THE DIVERSITY OF FLOWER-VISITING INSECTS IN THE GARDENS OF
ENGLISH COUNTRY HOUSES
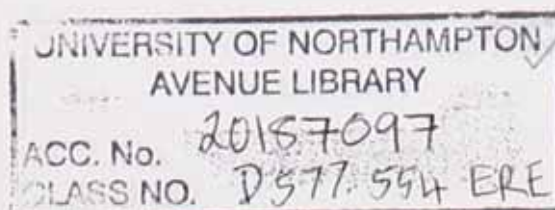
Submitted for the Degree of Doctor of Philosophy
at the University of Northampton

2013

Hilary E. Erenler

Abstract

Flower-visiting insects provide essential pollination services, ensuring both global food security and the continuity of wild plants. Recently documented declines in pollinators give cause for concern. Identifying previously unappreciated habitats that support diverse assemblages of these insects is an essential first step in mitigating further losses.

This study evaluates, for the first time, the role that large English country-house gardens play in supporting flower visitors within expanses of intensively farmed agricultural land. Focussing on 17 properties in lowland Central England, the results show that these novel ecosystems are important sites for hoverflies, bees and butterflies. In 2010 almost 10,000 flower-visitors from 174 species were recorded. Hoverflies were the only group to show a significant difference in species richness across the sites.

An important characteristic of these rural gardens is the high diversity of flowering plants available. More than a fifth of the world's plant families were represented, of which approximately 68% were non-native. The results showed that flower visitors did not prefer native plants over aliens, and that the dominance by aliens was no barrier for extensive use by the insects present. Both the species richness and abundance of flower visitors increased as plant richness increased.

The study revealed that half of all insect-plant interaction networks examined exhibited a nested structure, a common feature of natural environments that has not previously been assessed in rural gardens.

In addition to flower resources influencing insect species richness, landscape-scale effects were also significant. Insect groups responded differently to components in the landscape according to the time of year and the spatial scale considered. Bumblebees exhibited the greatest response to landscape factors and did so at larger scales than other groups.

The deployment of commercial trap-nests for solitary cavity-nesting red mason bees in walled gardens revealed new insights into the differential mortality suffered by male and female progeny. Female offspring were found to be disproportionately affected by a combination of development and parasitism losses. This finding suggests that effective mitigation strategies are needed before this species can be considered for use as a managed-pollinator.

Further research assessing the benefits crops such as oilseed rape derive from the presence of insects in nearby rural gardens would be a useful addition to this work.

Overall, the gardens of English country-houses emerge as sites of important natural as well as cultural heritage.

The beauty and genius of a work of art may be reconceived though its first material expression be destroyed.

A vanished harmony may yet again inspire the composer.

But when the last individual of a race of living beings breathes no more, another heaven and another earth must pass before such a one can be again.

William Beebe (1906)

From a plaque marking the site of Gerald Durrell's ashes.
Durrell Wildlife Park, Les Augrès Manor, Trinity, Jersey, Channel Islands.

To Michael and Tinaz.
For your love, support and encouragement every day and every step of the way.

Acknowledgements

Table of Contents

List of figures Page

List of tables

Chapter 1

Introduction

Chapter overview

This introductory chapter sets out the case for studying flower-visitor insect diversity. It identifies the main causes for insect pollinator declines and reviews the role gardens can play in providing suitable forage and nesting habitat. A brief synopsis of the changes English country-house gardens have experienced through the centuries is followed by a section outlining the scope of the project and the key research questions that will be explored. The chapter concludes with an overview of how the thesis is arranged.

Biodiversity and ecosystem services

As the human population continues its climb towards a predicted total of 10.1 billion by 2100 (United Nations, 2011), biodiversity is forecast to decline over the same period (Pereira et al., 2010). The pressures of a burgeoning global population on the Earth's remaining natural environments and their non-renewable capital are both a cause for concern and an incentive for urgent action (Wilson, 2001, Butchart et al., 2010). As the awareness of the consequences of biodiversity loss increases, so too does the interest in understanding the patterns and processes that drive it (Liu et al., 2011).

During the 1990s both regional and global biodiversity protection measures shifted from targeting individual species to placing increased importance on 'hotspots' of biodiversity (Mittermeier et al., 1998). Later, ecosystem services, defined as 'the benefits people obtain from ecosystems' (UNEP-WCMC, 2011), were identified as vulnerable entities in themselves that warranted assessment and conservation strategies. The focus on these services stems from a realization that the survival and well-being of humans is intricately related to the health and robustness of the ecosystems they interact with (Costanza et al., 1997, Daily et al., 1997).

Pollination: An essential ecosystem service

Ecosystem services can be categorised according to whether they are cultural, provisioning, regulating or supporting. Pollination, which is the transfer of male gametes within pollen to receptive female flower organs, is considered an essential *regulating* process (UNEP-WCMC, 2011). Following a pollination event a plant may set seed, thus facilitating future generations of that species (Kearns and Oliveras, 2009), as well as nutritionally supporting other organisms (Dias et al., 1999). Pollen transfer may be enabled by wind or water, but for the majority of angiosperms (approximately 88%, Ollerton et al., 2011) it is pollination by animals that facilitates

fertilisation and seed-set. Although animal mediated pollination does not guarantee the long-term survival of a plant population (and the organisms that rely on it), it can nevertheless act as a necessary first step in the process (Rathcke and Jules, 1993).

Pollinators belong to diverse groups within the animal kingdom and include birds, bats, opossums and reptiles (Dias *et al.*, 1999). It is, however, certain groups of invertebrates that are most associated with pollination. These include solitary and social bees and wasps (Hymenoptera), butterflies and moths (Lepidoptera), hoverflies (Diptera) and beetles (Coleoptera), (Waser, 2006). Globally, 3,000 species of plant are grown or used for food by humans and their domesticated animals, two–thirds of which require insect pollination (Dias *et al.*, 1999). As a measure of how important hymenopterans are in this process, bees have been recorded visiting 73% of these plants (Kremen and Chaplin-Kramer, 2007).

The importance of flower-visiting insects through their role as pollinators was formally recognised in the Saõ Paulo Declaration on Pollinators in 1999 (Dias *et al.*, 1999). The statement that 'Pollination is one of the most important mechanisms in the maintenance and promotion of biodiversity and, in general, life on earth' (Dias *et al.*, 1999, p. 18) heralded the start of what has subsequently become an area of intense research focus.

Research into pollinating insects stems from their acknowledged contribution to biodiversity together with a heightened awareness that declines in their abundance and richness could have ecological and economic consequences. Current international and national projects include: STEP (Status and Trends of European Pollinators) a European-wide collaboration aiming to understand and mitigate against the drivers and impacts of changes in pollinating insect diversity and abundance (STEP, 2012); and a suite of UK projects under the Insect Pollinators Initiative backed by a £10 million research investment to investigate biological and environmental factors affecting pollinating insects (NERC, 2009). The reason behind this increased research effort comes from reports that pollinating insect numbers are declining.

Pollinator declines

A decline in pollinators (in particular pollinating insects) is now accepted to be occurring on a global scale (Wratten *et al.*, 2012 and references therein). Potentially, this has major consequences for the humans and animals that rely on the nutritive and medicinal benefits that wild plants and crops provide (Klein *et al.*, 2007). Food

security issues already exist on our increasingly populated planet, and pollinator declines threaten to exacerbate these (Costanza *et al.*, 1997, Daily *et al.*, 1997, Fitzpatrick *et al.*, 2007).

Declining pollinator abundance and diversity can operate at local and global scales, generating productivity concerns for individual growers as well as threatening to destabilise world commodity markets (Dias *et al.*, 1999). The latter raises potential nutritional and health issues for many people (Allen-Wardell *et al.*, 1998, Steffan-Dewenter *et al.*, 2005, Kleijn and van Langevelde, 2006, Klein *et al.*, 2007). Countries such as China have already reported reductions in fruit and vegetable yields as a result of pollinator declines (Partap *et al.*, 2001).

The global decline of the world's most common managed pollinator, the honey bee (*Apis mellifera*, Apidae) has received a great deal of attention in both the scientific and popular press (vanEngelsdorp and Meixner, 2010, Breeze *et al.*, 2011, Thompson, 2012) and continues to exert what some consider to be a disproportionate claim on the scientific funding available for research into the loss of bee populations (Ollerton *et al.*, 2012). Although the reduction in the number of honey bees and their colonies is causing concern it is not, in the words of vanEngelsdorp and Meixner (2010), 'universal'. Indeed, these authors suggest that whilst North American and European populations have been hardest hit, within these areas some countries have not experienced declines. In places where losses have occurred the primary causes have been cited as disease, parasites, overwintering mortality, pesticides (both direct and indirect toxicity), reduced availability of forage and changes in climate (vanEngelsdorp and Meixner, 2010).

In contrast to the widely communicated reduction in honey bees, far less is known about losses affecting the majority of wild pollinators. Kearns and Inouye (1997, p.300) see this 'information imbalance' as a particular problem for wild bees, stating that issues relating to honey bees have been 'studied extensively, often at the expense of the other 20,000 – 30,000 bee species'. Some insect groups such as bumblebees and butterflies are notable exceptions to this, with reductions in the range and abundance of certain species well documented (Goulson, 2010, Fox *et al.*, 2012).

Parallel declines in pollinators and wild and cultivated plants have been reported in Europe (Biesmeijer *et al.*, 2006, Natural England, 2010, Potts *et al.*, 2010). These declines emphasize the risk that any disruption in pollination services may bring, including unpredictable, cascade-like effects that have the potential to disturb multiple food webs (Rathcke and Jules, 1993, Kearns and Oliveras, 2009).

Pollinating insects

Not all insects are pollinators, despite their often frequent visits to flowers, nor does each visit by a legitimate pollinator result in a pollination event (Kwak *et al.*, 1996). Classifying an insect group, genus or species according to its pollinating abilities is therefore a difficult task. In their seminal work 'The principles of pollination ecology', Faegri and van der Pijl (1966) described in detail the range of invertebrates that are considered as pollinators. They identified four key insect orders warranting particular attention: beetles (Coleoptera); flies (Diptera); bees (Hymenoptera) and butterflies and moths (Lepidoptera).

For the purposes of this study the general term 'flower-visiting insect' will be used. This recognises that although insects alighting on flowers may appear to be pollinating them, the occurrence of a pollination event cannot be assumed (Kevan and Baker, 1983).

Current state of native flower-visiting insect diversity in the UK

Assessing the state of current native flower-visitor insect diversity in the UK is complicated by the fact that no single organisation researches and reports on all insect groups. Instead, specialist recording societies, non-governmental organizations (NGOs), e.g. Friends of the Earth, Government organisations (Natural England) and academics have all taken the lead in highlighting the status of particular groups at different times. A selection of these is given in Table 1.1.

Table 1.1 Publications relating to the losses and current status of key flower-visitor groups in the United Kingdom.

Insect group	Key findings	Publication	Reference
Bumblebees	• 3 species extinct • 8 species in severe decline • Worst affected are long-tongued species	Decline and Conservation of bumblebees	Goulson et al. (2008)
Butterflies	• UK butterflies are in serious decline • Ten-year trends show 72% of species declined in abundance • Ongoing deterioration of habitats is main cause	The State of the UK's Butterflies, 2011	Fox et al. (2012)
Honey bees	• UK managed colonies declined by 53% between 1985 - 2005	Global pollinator declines: Trends, impacts and drivers	Potts et al. (2010)
Hoverflies	• 33% of species have declined over last 25 - 35 years • Species associated with conifers and wetlands experienced the greatest declines	Atlas of the Hoverflies of Great Britain (Diptera, Syrphidae)	Ball et al. (2011)
Solitary bees	• True status of most species not known but approx. 52% decline within English landscapes	The decline of England's Bees	Breeze et al. (2012)
All	• Since 1800, 23 bee, 18 butterfly and 88 moth species lost from England	Lost Life: England's lost and threatened species	Natural England (2010)

Threats to UK flower-visiting insect diversity

Flower-visiting insect populations in the UK are under pressure for many reasons. These include: changes in agricultural practices, fragmentation or alteration of land use (e.g. infrastructure creation or urbanisation) and the effects of climate change. These are now considered in turn.

Changes in agricultural practices

Major changes in the rural landscape have been a feature of the UK for centuries. From the increased use of ridge and furrow ploughing practices in the Middle Ages to the Parliamentary Enclosure Acts of the 18th and 19th century, land management has

been in a constant state of flux (Thomas, 1984). The changes since World War II are, however, some of the most extensive to date. In common with the majority of Northern Europe, agricultural intensification, in particular 'modern intensive farming', has been cited as the principal cause for the decline in biodiversity in the European countryside (Stoate *et al.*, 2001, Carvell *et al.*, 2004, Dormann *et al.*, 2007, Henle *et al.*, 2008). More land than ever before has been taken into agricultural production in the UK. Currently 17.2 million hectares (70% of the area of the UK) is designated as agricultural land (Defra, 2011).

High-yield crops such as wheat and barley rely on a mixture of agri-chemicals to control weeds, fungi and crop-pests (Defra, 2011). As such, managed and unmanaged pollinators are exposed to an ever-increasing range of treatments (Breeze *et al.*, 2012). The risks from acute toxicity following direct exposure have been largely mitigated by the introduction of pesticide-use regulations (vanEngelsdorp and Meixner, 2010), however the sub-lethal side-effects on insects following chemical applications are only now being fully explored. Recent research considering the effect of neonicotinoids on bumblebee queen production and bee foraging and homing behaviour has shown that, even at trace levels, these pesticides are able to impair reproductive and functional behaviour (Girolami *et al.*, 2012, Whitehorn *et al.*, 2012).

Global and national economic drivers such as rapidly increasing commodity prices (Mitchell, 2008), financial incentives to grow specific crops, e.g. the mass-flowering oilseed rape (OSR), *Brassica napus* (Diekotter *et al.*, 2010), and the removal of payments to landowners to leave land out of production (set-aside) (Defra, 2011) continue to alter how agricultural land is used in the UK. The increased presence of OSR since the 1970s has been described as one of the most dramatic changes to the floral landscape for centuries (Cussans *et al.*, 2010). Attempting to understand how the presence of OSR (which produces a single pulse of flowers in spring/early summer) alters pollinator foraging behaviour, and how this impacts on wild plant reproductive success, is an active research topic (Westphal *et al.*, 2003, Cussans *et al.*, 2010, Holzschuh *et al.*, 2011, Jauker *et al.*, 2012a,b).

The withdrawal of payments for set-aside has resulted in a sharp fall in uncultivated land on farms (Defra, 2011). The loss of field-margins that provide abundant flowering herbaceous perennials throughout the bee-foraging season is suggested as a major contributor to the decline in native pollinators (Osborne *et al.*, 1991, Comba *et al.*, 1999b), as is the loss of suitable sites for ground-nesting specialists (Kremen and Ricketts, 2000). Added to this, the inappropriate timing of hedgerow management and the regular cutting of flower-containing grass leys for silage (as

opposed to a single late cut for hay) has also altered forage availability for pollinating insects (Lagerlof *et al.*, 1992, Fitzpatrick *et al.*, 2007, Hannon and Sisk, 2009).

Fragmentation and urbanisation

Habitat fragmentation has been described as 'one of the greatest threats to biodiversity' (Rathcke and Jules, 1993). Through the reduction of patch sizes and the subsequent isolation of species, fragmentation alters the survival potential of insect populations (Westrich, 1998, Exeler *et al.*, 2010). Gene flow may be impeded and genetic diversity reduced as options to migrate to new sites diminish (Saunders *et al.*, 1991, Kwak *et al.*, 1998). Although insect pollinators with general rather than specific food requirements may respond differently to fragmentation, this form of disturbance has the overall potential to disrupt plant-pollinator interactions (Rathcke and Jules, 1993).

By 2030 83% of UK residents are expected to be living in urban environments (United Nations, 2011). The process of urbanisation is known to degrade existing vegetated areas through land-take for building and infrastructure as well as fragmenting remaining pockets of land that support wildlife (Fahrig, 2003). Urban fragmentation reduces biodiversity and can lead to biotic homogenisation (Goddard *et al.*, 2010). The latter can result in the over-representation of generalist flower-visiting insects at the detriment of specialist pollinators (Frankie *et al.* 2009, Matteson and Langellotto, 2010).

Climate change

Changes in the phenology of flowering plants have been attributed to global warming (UKCIP, 2012). As atmospheric CO_2 levels increase further, the flight periods of pollinating insects and the opening of flowers may become increasingly dissociated, leading to reduced food availability for insects and a reduction in pollination events (Bartomeus *et al.*, 2011). Although studies have suggested that the changes in the timing of the first-flowering of some plants may be matched by correspondingly earlier appearances of insects, e.g. butterflies (Roy and Sparks, 2000), the potential impact on the insects themselves and plant-pollinator interactions is difficult to gauge (Memmott *et al.*, 2007).

Summary of threats to insect diversity and potential opportunities

In summary, large-scale anthropogenic disturbance via agricultural intensification, fragmentation and through the effects of climate change suggests a continued and sustained negative impact on the world's insect pollinators. Despite this it is important to recognize that not all human actions are detrimental. Two examples of the positive effects of human-mediated interventions include the regular cutting of

unimproved meadows, such as in Baden-Württemberg (Germany), where more than 132 bee species have been recorded (Westrich, 1996), and allowing ivy (*Hedera helix*) to freely colonise walls in UK towns and villages, thereby indirectly encouraging populations of the oligolectic ivy bee (*Colletes hederae* Schmidt & Westrich, 1993) to establish in new areas (BWARS, 2012).

Ivy-covered walls are good examples of 'synthetic ecosystems' i.e., conditions and/or combinations of organisms not previously in existence (Odum, 1962). Hobbs *et al.* (2006) recently extended this idea by suggesting that in the new ecological world order, some ecosystems that do not fit into existing categories may be termed 'novel ecosystems'. The authors broadly define these ecosystems as areas containing alternative combinations of species to those found in nature, which have come into existence as a result of deliberate or inadvertent human intervention (Hobbs *et al.*, 2006). According to the definition, gardens may be considered novel ecosystems as they contain unusual combinations of plants not normally found together as a direct product of human actions. Gardens, as anthropogenic constructs, therefore possess attributes that are of interest when considering insect diversity, not least because the choice of plants used has the potential to alter the way plants and insects interact (Owen, 1981).

The role of gardens in supporting pollinating insects

Garden environments

Gardens throughout the world provide a mosaic of habitats that can support a diverse range of invertebrates (Owen, 1983, Miotk, 1996, Smith *et al.*, 2006c, Fetridge *et al.*, 2008, Frankie *et al.*, 2009). Plant assemblages in gardens are regarded as notably species rich (Galluzzi *et al.*, 2010) and often represent an eclectic mix of native and non-native species not normally found together. These 'contrived plant collections' (Owen, 2010) offer rich habitats with the potential to provide suitable feeding and nesting opportunities for a range of fauna (Goulson *et al.*, 2002, Loram *et al.*, 2008b). The floral and structural resources in gardens, e.g. woody shrubs and trees, have also been shown to extend temporally and spatially beyond those found in nearby 'semi-natural' areas (Goddard *et al.*, 2010). The presence (or otherwise) of these resources can act as variables that shape pollinator diversity in an area (Potts *et al.*, 2003, Smith *et al.*, 2006c).

The findings of a recent Defra report into the attitudes and knowledge relating to biodiversity and the natural environment in the UK show that of those UK residents who had access to a garden, 74% took steps to actively encourage wildlife into it. Additionally, 78% of respondents said they 'worry about changes to the countryside

in the UK and the loss of native animals and plants' (Defra Environment Statistics Service, 2011). As gardens represent the most frequent contact between humans and nature in an increasingly urbanised society, they play an important role in supporting and maintaining human physical and psychological health, as well as providing educational opportunities for the next generation (Dunnett and Quasim, 2000).

Although individual gardens in city and urban settings may be relatively small, aggregations of these domestic green spaces can allow the maintenance of biodiversity in an otherwise inhospitable landscape (Loram et al., 2008a,b, Davies et al., 2009, Sattler et al., 2010). Indeed some regard urban green spaces as an 'increasingly important refuge for native biodiversity' (Goddard et al., 2010, p.90). Detailed investigations into urban garden habitat structure and management have revealed they make a major contribution towards providing resources for wildlife (Smith et al., 2006a, Sattler et al., 2010). Both local (within garden) and landscape-scale factors are possible drivers for the different levels of flower-visitors observed (Smith et al., 2006b,c, Matteson and Langellotto, 2010).

In contrast to urban gardens, far less is known about gardens in rural areas. Engels (2001) notes rural gardens have the potential to contribute to the functioning, sustainability and resilience of nearby agricultural ecosystems. An example is the nutritional support garden flowers provide to adult hoverflies. The presence of flower resources can benefit nearby food crops through reduced herbivory. This arises because the larvae of many species of hoverfly are important predators of aphids (Hogg et al., 2011). The potential of forage resources in gardens is yet to be assessed in a rigorous way, and reflects the limited evidence available generally about how non-native flowers influence pollinator visitation (Ghazoul, 2006, Fründ et al., 2010, but see Cussans et al., 2010 and Salisbury, 2012).

Within agriculture-dominated zones, flower-rich areas such as orchard meadows and field margins have been assessed to establish whether a diverse array of flower-visiting insects make use of available floral and nesting resources (Steffan-Dewenter and Tscharntke, 2001, Steffan-Dewenter and Leschke, 2003, Osborne et al., 2008a). However, to my knowledge, no published research has examined the potential of large rural gardens to support these insects. This is somewhat surprising considering the continuity and well-documented floral resources large rural gardens possess.

English country house gardens

English country houses represent more than simply a 'large house in the country' (Aslet, 1982). These properties frequently function as the centre piece of a landed estate and are often accompanied by lodges and gardens associated with the pastimes of wealthy occupants (Aslet, 1982). Littlejohn (1997) offers a more precise definition. He describes country houses as being large private residences with twenty rooms or more that are set in their own gardens and parkland. He adds that when such properties were constructed they were intended to serve as the family home for several generations and that the occupants would derive at least part of their income from the associated agricultural estate.

Throughout the centuries English country houses have been regarded as important architectural, artistic and economic entities that represent significant features of British heritage (Christie, 2000). Despite a continued interest in these cultural sites - The National Trust has more than four million members and received over nineteen million paid visits to their sites in 2011[1] (The National Trust, 2012b), the fate of country houses has often been in question.

The 1974 exhibition at the Victoria and Albert Museum entitled 'The Destruction of the Country House', brought the plight of these properties to the fore by revealing that a thousand country houses were lost between 1874 – 1974 (Binney, 1974). The post-war years were particularly unforgiving; with an estimated one house lost every five days in 1955 alone (Beckett, 2012).

Although the demise of physical structures relating to country estates is reasonably well documented (Beckett, 2012), the parallel decline of their gardens and landscapes has received far less attention. Elton et al. (1992, p.50) note 'houses may be burned to the ground or knocked down and replaced, but gardens are even more likely to disappear as fashion succeeds fashion'. Despite their apparent transient nature, Christie (2000) highlights the importance of gardens by referring to them as integral parts of each estate.

The initial design of landscapes surrounding country houses often varied significantly. Some gardens followed the trends of the time, whilst others showed a more individualistic style, whereby the wishes of the owner (bound up in his political, social and educational fabric) were catered for by well-known and novice landscape designers alike (Christie, 2000). Areas within individual gardens often ranged between two extremes; ultra-formal terraces and parterres to self-created

---

[1] This is the number of visits to all NT sites (including the 200 country houses it manages)

'naturalness' (Christie, 2000, p. 138). An example of 'designed naturalness' was that of Alexander Pope's garden at Twickenham (Figure 1.1).
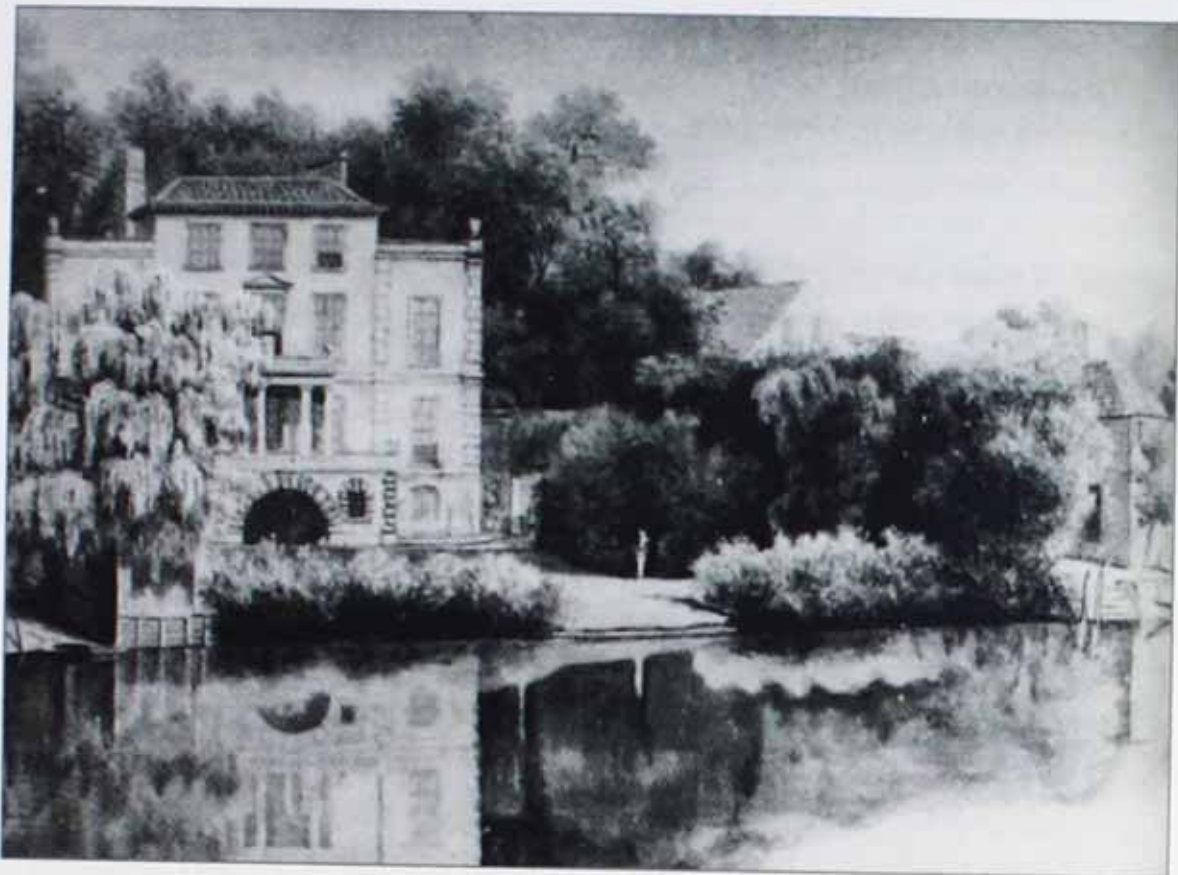
Figure 1.1 Alexander Pope's house at Twickenham (From an original painting at Orleans House Gallery, Richmond, painter unknown). Published here with kind permission from the Richmond Borough Art Collection, Orleans House Gallery, Richmond. (WikiMedia Commons, 2005).

Pope experimented by laying out his garden in harmony with nature noting, 'The first rule - to adapt all to the nature and use of the place; the beauties not forced into, but resulting from it' (Dutton, 1949, p. 105). He expanded on this theme in his verse Epistles to Several Persons: Epistle IV (Warton, 1822).

> To build, to plant, whatever you intend,
> To rear the column, or the arch to bend,
> To swell the terrace, or to sink the grot;
> In all, let Nature never be forgot.

> Alexander Pope (1688 – 1774)

Informed by classical texts such as Virgil's *Georgics* and the pastoral poems *Ecologues*, Pope combined contemporary ideas about the countryside with a deeper

appreciation of the human psyche which affected how people interacted with the natural world (Christie, 2000). Additionally he moved the focus away from the house and turned the attention to the different components of the garden: in his case an orangery, orchard, kitchen garden and grotto (Christie, 2000). Tree planting achieved the effect of dividing the garden up into small but distinct parcels. The latter were not only aesthetically pleasing but had the effect of creating a nested set of distinct habitats within a larger whole.

Pope's garden was more an exception than the rule, as few owners seem to have been as keen to immerse their gardens into the surrounding landscape. Instead, they wished to make a statement demonstrating what their wealth could achieve (Musgrave, 2009). The sixteenth century saw the arrival of many new plants from abroad and this gave rise to a renewed interest in gardening. William Harrison wrote in his *Description of England* in 1587 that 'Many strange herbs, plants and annual fruits are daily brought unto us from the Indies, Americas, Canary Isles and all parts of the world' (Dutton, 1949, p.95). In parallel with the availability of new plants, the influence of continental landscaping styles started to alter the layout of English gardens. The skills of Italian craftsmen brought to England by Henry VIII did not stop at the adornment of buildings; they introduced architectural and formal gardens, complementing them with clipped yew and box, ornate marble fountains and sundials (Dutton, 1949).

Today the gardens of large English country houses are still influenced and characterised by these two seeming incompatible trends; that of sweeping nature-inspired landscapes versus formal flower beds, borders and parterres containing species that boast their origins far beyond the country's shores. It is this unique blend of mixed habitat types, often within small geographic areas, that contributes to their potential importance as novel ecosystems.

The demand, most usually by the lady of the house, for the garden to produce abundant cut flowers throughout the year to decorate reception rooms is all but gone. Despite this, there is still a requirement for country house gardens to provide flowering periods that extend well beyond the summer flush of traditional roses. The reason behind this is related to the new ways in which some country houses are managed. The opening of estates to the public is one of several ways that income can be generated, thus allowing continuity of existence (Elton et al., 1992). The fashion of opening stately homes to paying visitors saw dramatic post-war growth when, in 1949, the sixth Marquis of Bath opened his house at Longleat. It was his success in attracting 138,000 visitors in the first year that paved the way for other house owners to follow (Elton et al., 1992). Today, gardens can be hired for use as

wedding venues or film sets as well as continuing to be places where the paying public can visit to get inspiration and planting ideas for their own gardens (Althorp Estate, 2012, Boughton House, 2012).

Although present-day English country-house gardens are diverse from the perspective of ownership and design, they share a common theme. They represent flower-rich 'islands' (Fahrig, 2003) within expanses of intensively farmed land (Figure 1.2). As this form of agriculture is known to suppress biodiversity (Tscharntke *et al.*, 2005) this raises the possibility that rural gardens may be sites where flower-visitors successfully persist and even act as source populations which can disperse into the wider landscape. This is an extension of the 'Circe principle' described by Lander *et al.* (2011) who suggest that the existence of resource-rich land in an otherwise inhospitable matrix may waylay flower visitors as they pass from one area to another. Establishing whether these gardens possess an, as yet, unappreciated natural-heritage value in addition to their acknowledged cultural importance is central to this project.

Figure 1.2 Waddesdon Manor, Buckinghamshire (centre), set within a mosaic of intensively farmed land. Scale bar = 0.5km. Image GetMapping PLC, 2012.

Scope of the research project

This project explores flower-visiting insect richness, diversity and community interactions in gardens in rural areas by focussing on English country-house estates. It utilises a suite of properties in lowland Central England to achieve this, concentrating on several key insect groups.

Defining the area of study

Research in the field of pollination ecology is a dynamic and on-going process. A recent poll of 66 active researchers in the field yielded 86 questions in 14 categories which warranted further consideration (Mayer *et al.*, 2011). Clearly, the scope for any research project is limited by time and resources. A Ph.D. project is no exception. In order to incorporate as many gardens as possible into the study, whilst balancing the need to sample them regularly, identify the species observed and analyse the data collected, a single geographic area (that of Northamptonshire and the nearby counties of Bedfordshire, Buckinghamshire and Warwickshire) is used.

Land use in Northamptonshire is dominated by agriculture. In 1930, 99% of the county was used for agricultural activities; however by 2000 this had fallen to 78% (McCollin *et al.*, 2000). Although wheat and barley continue to be sown, there has been a major shift towards planting oilseed rape (OSR) (Defra, 2011). Northamptonshire, together with others in the region, has been described as a 'yellow county' (ITV, 2012) due to the dominance of this mass-flowering crop in early summer. The shift to OSR (with a corresponding reduction in barley) reflects a UK-wide trend that started in the mid-1970s. The total area occupied by this crop has increased dramatically, from 402,000ha in 2000 to 705,000ha in 2011 (Defra, 2011). It is not just this change from one intensively grown arable crop to another that presents unknown challenges for flower-visiting insects however. Northamptonshire, together with many other lowland central English counties, has also seen a dramatic shift in the ratio of land described as unimproved pasture to that of intensive agriculture, of which the latter includes grass leys for silage purposes (King, 2002). In the 1930s two-thirds of farmland in the county was left as pasture, but by 2000 this had dropped to just a quarter (McCollin *et al.*, 2000). Across the UK the most valuable areas of unimproved grassland (described as flower-rich meadows) have decreased dramatically, with 97% reportedly lost over a seventy year period (King, 2002, 2011).

In addition to these documented land-use changes, Northamptonshire has found itself infamous for being known as the county with the highest number of wild-plant extinctions since 1900 (Marren, 2000, 2001, but see Walker (2003) who placed it second). Walker and Preston (2006) suggest that the county has lost 11% of its

native flora since 1700 and that from the 1950s onwards an average of six to eight species have been lost each decade (Walker and Preston, 2006).

Target insect groups

As discussed above, flower-visiting invertebrates include taxa from several orders. In the past, many studies have focussed on a single plant or pollinator species, particularly when they are believed to have closely evolved (Burkle and Alarcón, 2011). Considering a suite of flower-visiting insects from a number of different groups has advantages over this method as it enables a community level approach to be taken as well as permitting the degree of generalization and specialization between plants and insects in a geographical area to be explored (Waser and Ollerton, 2006). For the purposes of this project, insect species from the orders Diptera, Hymenoptera and Lepidoptera are included (Table 1.2). By concentrating on three groups a sound understanding of the main flower-visitors in rural garden landscapes and the plants they interact with can be formally documented for the first time. Detailed information on the study sites and organisms selected is presented in Chapter 2.

Table 1.2 The three insect orders containing nine target groups used in the study.

Order	Common name
Diptera	Hoverflies (flower flies)
	Other flies
Hymenoptera	Bees (honey)
	Bees (native, solitary)
	Bumblebees
	Wasps (social)
	Wasps (solitary)
Lepidoptera	Butterflies
	Day-flying moths

Project aims

The overall aim of this project is to explore the structure and composition of plant-pollinator assemblages in English country house gardens.

Specifically, the work seeks to elicit how novel ecosystems are structured by taking a community-level approach that considers interactions between flower-visiting insects and the plants available.

Furthermore, by quantifying within-garden and landscape-scale factors, the project examines whether spatial attributes help explain the observed flower-visitor richness.

Finally, through the use of artificial trap nests, the study seeks to determine which factors affect reproductive success for a single species of cavity-nesting bee.

Research questions

The project seeks to answer the following broad questions:

1. What is the composition of flower-visiting insect communities in large English country house gardens and how do these compare to other sites?
2. Do communities of flower-visiting insects and the plants they visit exhibit non-random interaction patterns?
3. How do flower-visitors respond to the temporal and spatial variation associated with local and landscape-scale factors in and around gardens?
4. Can artificial trap nests in walled kitchen gardens provide new insights into solitary bee nesting behaviour and reproductive success?

Overview of the thesis

Chapter 1 INTRODUCTION

This is a broad introduction to the project establishing the importance of pollination as an ecosystem service and the threats it faces. The role of large gardens in supporting biodiversity is discussed in general and the dearth of information relating to rural gardens established. The chapter concludes by stating the scope of the project and identifying the overall aims for the work.

Chapter 2 STUDY SITES, STUDY ORGANISMS AND GENERAL METHODS

Chapter two explains the process for selecting study sites. It describes the target flower-visiting groups and the methods employed to gather data about them. Procedures specific to the field study seasons in 2010 and 2011 are detailed, as are generic statistical techniques.

Chapter 3 **FLOWER-VISITOR SPECIES RICHNESS AND DIVERSITY**
In the third chapter the species richness (both actual and estimated) of flower-visiting insects in seventeen gardens is analysed and compared to other datasets. Differences in species diversity across gardens and between key groups are also elucidated. Finally, community composition similarity is explored as well as the notion of rarity.

Chapter 4 **THE STRUCTURE OF PLANT AND FLOWER-VISITOR COMMUNITIES**
Chapter four starts by assessing the species richness of the plants available. It quantifies the use of floral resources by flower-visiting insects across the season and explores non-random patterns in community interactions.

Chapter 5 **SPATIAL AND SEASONAL FACTORS AFFECTING THE DIVERSITY OF FLOWER-VISITORS**
Within-garden and landscape-scale factors are considered in Chapter five to establish whether any observed differences in flower-visitor species richness between properties can be explained by environmental factors.

Chapter 6 **TRAP-NEST BEES IN WALLED GARDENS**
Chapter six focuses on a subset of the gardens and looks specifically at trap-nest usage by the solitary bee *Osmia bicornis*. It focuses on differential survival rates of males and females as a result of two different causes of mortality.

Chapter 7 **CONCLUSIONS**
The thesis concludes with a summary of the findings, a critique of the study and recommendations for future work.

Chapter 2

Study sites, study organisms
and general methods

Chapter overview

In this chapter the location of the study and sites are introduced. The target taxa are described, with their feeding preferences and UK status included where known. Information on the two field seasons is given, together with generic procedures for statistical tests.

Introduction

The observation and accurate identification of flower-visiting insects in the gardens of English country-house estates was a prerequisite to achieve the aims of the project, as set out in Chapter 1. The sections that follow describe the selection criteria for the study sites and the methods used to collect the raw data during the 2010 and 2011 field seasons. All data (unless otherwise stated) are original field data collected solely by the author.

Study sites

English country-house estates

Properties defined as large country houses in Britain exist along a continuum of size and age-range. Ownership also varies, and includes national organisations such as English Heritage and The National Trust as well as private trusts set up specifically to maintain the heritage of a site. Another cornerstone of English country-house ownership is that of wealthy individuals. Properties of this type can be subdivided into those estates that have been passed down from generation to generation within the same family, such as Althorp and Courteenhall in Northamptonshire, or those that have been acquired by individuals with no prior connection to the site e.g. Easton Neston, Northamptonshire.

Shortlisting potential garden sites

The county of Northamptonshire in lowland Central England boasts some 63 historic gardens (Mowl and Hickman, 2008), the majority of which are associated with country-houses. In order to minimise climatic differences, gardens were considered as potential sites if they were located within a 50km radius of central Northampton. This criterion extended to properties in nearby counties.

A limiting factor in the success of the research project was identified early on as the obtaining of land-owner permission to conduct repeat sampling at country house locations over a two-year period. In particular it was anticipated that securing permission to access the gardens of privately owned houses which are rarely, if ever, open to the public might prove difficult. In the light of this, the list of potential properties to sample was compiled with the aid of published sources

that cited owners amenable to research taking place. The reference work of Mowl and Hickman (2008), who documented Northamptonshire's historic gardens, was particularly useful, as was Heward and Taylor's 1996 work on the county's main estate homes.

Selection of gardens

Favourable responses to requests to conduct garden surveys were received from owners and estate managers at twenty-two of twenty-eight properties approached. From these, seventeen were selected. The final selection reflected a range of ownership types (trust, private and organisational), with house construction dates spanning approximately five centuries (Appendix I).

As the sampling of flower-visiting insects is a weather and temperature dependent activity (all are poikilotherms), maximum flexibility for potential site visits was necessary. To this end, an additional criterion at the time of selection was that no stringent access rules existed, e.g. sampling was not limited to a specific day a week. The gardens chosen for sampling are detailed in Figure 2.1, Table 2.1 and Appendix 1, and are hereafter referred to using the abbreviations given.
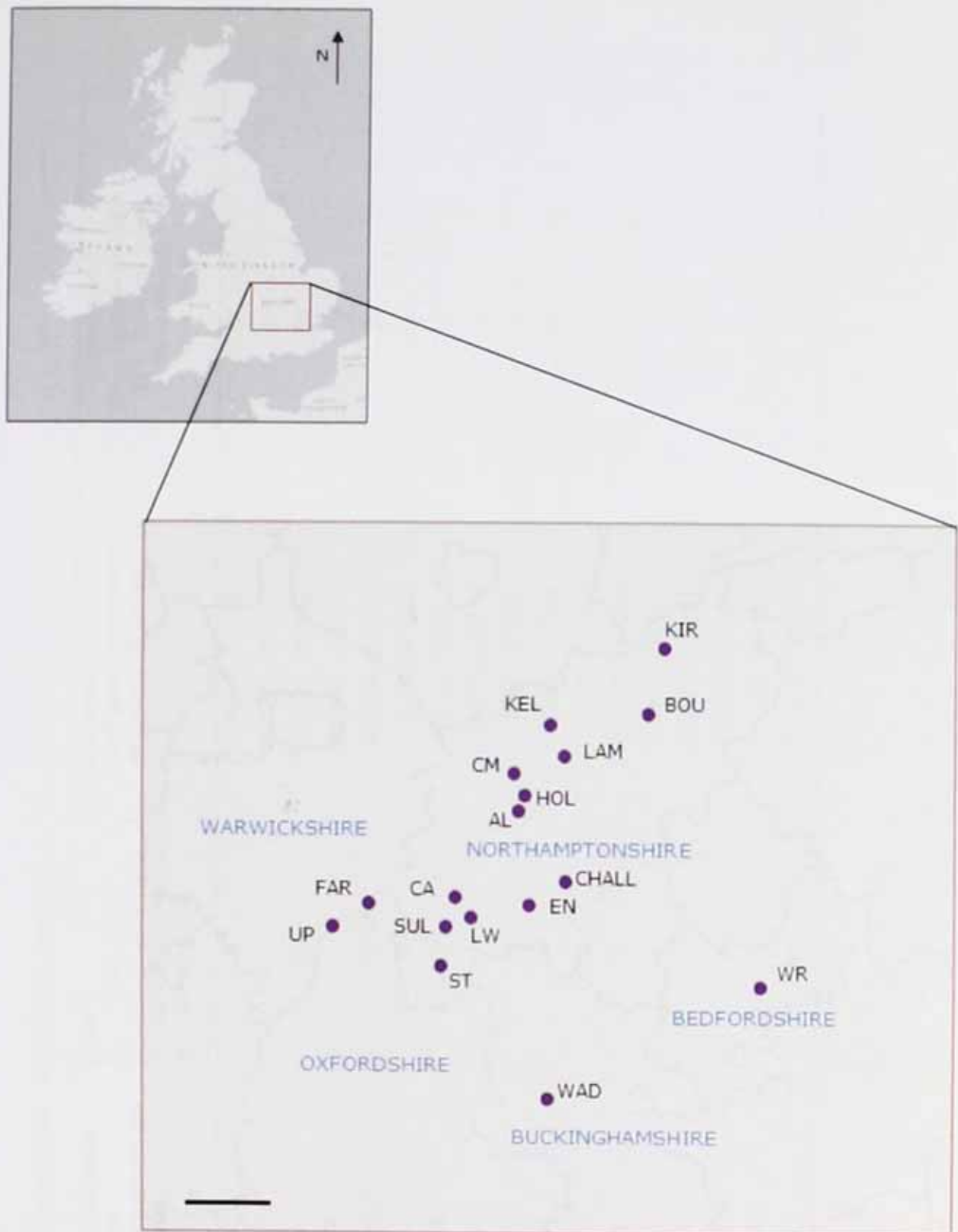
Figure 2.1 Location of the 17 gardens in central lowland England used in the study. Abbreviations for property names as per Table 2.1. Scale bar = 10km. Map created in ArcMap (ESRI, 2011).

Table 2.1 Details of the 17 properties selected for sampling.

Property name	Abbreviation used throughout the thesis	County Be = Bedfordshire Bu = Buckinghamshire N = Northamptonshire W = Warwickshire	Location (OS grid coordinates at centre of house)	Ownership EH = English Heritage NT = National Trust Pr = Private Tr = Trust
Althorp Estate	AL	N	468200, 265105	Pr
Boughton House	BOU	N	489970, 281548	Pr
Canons Ashby	CA	N	457715, 250658	NT
Coton Manor	CM	N	467449, 271604	Pr
Courteenhall	CHALL	N	476136, 253129	Pr
Easton Neston	EN	N	470174, 249280	Pr
Farnborough Hall	FAR	W	443067, 249419	NT
Holdenby House	HOL	N	469267, 267749	Pr
Kelmarsh Hall	KEL	N	473619, 279594	Tr
Kirby Hall	KIR	N	492566, 292709	EH
Lamport Hall	LAM	N	475868, 174493	Tr
Lois Weedon House	LW	N	460459, 247194	Pr
Steane Park	ST	N	455396, 238987	Pr
Sulgrave Manor	SUL	N	456053, 245587	Tr
Upton House	UP	W	436956, 245699	NT
Waddesdon Manor	WAD	Bu	473265, 216497	NT
Wrest Park	WR	Be	509085, 235588	EH

Study organisms

As discussed in Chapter one, three insect orders containing nine flower-visiting groups were identified for inclusion in the study (Figure 2.2). These are now considered in detail.

Figure 2.2 Examples of flower-visitors recorded in the current study. **Hymenoptera** - **A** Bumblebee - *Bombus hortorum*, **B** Honey bee - *Apis mellifera*, **C** Solitary bee - *Lasioglossum* sp., **D** Social wasp - *Vespula/Dolichovespula* sp., **E** Solitary wasp – species unconfirmed, **Diptera** – **F** Hoverfly - *Eristalis tenax*, **G** Bombyliid fly - *Bombylius major*, **Lepidoptera** – **H** Butterfly – *Aglais urticae*, **I** Day-flying moth - *Adela rufimitrella*. Images: Erenler (2010 and 2011).

Hymenoptera

The aculeate Hymenoptera (bees, wasps and ants) comprise some of the most economically important pollinating insects throughout the world (Faegri and van der Pijl, 1966, Michener, 2007). Within the aculeates, bees (Apoidea) are the most frequent flower-visitors, often collecting both pollen and nectar for their brood, as well as imbibing nectar to meet their own energy needs (Michener, 2007).

Bees

Bumblebees (Apidae: *Bombus*)

Bumblebees (Figure 2.2 A) include social nesters ('true' bumblebees) and cuckoo species (those that select the nests of other species in which to raise their young) (Goulson, 2010). Depending on species, bumblebees make nests underground, amongst vegetation or in tree holes (Prŷs-Jones and Corbet, 2011). Tongue length also varies according to species, with longer-tongued bumblebees able to remove nectar from flowers with tubular corollas (Prŷs-Jones and Corbet, 2011). Most bumblebee colonies complete a single nesting event a year, with newly reared queens being the only individuals to survive the winter. The following spring the overwintered 'true' bumblebee queens emerge and commence nest building (Goulson, 2010, Prŷs-Jones and Corbet, 2011).

The foraging range of most bumblebee species remains poorly understood (Goulson, 2010); however certain species have been the focus of spatial studies. Osborne *et al.* (1999) found workers of *Bombus terrestris* L. regularly travelling 200m to forage in an agricultural setting in the UK, whilst Kreyer *et al.* (2004) noted the maximum forage distance for *B. terrestris* agg. in a German forested landscape was 2.2km.

In the UK there are 24 species of bumblebee. Three additional species that were regularly found in the early part of the twentieth century are now considered extinct (BWARS, 2012).

Honey bees (Apidae: *Apis*)

Honey bees (Figure 2.2 B) live in colonies consisting of a single queen and many workers, often reaching up to 60,000 individuals (Hooper, 1991). They are classed as highly eusocial. Eusociality involves adult females from two generations working cooperatively together, with a clearly demarked division of labour (Michener, 2007).

Within a colony the queen is responsible for egg-laying, whilst members of the worker caste engage in a range of activities including foraging, nursing developing brood and general guard duties (Hooper, 1991, Michener, 2007).

Honey bees are managed pollinators, with *Apis mellifera* (the European honey bee) classed as the most managed bee in the world (vanEngelsdorp and Meixner, 2010). Human intervention, in the form of nest provision and nourishment through the winter months (usually after honey reserves have been removed), means managed honey bees no longer function as fully autonomous organisms (Hooper, 1991).

Honey bees make a major contribution to agriculture through the pollination services they provide, with 52 of the leading 115 global food commodities dependent to some extent on their presence (Klein *et al.*, 2007). They are classed as super-generalists making them extremely versatile for commercial use (Michener, 2007, Kaiser-Bunbury *et al.*, 2009, vanEngelsdorp and Meixner, 2010). Honey bees are known to have long foraging ranges; Beekman and Ratnieks (2000) found the mean range of honey bees on heather (*Calluna vulgaris*) in the UK to be 5.5km, with 10% of workers travelling more than 9.5km.

In the UK the native status of the dark honey bee, *Apis mellifera mellifera* is unclear. Carreck (2008) makes a case for its existence based on archaeological evidence and a study mapping its European distribution, however no formal assessment has been made to establish the location of colonies in the UK (BWARS, 2012). It is therefore reasonable to assume that encounters with honey bees in the UK are likely to be with the non-native, managed, European species, *Apis mellifera* (Breeze *et al.* 2011, 2012).

A 78% decline in beekeeping between 1953 and 2010 (Potts *et al.*, 2010) together with a number of diseases and parasites has drastically reduced the number of honey bee hives in existence in the UK (Breeze *et al.*, 2012).

Solitary bees
(Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae, Melittidae)

Solitary bees (Figure 2.2 C) include aerial nesters and those that nest in the ground. They can be further sub-divided into two distinct reproductive types: those that provision their own nests and those that are cleptoparasitic, i.e., making use of the resources collected by other bees (Westrich, 1996). Solitary bees that construct their own nests do so without the assistance of other females and usually take no part in rearing the offspring (Michener, 2007). Cleptoparasites also usually die or depart without encountering the emergence of their progeny (Michener, 2007).

Habitats that support solitary bees possess three key features: suitable space for nests, material for nest building, and sufficient food plants to supply nectar and pollen needs (Westrich, 1996). Some solitary bees have general pollen requirements and are termed polylectic, whilst others are specialised on particular plants (oligolectic). Monolectic bees restrict their visits to a single plant species (Westrich, 1996; Cane and Sipes, 2006; Michener, 2007).

Solitary bees are active from early spring to late autumn in Europe (Westrich, 1996). Most are univoltine, timing their emergence to coincide with the peak flowering of plants they commonly visit (Westrich, 1996). The foraging distance of solitary bees is positively correlated with body length, with Gathmann and Tscharntke (2002) noting that the foraging range of sixteen European solitary bee species typically varies between 150 and 600m.

Westrich (1996) suggests that solitary bees are likely to have evolved in a variety of dynamic habitats such as shifting flood plains within large riverine systems. As anthropogenic influences on the landscape spread, bees subsequently dispersed into new habitats (Westrich, 1996).

Solitary bees are regarded as increasingly important pollinators, due in no small part to the dramatic declines observed in honey bee populations in some northern temperate areas (Winfree *et al.*, 2007, Breeze *et al.*, 2011). Added to this is the realisation that although honey bees are good generalist foragers, there are certain crops for which their pollinating success is inferior to solitary bees. An example of this is alfalfa (*Medicago sativa*). The solitary leaf-cutter bee (*Megachile rotundifolia*) is used as a managed pollinator on this crop (Michener, 2007).

In the UK there are approximately 228 species of solitary bee (BWARS, 2012).

Wasps

In the majority of cases, wasps do not forage for resources from flowers to feed their young; the exception being the pollen wasps (Vespidae; subfamily Masarinae). Instead, they gather animal protein such as live or masticated insects or spiders which they take back to communal nests (in the case of social wasps), or use them to provision cells that will contain offspring (solitary wasps) (BWARS, 2012). The target prey is generally specific to the species of wasp collecting it. Prey items include aphids, caterpillars, flies, hoverflies, spiders and weevils, all of which may be immobilised by sting or paralysis (BWARS, 2012). Certain wasp species do not

collect prey; instead they are parasitoids which oviposit directly into their hosts or, alternatively, they are cuckoos that use the nests of bees to raise their offspring in (BWARS, 2012).

Social wasps (Vespidae: *Dolichovespula, Vespa, Vespula*)

Social wasps (Figure 2.2 D) consist of colonies that may be ground or aerial nesting. They visit flowers for nectar to fuel their flight activity and to look for prey items. Whilst searching, pollen adheres to hairs on the thorax and abdomen, which may later be transferred to receptive flowers.

There are nine species of social wasp in the UK. Some of these have particularly large populations. Crawshay (1905) noted more than 5,000 *Vespula vulgaris* individuals present in a single nest. The total number of *V. vulgaris* workers that are reared throughout a season can approach 10,000 (BWARS, 2012). Virtually nothing is known about the foraging ranges of social wasps.

Solitary wasps (12 families)

Solitary wasps (Figure 2.2 E) can be either ground or aerial nesting. As with social wasps, flower visiting is limited to trips to obtain resources to fuel flight and to search plants for prey items. Females prepare nests and cells without assistance from a worker caste and die or disperse before their offspring emerge (BWARS, 2012). There are approximately 314 species of solitary wasp in the UK. Virtually nothing is known about their foraging ranges.

Diptera

Flies are an important group of flower visitors and play a key role in pollination, second only to hymenopterans (Yeates and Wiegmann, 2005). Hoverflies are regarded as particularly important flower visitors (Rotheray and Gilbert, 2011).

Hoverflies (Syrphidae: 3 sub-families, Eristalinae, Microdontinae, Syrphinae)

Also known as flower flies, hoverflies (Figure 2.2 F) occur on all continents except Antarctica (Rotheray and Gilbert, 2011). Most species can be categorised according to their larval feeding type which includes: predation of aphids and ants – termed zoophagy; consumption of live plant material - phytophagy, and the breakdown of detritus in soil and water – saprophagy (Gilbert *et al.*, 1994, Rotheray and Gilbert, 2011). In the case of zoophages, eggs are laid near food sources such as aphid colonies or ant nests, whilst for saprophages tree sap, farmyard ditches or bumblebee nests are sought out and used (Stubbs and Falk, 2002).

Hoverflies do not visit flowers to collect food for their offspring; instead they visit them to satisfy their own nutritional and energy needs (Faegri and van der Pijl, 1966). Pollen and nectar are the two most important sources of energy for adult hoverflies, the third being honeydew excreted by aphids (Rotheray and Gilbert, 2011).

The foraging ranges of hoverflies remain poorly understood, although they are easily capable of long distance flight. This is exemplified by the migration of certain species such as *Episyrphus balteatus* across the English Channel (Stubbs and Falk, 2002).

Hoverflies are usually considered generalists, visiting a range of flowers across the season (Rotheray and Gilbert, 2011).

There are currently 282 species of hoverfly recorded from the UK (Ball *et al.*, 2011).

Other flies (including: Bombyliidae, Conopidae and Tachinidae)
In addition to hoverflies, several other fly families contain species that are notable flower visitors. These include (but are not limited to): Bombyliidae, Conopidae and Tachinidae.

Bombyliids (Figure 2.2 G) are bee mimics with a rigid proboscis. They hover to nectar-feed from flowers and their larvae are scavengers or parasites in the nests of solitary bees. Conopids (thick-headed flies) have a long proboscis and regularly visit flowers to feed on nectar. Their larvae are internal parasites of bees. Tachinids are robust and often bristly flies that feed on nectar and pollen from flowers. Their larvae are endoparasites of butterflies and moths (Colyer and Hammond, 1968).

In the UK there are 287 species of fly within these three families: Bombyliidae (9), Conopidae (24) and Tachinidae (254) (Dipterists' Forum, 2012), however only five commonly occurring garden species are included for the purpose of this study: *Bombylius major* (Bombyliidae), *Conops quadrifasciata* (Conopidae), *Phasia hemiptera* (Tachinidae), *Sicus ferrugineus* (Conopidae) and *Tachina fera* (Tachinidae).

Lepidoptera

Both butterflies and moths visit flowers for nectar and pollen, with the latter considered necessary for oogenesis (O'Brien *et al.*, 2003). These two groups often have strong links to specific plants which are used as host sites for larval feeding,

the exception being the lycaenids that are ant-nest associates (Brooks and Knight, 1982). For the purposes of this study, butterflies and moths are recorded together.

Butterflies (Hesperiidae, Lycaenidae, Nymphalidae, Papilionidae, Pieridae, Riodinidae)

Although butterflies (Figure 2.2 H) are a small group, representing only about 360 of the 5,000 species of Lepidoptera in Europe (Chinery, 1989), they are more likely to be observed on flowers during the day than moths. Their seasonal emergence is closely tied to the availability of their larval host plants (Brooks and Knight, 1982, Chinery, 2005). There are 59 species of butterfly that regularly breed in the UK (Fox et al., 2012).

Day-flying moths (multiple families)

Few of the > 2,400 species of moth recorded in the UK are observed visiting flowers during the day, although some, such as the micro-moth *Adela rufimitrella* (Adelidae) (Figure 2.2 I) and the macro-moth, the silver Y, *Autographa gamma* (Plusiinae), are almost exclusively day feeders (Kimber, 2012).

Summary

These nine insect groups encompass a suite of species that are known from urban gardens and parks, as well as agriculture-dominated landscapes (Carter, 2001, Frankie et al., 2009, Bates et al., 2011b). English country-house gardens have the potential to meet some or all of the food, nesting and egg-laying requirements for these groups.

General fieldwork principles

Fieldwork took place over two years (2010 and 2011) and was conducted between the months of April and September. This six-month period was chosen as it corresponds to the maximum number of days when weather conditions meet the criteria for insect surveys (UKBMS, 2010a).

The following describes the general fieldwork principles for the two years.

2010 Field season

The 2010 field season involved sampling predefined areas in each of the 17 gardens on four occasions during the year.

Establishing survey areas within the seventeen gardens

The types of garden area that are common to most country-house estates, such as beds, borders and rose gardens, were identified early in 2010 using online resources (The National Trust, 2012a) and published literature (Mowl and Hickman, 2008 and Musgrave, 2009). From these, a list of potential garden-area categories (hereafter referred to as components) was compiled. During initial site visits to the seventeen properties in February and March of 2010 the presence or absence of these components was assessed. By conducting late-winter site visits (when the majority of garden perennials were in their dormant phase), potential areas for sampling could be identified without bias. This was particularly important for gardens with several flower beds and borders, as it meant the most floristically rich areas were unknown to the researcher during the selection process.

The aim when selecting areas to sample at each location followed a two-stage process: firstly, components shared by many gardens were chosen for inclusion, e.g. herb areas and flower beds and borders. Secondly, an attempt was made to include all other habitats available (UKBMS, 2010b). To achieve this, a sketch map was drawn of each garden and annotated with the components present. During a separate visit non-contiguous transects (with a combined length of 600m per property) were measured out using a trundle wheel. Where only one or two component types were present in a garden, all available flower beds and borders were measured to their full extent first, followed by any other available components. The category 'semi-wild' made up the remaining length of the 600m transect (Table 2.2). Conversely, where gardens had extensive flower borders, only a proportion of these were measured. This approach ensured that area selection did not place a disproportionate importance on flower-rich patches in gardens where several habitat types were present.

Having measured the transects the sketch maps were updated with the start and end locations of each area to be sampled, enabling quick and accurate relocation of transects on subsequent sampling visits.

By following this method, transects of equal length based on a stratified sampling approach were identified in all gardens. This enabled areas to be repeat-sampled throughout the season. This type of sampling is similar to that of Pollard walks for

butterfly monitoring (Pollard, 1977), a robust sampling method that has been used for over thirty years.

The components included and their respective lengths at each of the seventeen gardens are given in Table 2.2.

Although walled ('kitchen' or 'productive') gardens were identified as ubiquitous features that would have originally been present at most country-house estates, only half of the properties selected for sampling still had these in existence. The category 'beds and borders' therefore includes areas both within and beyond walled gardens. These walled areas became the focus of the 2011 field season (see below) and their history, and importance is discussed in greater detail in Chapter 6.

Table 2.2 Description of the 2010 sampled components at each garden, the total transect length per component (m) and (in brackets) the number of individual areas they comprised.

Property	Garden components							
	beds and borders	fruit[1]	herbs	pond edges	roses	semi-wild[2]	vegetables	TOTAL
AL	221 (5)	-	-	53 (1)	166 (3)	160 (4)	-	600
BOU*	262 (3)	-	78 (1)	53 (1)	-	207 (2)	-	600
CA*	350 (7)	31 (1)	27 (1)	-	-	192 (4)	-	600
CM	294 (6)	21 (1)	49 (1)	47 (1)	20 (1)	169 (2)	-	600
CHALL*	281 (7)	-	-	83 (1)	-	222 (5)	-	600
EN*	192 (5)	83 (2)	6 (1)	80 (1)	37 (1)	184 (2)	14 (1)	600
FAR*	203 (4)	-	-	-	61 (1)	336 (3)	18 (1)	600
HOL*	375 (8)	-	103 (2)	-	-	122 (2)	-	600
KEL*	325 (6)	-	-	-	68 (2)	174 (4)	33 (1)	600
KIR	136 (2)	-	-	-	-	464 (4)	-	600
LAM*	403 (10)	52 (1)	-	-	-	145 (2)	-	600
LW*	425 (9)	-	-	29 (1)	30 (1)	116 (1)	-	600
ST	245 (8)	14 (1)	10 (1)	78 (2)	-	181 (3)	-	600
SUL	238 (9)	69 (1)	188 (1)	-	23 (1)	39 (3)	72 (1)	600
UP	311 (9)	55 (1)	20 (1)	77 (1)	43 (1)	94 (2)	43 (2)	600
WAD	255 (9)	-	-	-	60 (1)	285 (4)	-	600
WR	425 (4)	61 (1)	-	-	-	114 (1)	-	600

[1] Fruit = soft fruit or orchard, [2] Semi-wild = un-mown patches or non-lawn, grassy areas, * Site includes walled garden sampled in 2011

33

Insect surveys and timing of sampling sessions

The need to accurately identify insects to species level, together with noting the plants they were visiting, was deemed of paramount importance to achieve the stated aims of the project. For this reason the collection of insects using malaise or pan traps was not considered appropriate. Although these two methods have been used to record the species richness of a range of invertebrates in gardens (Smith *et al.*, 2006c, Owen, 2010) the data collected provides no information about the flowers the insects visit. More importantly, these methods can underestimate the presence of some species and lead to the destructive sampling of large numbers of others (Cane *et al.*, 2000). To avoid these problems the technique of hand netting using a standard butterfly net was used (NHBS, 2012, Pocock *et al.*, 2012).

Between the 27th April and the 30th September 2010 the seventeen properties were each sampled four times. The gardens were sampled on a rotational basis in each of four broad sampling periods between spring and late summer (22 April – 5 June, 6 June – 18 July, 19 July – 9 August and 10 August – 30 September). Properties were selected for sampling by generating random numbers from one to seventeen in a spreadsheet then matching the number drawn with the alphabetically sorted properties. As a courtesy to property owners it was agreed that a minimum of twenty-four hours' notice would be given prior to any visit.

Potential sampling days were chosen using the BBC's 'next 24-hours' weather forecast website for the region (BBC website). Permission to sample was only sought if weather conditions were predicted to meet the standards necessary for flower-visiting insect activity. This was either a temperature of $\geq 13°C$ with clear skies, or alternatively $\geq 17°C$ and no rain. In accordance with the UK Butterfly Monitoring Scheme protocol (UKBMS, 2010a), days when wind speeds were predicted to reach five or more on the Beaufort scale were discounted for sampling purposes.

If a planned visit was inconvenient for the owner e.g. there was a pre-arranged event taking place, the next randomly drawn property was contacted and the visit to the first site rearranged. Selecting properties in this way ensured that gardens were not visited in the same order each time. The mean number of days ($\pm$ SE) between sampling sessions per property was 39.8 $\pm$ 1.06, $n = 17$.

Cancellation of visits and inclement weather meant a small overlap in sampling sessions occurred. Of the 68 sampling sessions, 91% were within the broad

sampling periods stated above. The remainder were within ± 4 days (range 1 – 10 days) of the previous sampling session.

Whilst walking along a transect, a distance 1.5m perpendicular to the route was included for surveying purposes. Where transects were contiguous with linear components such as beds or borders, 1.5m on the flower bed or border side of the surveyor was sampled. This observational area was set as a realistic 'space' for observations without requiring the researcher to step onto tilled/managed flower beds. Where transects passed through open components, e.g. orchards, 0.75m either side of the surveyor was included in the sampling. This method of belt transect sampling is similar to other studies assessing the diversity and abundance of flower-visiting insects e.g. Lagerlof *et al.* (1992), Colla *et al.* (2008) and Fründ *et al.* (2010). Sampling in this way gave a total surveyed area of 900m² per property per session (600m x 1.5m = 900m²).

Sampling took place between the hours of 10.45 and 15.45, unless daytime temperatures exceeded > 25°C, when sampling was deferred between the hours of 12.45 and 13.45 due to potential reduced insect activity. Transects were walked at a standard pace of approximately 6m per minute (UKBMS, 2010b). In 2010, an area totalling 6.12ha was sampled in approximately 113 hours.

If a garden was open to the public on the day of the visit, care was taken to avoid sampling in areas where visitors were present to avoid disturbance of insects.

Insects alighting on flowers and legitimately in contact with either male or female plant reproductive organs were recorded, irrespective of whether they appeared to be transporting pollen in scopae, corbiculae or on hairs on the body. In addition to recording the insect, the species of plant that was visited was noted. Flower-visitors observed to be robbing nectar resources without coming into contact with reproductive structures, e.g. *Bombus* spp. biting through the back of *Salvia* spp. flowers, were not included.

Where possible, flower-visitors were recorded to species level in the field. If an immediate identification was not possible, insects were netted and placed in a small, labelled plastic jar containing a ball of paper tissue to absorb excess moisture. The plastic jars were not tightly sealed, thus allowing insects to respire. To avoid heat-stress the jars were placed in an insulated cooler bag for later identification. The time taken to net and tube each insect was excluded from the observation time. At the end of each sampling session insects in jars were

identified and released. Where identification was not possible, individuals were retained for processing as voucher specimens. Only those insects required under the aims of the study were taken as voucher specimens as per the published code of conduct for collecting insects (Joint Committee for the Conservation of British Invertebrates, 2002).

The castes of certain species of bumblebee and some morphologically similar groups of hoverfly could not accurately be separated in the field. Their high abundance meant taking all as voucher specimens was both impractical and unethical. For these insects, broad classifications were made as per Dicks *et al.* (2002). These included the categories: *Bombus terrestris/lucorum* (combining the workers of the species *B. terrestris* and the species complex *B. lucorum sensu lato*), *B. vestalis/bohemicus* (combining the males and females of both species) and *Syrphus* spp. (combining *rectus, ribesii, torvus* and *vitripennis*).

Preparation and storage of voucher specimens

Insects taken as voucher specimens for identification were prepared using ethyl acetate or by freezing, following the descriptions in Eversham (2010). Voucher specimens are held at The University of Northampton, School of Science and Technology, Newton Building, St George's Avenue, Northampton, NN2 6JD, UK.

Identification of species

The identification of flower-visiting insects required the use of identification guides, handbooks, dichotomous keys, consultation with specialists and visits to institutions with insect collections, e.g. The Angela Marmont Centre for UK Biodiversity at the Natural History Museum, London. The main identification sources used are listed in Table 2.3. Eleven individuals (all solitary bees) remained unidentified at the end of the season. As these were morphologically distinct from all other specimens they were included in the species richness calculations for the 2010 field season, despite lacking a formal identification.

Table 2.3 List of resources used to identify voucher specimens and flower-visiting insects observed in the field.

Order	Target group	Resources used		Specialists consulted
		Books and keys	**Other resources**	
Hymenoptera	Bumblebees	Bumblebees (Prŷs-Jones and Corbet, 2011), Field Guide to the Bumblebees of Great Britain and Ireland (Edwards and Jenner, 2009)	www.bwars.com (BWARS, 2012) www.bumblebeeconservation.org (BBCT, 2012)	Mike Edwards, Stuart Roberts (BWARS)
	Honey bees	Guide to Bees and Honey (Hooper, 1991)	-	-
	Solitary bees	Guide to the Bees of Britain (Field Studies Council, 2007) Keys to species (Trial keys from BWARS for Andrena, Chelostoma, Coelioxys, Colletes, Halictus, Hylaeus, Lasioglossum, Megachile, Nomada, Osmia, Sphecodes)	www.bwars.com (BWARS, 2012) Angela Marmont Centre for Biodiversity, Natural History Museum, London	Mike Edwards (BWARS), Chris O'Toole
	Social wasps	Wasps: An account of the biology and natural history of social and solitary wasps (Spradbury, 1973)	-	-
	Solitary wasps	Solitary Wasps: Naturalists' Handbook 3 (Yeo and Corbet, 2005)	www.bwars.com (BWARS, 2012)	David Baldock (BWARS)
Diptera	Hoverflies	British Hoverflies (Stubbs and Falk, 2002)	www.hoverfly.org.uk (Hoverfly Recording Scheme, 2012)	John Showers (Northants Diptera VC recorder)
	Other flies	Flies of the British Isles (Colyer, 1968)		John Showers
Lepidoptera	Butterflies	Guide to the Butterflies of Britain (Field Studies Council, 2005) A Complete Guide to British Butterflies (Brooks and Knight, 1982)	www.butterfly-conservation.org (Butterfly Conservation, 2012)	-
	Day-flying moths	Butterflies and Day-Flying Moths (Chinery, 1989)	www.ukmoths.org.uk (Kimber, 2012)	Ian Kimber (UK Moths)

Floral surveys

On the same day that insects were surveyed, a complete inventory of all plants in flower along the sampled transects was made. This was achieved by re-walking each transect route.

A plant species was recorded as present and in flower when a minimum of three flowering units were observed. A flowering unit consisted of either: a solitary flower e.g. *Tulipa* spp., an umbel e.g. *Verbena bonariensis,* a head e.g. *Dipsacus fullonum*, a spike e.g. *Ajuga reptans* or a capitulum e.g. *Doronicum orientale* (Dramstad and Fry, 1995, Carvell *et al.*, 2007). Flowers were only included when they possessed an intact, fresh perianth that showed stamens presenting pollen and/or a non-wilted stigma, as per the methods of Primack (1985).

Flowering plants were identified to species level in the field. If this was not possible, a photograph was taken and the image number noted next to a hand-written description. Identification books were later used to identify plants to at least genus level. A list of any plants remaining unidentified at the end of the field season was sent to the head gardener at each property together with an electronic folder containing flower images, site locations and dates. At the end of 2010 less than 0.3% of all plants observed remained unidentified to genus. These were excluded from analyses.

A range of resources were used to identify plants in flower. These are detailed in Table 2.4. Nomenclature follows the most recent Angiosperm Phylogeny Group publication (APG III, 2009).

Table 2.4 Resources used to identify flowering plants.

Book title/Website	Reference
New flora of the British Isles	Stace (1997)
RHS website	RHS (2012b)
RHS New encyclopedia of plants and flowers	Brickell (1999)
The encyclopedia of planting combinations	Lord (2002)
The flower expert	Hessayon (1995)
The tree and shrub expert	Hessayon (1993)
Wild flowers of Britain and Ireland	Blamey *et al.* (2003)

2011 Field season

In 2011 a subset of the seventeen properties was sampled. Sampling took place on three occasions at nine properties.

Survey areas

Properties that possessed walled 'kitchen' or 'productive' gardens were the focus of the 2011 field season (marked with an asterisk in Table 2.1).

Insect surveys and timing of sampling sessions

Each walled garden was visited on three occasions between the 11th April and 15th September 2011. The selection protocol of 2010 was followed to decide the order in which the properties would be visited.

A standard sampling time of 1 hour 15 minutes was allocated for insect sampling on each of the three visits to a garden. During this time, the inner perimeter of the walled garden was walked at a standard pace (as per 2010), followed by two diagonal transects, each starting at a corner, passing through the centre and ending at the opposite corner. Finally any beds or borders not covered by the above perimeter or diagonal walks were sampled individually. This procedure was repeated several times during each visit until the allocated sampling time elapsed.

The 2011 insect sampling differed from 2010 in that all flower-visiting insects observed were noted, regardless of whether they were in contact with the reproductive parts of flowers. This method meant individuals on the wing, those that were resting on the ground or walls, or those walking over plants in search of prey items were included. In addition, the activity of each insect was noted. Where individuals were noted to be legitimately in contact with flowers an identification of the plant species was made. During the third visit to each property large numbers of social wasps were often found aggregating on fallen fruit. If this occurred, the species was noted but no attempt was made to accurately assess the number of wasps present.

Insects were identified, netted, prepared and identified using the same methods as in 2010.

Floral surveys

As with the 2010 sampling season an inventory of all flowering plants in the transects was made. This included all items in flower; from flowers present in lawns, to climbers on walls as well as both free-standing and espalier fruit trees.

In addition to flowering-plant richness, an estimate of abundance (blossom cover) was made. The mean area of inflorescences was measured in cm^2. For actinomorphic flowers a circular shape was assumed, with the radius measured, whilst for zygomorphic flowers lengths and widths were measured, as per Hegland and Boeke (2006). The measured parts of flowers included both plant reproductive organs and petals (perianth).

Analyses

Information relating to individual statistical tests is detailed within each chapter. The following refers to generic procedures.

Tests for normality were conducted using Shapiro-Wilk, with homogeneity of variance established using Levene's test. Where tests violated assumptions, data were transformed accordingly and re-tested. Where necessary, non-parametric tests (e.g. Kruskal-Wallis) were used.

Means are presented with ± 1 standard deviation, 1 standard error or 95% confidence intervals (detailed in text).

Unless otherwise stated, tests were performed using IBM SPSS Version 20 (IBM Corp., 2012).

Abbreviations

Abbreviations used throughout the thesis are listed in Appendix II.

Chapter 3

Flower-visitor species richness and diversity

Chapter overview

This chapter describes the communities of flower-visiting insects in the gardens of large English country houses. Species richness and diversity are quantified and comparisons are made with independently collected data as well as with vice-county lists. Similarity in flower-visitor community composition is considered, and both seasonal and insect taxa-specific patterns are explored.

Introduction

Documenting insect communities

The collecting and cataloguing of pollinating insects to establish their diversity has a long history (Donovan, 1792, Riley, 1892). Despite numerous academic publications on the subject (the search term 'pollinator diversity' in Web of Science reveals 1,511 journal articles published between 1982 and 2012), the assessment of, and explanation for, the exact composition of any particular group of flower-visiting insects continues to generate scientific interest (Franzén and Öckinger, 2012).

The focus on pollinator diversity stems from an appreciation that many natural ecosystems rely on a range of pollinators to ensure continuity of existence (Potts *et al.*, 2006). In addition, diverse pollinator assemblages benefit crop yields, the true economic value of which is only now being fully realised (Greenleaf and Kremen, 2006, Bommarco *et al.*, 2012). A greater understanding of pollinator diversity allows informed decisions to be made about how best to encourage, monitor and preserve pollinating insect communities in diverse habitats (STEP, 2012).

Target insect groups

As discussed in Chapters 1 and 2, a number of flower-visiting insect groups are important ecosystem-service providers and therefore warrant investigation. For the purposes of academic study, the decision to focus on particular groups has often been driven by the specialism(s) of the lead investigator (Westphal *et al.*, 2008, Lye *et al.*, 2009, Keil *et al.*, 2011). Concentrating research effort on only one or two insect orders is common, and has tangible advantages including the accurate identification of samples to species level with the aid of specialist entomologists (Westphal *et al.*, 2008). This task is made harder if many orders are involved and funding is limited. By focussing on identifying only bees and hoverflies Fründ *et al.* (2010) were able to answer questions about the response of insects to flower diversity, whilst Bates *et al.* (2011b) used the same two groups to address questions on how pollinator assemblages vary over urban-rural gradients. Only by working to

species resolution can the biology and life history traits of an organism be taken into consideration when interpreting results. For example, Bates *et al.* (2011b) used this approach to comment on the larval requirements of specific hoverfly species in relation to features in the landscape.

In contrast to a species-led approach, research that takes a more holistic view may reveal hitherto unappreciated interactions between different pollinator groups and the flowers they visit (Alarcón *et al.*, 2008). However, what is gained in describing 'the bigger picture' is often tempered by a loss of resolution. For example, Lazaro and Totland (2010) recorded the abundance of ten flower-visitor groups by assigning individuals to broad morphospecies classes. These were then used as surrogates for taxonomic classifications. Although the morphospecies method is presented as a valuable tool where rapid assessment of biodiversity is necessary (Oliver and Beattie, 1996), it is known to have several disadvantages. These include the artificial inflation of species richness that occurs when sexual dimorphism results in male and female specimens from the same species being erroneously classed as two separate species (Derraik *et al.*, 2002).

Insect assemblages within gardens

Gardens provide an excellent opportunity to observe insects visiting flowers. The records obtained by intensively cataloguing a single-garden location, such as Jennifer Owen's 30-year study of her Leicestershire garden (Owen, 2010), benefit from repeat sampling over many years. Despite the sustained sampling effort, these results are limited to a single site, thus restricting the interpretation of whether the garden is 'typical' or not.

Studies of gardens that incorporate a replicated sampling strategy, such as that of Smith *et al.* (2006c) who assessed the presence and abundance of twelve invertebrate groups in 61 urban domestic gardens in Sheffield, increase the robustness of species richness estimates, but also suffer limitations. In common with other invertebrate assessments in gardens, Smith *et al.* (2006c) employed capture methods (malaise traps) that failed to reveal information about the plant species the insects were visiting. Without this detail it is difficult to interpret whether individuals were caught simply as they passed through gardens, or whether they were visiting specifically to use the floral resources available.

A means of overcoming the limitations described above is to use a combination of a repeated sampling design (which focuses on several insect groups that are identified to species rather than morphospecies level), whilst also incorporating information on

43

the flowers the target insect groups are using. In this way, accurate species richness and diversity indices can be calculated and, additionally, the community structure of the plants and insects can be described. To my knowledge, no published data exist using this combination of methods for insect communities in large rural gardens. The current study offers a unique insight into the potential role these sites play in supporting flower-visiting insects in the countryside.

In this chapter flower-visitor species richness, diversity and community structure is documented for a suite of properties. Individual sites are compared to establish whether the communities observed are similar. Additionally, the data are explored in the context of other rural and large gardens. This is achieved by comparing the results from the current study with those from a dataset of 20 National Trust (NT) gardens in England and a published list of species compiled from three years' sampling at Buckingham Palace Garden (BPG). The results are also considered on a regional scale by placing them in the context of county-level records.

Flower-visitor species richness

Baltanas (1992, p. 484) describes species richness as 'the most fundamental meaning of biological diversity'. Evaluating species richness has often been considered a prerequisite when setting conservation targets or priorities (Margules and Pressey, 2000) or comparing multiple sites of interest (Beccaloni and Gaston, 1995). For example Kearns and Oliveras (2009) used species richness to compare urban and remote grassland areas in the USA to establish which environmental factors had the greatest effect on bee diversity. Two major limitations are associated with the species richness metric however. Firstly, species richness is dependent on both sample size and the extent of the area being studied (Peet, 1974). Greater intensity of sampling generally produces a higher number of species records, whilst larger areas often support more species (MacArthur and Wilson, 1967). A second issue is the presence of rare or hard-to-detect species at the study site of interest. Typically, the results from a sampling session document what is found, not what *might* have been found if all species were equally abundant and had similar levels of crypsis. The absence of a species from a dataset may therefore represent a *true* absence (it is genuinely not present) or a *false* absence (the species is there but remains undetected) (Gotelli and Colwell, 2011).

To overcome the observation that the total number of species recorded is generally a 'downward-biased' estimator for the true richness of a local assemblage (Gotelli and Colwell, 2011), methods and tools have been developed to correct for this. Using

species accumulation curves as a starting point, richness estimators extrapolate forward to a hypothetical asymptote of a curve to predict the estimated species richness for an assemblage. The methods use the observed number of rare species present to adjust for those predicted to be present but not detected (Colwell and Coddington, 1994, Gotelli and Colwell, 2011).

Non-parametric methods currently provide the most reliable species richness estimates (Chazdon et al., 1998, Walther and Morand, 1998). They comprise seven main estimators (Appendix III). Of these, three are particularly appropriate for use with abundance or count data, namely: ACE (abundance-based coverage estimator), Chao 1 and Jack 1 (Gotelli and Colwell, 2011). The choice of which estimator to use depends on the size of the dataset available, the relative importance of the singletons and doubletons present and the variance and confidence intervals associated with the estimated species richness values (Chazdon et al., 1998). Whilst all methods have their strengths and weaknesses, several authors have reported favourably on a number of them. For example, Chao 1 and Jack 1 were found to be the most robust estimators for parasite species richness when considering hosts from different taxonomic groups, as these two indicators were less biased and more precise than ACE (Walther and Morand, 1998). The reliability of Jack 1 has also been reported for artificial stream-influenced communities (Baltanas, 1992), as well as plant assemblages under hardwood stands (Palmer, 1990).

Species diversity

An assemblage of organisms is composed of a number of discrete units, with unit classification at species level being the most common (Magurran and McGill, 2011). The number of species occupying a site (the species richness) can be quantified or estimated by sampling subsets of the total area. Despite generating a quantitative measure for richness that can be used to compare one area to another, species richness does not adequately portray the variation in abundance of individuals that occurs between species. In short, both common and rare species are treated equally (Krebs, 2009).

Diversity indices combine evenness with richness to give a measure of how abundance is spread between the species observed (Colwell, 2009). Both Shannon and Simpson diversity indices are regularly used when considering pollinating insect communities. For example, Lazaro and Totland (2010) used Simpson's diversity index when investigating pollinator behaviour in relation to local flower composition, as this index gives a higher weight to common taxa. In contrast to this, Hennig and Ghazoul (2011) used the Shannon H' index to assess plant-pollinator interactions in

an urban setting, whilst Fründ *et al.* (2010) used the same index to examine whether plant diversity and flower-visitor diversity were correlated. The Shannon *H'* index is particularly useful for measuring diversity in gardens as, in addition to considering richness and evenness, it is weighted towards rarer species (Krebs, 1994).

Similarity of flower-visiting communities

In addition to measures of species richness and diversity, the composition of species present can provide a valuable measure that allows sites to be compared with one another (Su *et al.*, 2004). This has implications for research looking to quantify whether anthropogenic disturbance, e.g. agricultural intensification, has a homogenizing or diversifying effect on insect communities (Jost *et al.*, 2011). Assemblages can be measured according to their similarity or differentiation. In assessing two assemblages for similarity, the relative abundance of individual species shared by the two groups is assessed and a value is returned that acts as a proxy for the closeness of the two. The value can range from zero to one, with assemblages sharing no species assigned a zero score whilst those that are deemed identical are valued at one (Jost *et al.*, 2011). A multitude of metrics exist to measure similarity based on incidence, abundance and estimated data (Jost *et al.*, 2011).

Species abundance distributions

Assessing two communities on the basis of the similarity of their component parts has its advantages where overlap between the two allows meaningful comparisons to be made. A limitation of community similarity methods is that a single index value is calculated.

A more informative approach is to use species abundance distributions (SADs) (Magurran, 2011). Although these provide no information on species composition, they describe (and illustrate) the distribution of species within a community based on the frequency of species represented by *n* individuals. They represent a useful measure of the commonness and rarity of species that comprise any given sample, site or region (McGill, 2011).

SADs typically take the form of histograms (on arithmetic or log scales) or rank abundance distributions (RADs) (Krebs, 2009, Figure 3.1).

The shape of a SAD, frequently described as a hollow or 'lazy-J' curve when plotted as a histogram (McGill *et al.*, 2007), is a ubiquitous feature that occurs in many

multispecies communities ranging from marine benthic environments to Amazonian rainforests (McGill *et al.*, 2007). In fact these authors describe the hollow-curve SAD on an arithmetic scale as 'one of ecology's true universal laws' (McGill *et al.*, 2007).

A drawback of using RADs is that long 'tails' representing species characterised by one or a few individuals vary according to the diversity of the community. This creates problems when trying to make meaningful mathematical comparisons between two or more datasets (McGill, 2011). A useful extension to SADs are empirical cumulative distribution functions (ECDFs), described by McGill (2011, p. 122) as 'the optimal way to plot SADs'. ECDFs facilitate robust testing of data (either between distinct samples or against a standard distribution) using Kolmogorov-Smirnov procedures (McGill, 2011).
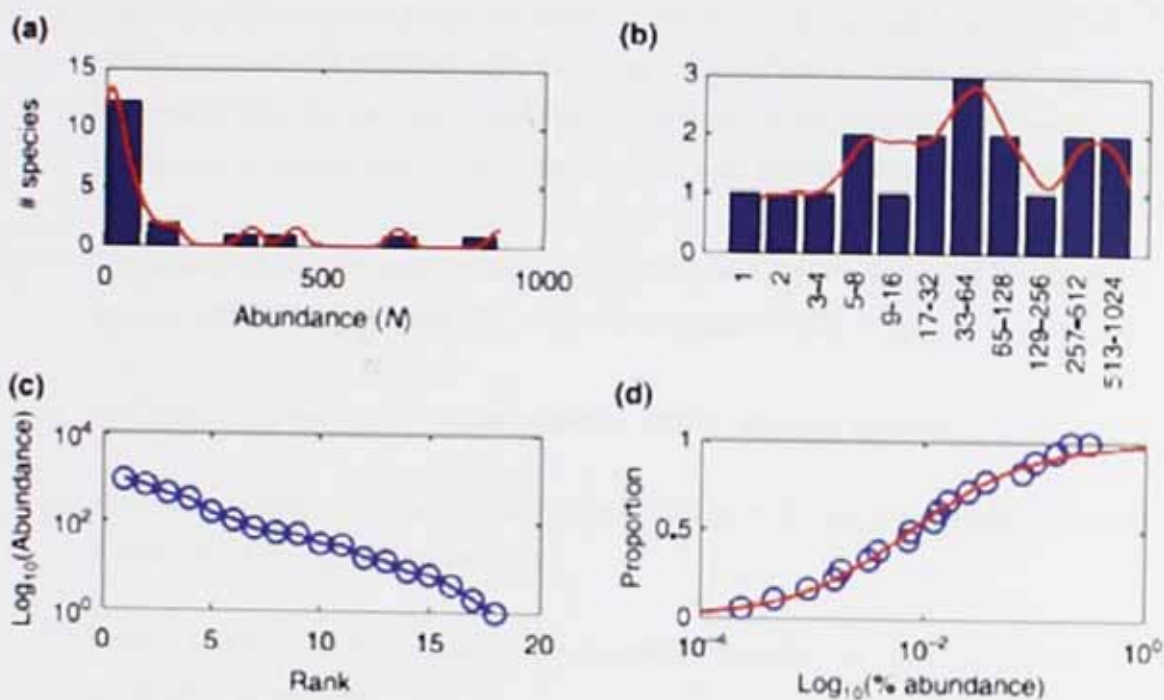
Figure 3.1 Four ways of plotting species abundance distributions. (a) Histogram showing the number of species (binned) for a given abundance on an arithmetic scale, (b) Histogram with abundance on a $\log_2$ scale, (c) Rank abundance distribution and (d) Scaled empirical cumulative distribution frequency with a logistic curve fitted through the data points. Copyright (2007) Wiley. Used with permission from McGill *et al.* (2007), Ecology Letters, Wiley publishing.

Aims

The aims of this chapter are to evaluate flower-visitor species richness, diversity and community similarity in 17 English country-house gardens and to compare these results to other large gardens where data exist.

Research questions

1. What is the *estimated* flower-visitor species richness for the seventeen gardens and how does this compare to the *actual* number of species recorded?

2. Does overall flower-visitor species richness and the richness of the four most speciose groups - bumblebees (BB), solitary bees (SB), butterflies and day-flying moths (BDM) and hoverflies (HF), vary between gardens?

3. How does the species richness data collected for this project compare to others, namely: a dataset summarising the species recorded at twenty National Trust properties, a dataset recording the abundance of flower-visitors at a single large urban garden site and finally to county-level data?

4. Does overall flower-visitor species diversity and the diversity of the four groups (BB, SB, BDM and HF) vary among gardens?

5. Are the communities of flower-visitors similar at each garden?

6. Are the species abundance distributions for each of the four groups consistent across the four sampling periods?

7. Within the assemblage as a whole do any of the groups show patterns according to season?

Methods

Data collection

Empirical data were collected by sampling gardens in 17 large English country house estates. Sampling took place between April and September 2010. Full details of the sites and methods for recording and identifying flower visitors are given in Chapter 2 (2010 field season).

Additional data were collated from a report prepared by Edwards (2003) for The National Trust. This report described entomological surveys undertaken in 20 of the Trust's gardens in seven counties between 7 July and 22 August 2003 (Appendix IV). For each garden a species list was provided, but this did not include insect abundance. Only data that could be compared directly with that of the present survey were selected from the report e.g. within the group Diptera – other flies (Chapter 2), only fly species that corresponded to those recorded in the current study were considered for inclusion. The data were prepared by compiling species lists for each of the twenty properties, with each species coded according to whether it was within the group bumblebees (BB), solitary bees (SB), butterflies and day-flying moths (BDM), hoverflies (HF), flies (F), solitary wasps (SOLW) or social wasps (SOCW). By doing this it was possible to calculate the overall species richness for the twenty properties, as well as assessing the species richness of the groups of interest. This facilitated a direct comparison between the report and the results of the present study.

A second dataset listing the aculeate Hymenoptera (hereafter referred to as aculeates) and hoverflies recorded at Buckingham Palace Garden was also obtained. These data, prepared by Harvey (2001) and Plant (2001), list the species recorded in the Royal family's garden between 1995 and 1997. The dataset differs from the current study and that of Edwards (2003) for two reasons. Firstly it represents only a single site, and secondly the data were obtained primarily as a result of malaise and pitfall trapping rather than hand-netting. Notwithstanding these differences, this garden merits inclusion as it represents one of only a handful of studies that have considered invertebrate populations in large gardens over a sustained sampling period. Another positive aspect of using these data is that the number of individuals recorded is given.

To consider the species richness of the seventeen gardens sampled in a broader context (and therefore their potential importance), applications for vice-county (VC) data were made to national insect recording schemes. Aculeate data for the four counties visited during the current study were provided by the Bees, Wasps and Ants

Recording Society (BWARS, 2012). On receipt, the data for each county were sorted according to age. Any species recorded prior to 1938, and not seen after that time, were excluded e.g., *Bombus cullumanus*, *B. distinguendus* and *B. subterraneus*. All records for ants (Formicidae) were then removed, thereby creating an overall list for aculeates (minus ants) for each county. These records were further subdivided into four groups: bumblebees (BB), solitary bees (SB), solitary wasps (SOLW) and social wasps (SOCW). The data represent all species recorded per county from January 1939 to September 2012.

Vice-county data for hoverflies were provided by the Dipterists' Forum Hoverfly Recording Scheme, the national recording body for hoverflies in the UK (Hoverfly Recording Scheme, 2012). The data represent all hoverfly records submitted for the four counties of interest from January 1975 to September 2012.

Species richness estimates

The statistical program EstimateS (Colwell, 2012) was used to calculate the estimated species richness for the 2010 field data and that of the twenty National Trust properties (Edwards, 2003). The other datasets (BPG and vice-county lists) were not suitable for examination using these methods as they were not derived from replicated sampling sessions. The data collected during the current project included abundance data, whilst that of Edwards was incidence (presence/absence data). This meant that although species richness calculations could be performed for both, they were performed using different indices (non-parametric abundance and non-parametric incidence metrics, Appendix III).

Several calculations were performed using the data from the current project. These were as follows: (i) each property was considered separately by using the four sampling sessions to derive a per-property species richness estimate, (ii) all properties ($n = 17$) were combined using the per-property total from each of the four sessions to generate a single species richness value, (iii) the four most speciose groups: BB, SB, BDM and HF were each assessed by using the total of four sampling sessions for each property ($n = 17$) to generate a per-group species richness value. For each calculation the recommended default settings for the software were used. This resulted in the bias–corrected formula for Chao 1 being used unless the value for doubletons was nil, in which case the alternative 'classic' formula was used (Colwell, 2012). Two of the three non-parametric species richness estimates that use abundance data (Chao 1 and Jack 1) are presented for comparison purposes.

As some of the gardens sampled in the current study were sufficiently close for target species to potentially fly between them, the data were checked for spatial autocorrelation using Moran's I test in R (package Ape) (R Development Core Team, 2012). The variables used for this analysis were the Jack 1 species estimate values and British national grid coordinates (Ordnance Survey, 2012).

Having checked for normality and homoscedasticity, one-way ANOVAs were used to check for differences in species richness between properties (all species across four sampling sessions and also for the four groups). These were followed up with Ryan-Einot-Gabriel-Welsch Q (REGWQ) *post hoc* tests.

For the Edwards dataset (Edwards, 2003), only incidence data were available. Using EstimateS (Colwell, 2012), the species richness estimates for (i) all properties combined ($n = 20$) and (ii) the four groups (BB, SB, BDM and HF) were calculated. The non-parametric incidence estimators Chao 2 and Boot (Appendix III), which are equivalent to the abundance estimators used for the current study, are presented.

Species diversity

Shannon H' diversity indices (hereafter referred to as Shannon), were calculated for the 17 properties using EstimateS (Colwell, 2012). Indices are presented for (i) all properties combined and (ii) each of the four groups (BB, SB, BDM and HF). The software generates a single diversity value and 95% confidence intervals (CI).

Community similarity

The similarity between assemblages of flower-visiting insects across the 17 gardens was assessed using EstimateS (Colwell, 2012). The Morisita-Horn and also Chao's Abundance-based Estimated Sørensen indices were calculated for comparison purposes as they are generated using different criteria (Chao et al., 2005, 2006; Colwell, 2012). The former compares abundance between two sites on a species-by-species basis and benefits from a lack of sensitivity to sample size. The downside of this index is that similarity is measured according to the composition of dominant species and largely ignores the effect of rare species, which can be key components in insect communities (Magurran and McGill, 2011). The latter index is based on the probability that two randomly chosen individuals, each drawn from one of two samples, are both representatives of a species that is present in both samples, but are not necessarily the same species (Chao et al., 2005, 2006; Colwell, 2012).

The software used to compute these values allows for re-sampling to create bootstrap-generated standard errors. In the current analysis the recommended '200 re-samples' setting was used.

An advantage of using Chao's abundance-based method is that it incorporates unseen species, i.e. it takes into account the contribution that a species can make when it is present at both sites but not necessarily detected at one of these (Chao *et al.*, 2005; Colwell, 2012), thus reducing the negative bias associated with more traditional indices (Chao *et al.*, 2005). Although this index is less likely to be affected by dominant species (as per Morisita-Horn), it does not benefit from the detailed species-by-species analysis that the aforementioned metric performs (Magurran and McGill, 2011).

As yet, multiple comparisons across sites remain too complex to be computed easily (Jost *et al.*, 2011) and therefore community similarity remains a calculation typically performed between two sites only. This produces multiple pair-wise results that require individual testing to establish whether a result is significantly different from another. Although Bonferroni (Field, 2009) or Dunn Šidák (Sokal and Rohlf, 1981) corrections help to avoid the Type I errors associated with multiple testing, when used at such a large scale they risk introducing Type II errors.

To overcome this, a different approach was taken to assess the results generated. Firstly, the values produced from the multiple comparisons were ranked according to their value ($n = 136$). As a low similarity score represents poor congruence in species overlap between sites, the lowest 5% of values were determined. These values ($n = 7$) were then examined to establish whether a disproportionate number were represented by an individual property. This approach was taken for both the Morisita-Horn and the Chao Abundance-based Estimated Sørensen values.

An independent, but complementary, method of looking at community similarity is the creation of a dendrogram using nearest neighbour hierarchical classification techniques (Oertli *et al.*, 2005). The Jaccard dendrogram created using SPSS (IBM Corp., 2012) represents a binary index that discards joint absences and gives equal weight to matches and non-matches alike.

Species abundance distributions

To overcome the problems associated with testing rank abundance distributions, empirical cumulative distribution function (ECDF) plots were created. For each insect group the abundance of individuals from each species was used to examine differences across four sampling sessions. Complementing this, the insect data were incorporated into plots categorised by each of the four sampling sessions.

In order to create the ECDFs for each insect group, the abundance of each species (per session) was ranked in ascending order and the fraction of the total abundance calculated. This was then plotted on a log-transformed x axis. The species data were maintained in the same ranked order and plotted as fractions of the total species richness on the y axis (McGill, 2011). The resulting ECDFs were tested for differences using a two-tailed Kolmogorov-Smirnov test with critical values (α) adjusted using the Dunn-Šidák method (Sokal and Rohlf, 1981, Appendix V). ECDFs for the four sampling sessions in the season were created in the same way.

As honey bees are classed as a single species for the purposes of this study, the data could not be used to prepare ECDFs. To compare the difference in honey bee abundance across sessions, the number of honey bees observed at each property was summed. The original and transformed data did not meet assumptions for normality, therefore the non-parametric Wilcoxon signed ranks test was used.

Results

Overview of results

The sampling of seventeen properties in 2010 (each on four occasions) yielded a total of 9,893 records of flower-visiting insects from 174 species (Appendix VI). Approximately 1.5 insects were recorded per minute over a total area of 6.12ha. Hoverflies were the most abundant group (4,430 individuals) followed by bumblebees (2,870), honey bees (801), solitary bees (674), and butterflies and day-flying moths (613). The remainder (505) were comprised of other flies, solitary and social wasps.

Of the four sampling sessions, Session 3 produced the most insect records (4,935). Almost 50% of all individuals recorded in 2010 were from this session (mean 290.3 ± 148.1 individuals per property).

The results of Moran's I test showed no significant autocorrelation between sites, $P = 0.87$, therefore independence of locations was assumed.

Species richness

The total number of species recorded for each of the 17 properties ranged from 23 at Kirby (KIR) to 75 at Courteenhall (CHALL) and Steane (ST), mean 61.6 ± 12.1. These values, together with the results of the Chao 1 and Jack 1 species richness estimators for each property, are presented in Table 3.1 and Figure 3.2.

The per-property species richness estimates were plotted against the pooled total of flower-visiting insects per property (Figure 3.3). The lines of best fit for Chao 1 and Jack 1 were almost identical, although the spread of data points around the trend line for Chao 1 was greater.

Table 3.1 Results of EstimateS (Colwell, 2012) Chao 1 and Jack 1 species richness estimations for the 17 properties together with the actual number of species recorded.

Property	Species recorded (4 samples)	Chao 1	(SD)	Jack 1	(SD)
AL	51	89.00	(23.9)	75.00	(8.8)
BOU	65	110.56	(24.8)	95.75	(11.3)
CA	70	95.00	(13.3)	100.00	(3.2)
CM	58	83.79	(16.2)	87.25	(7.0)
CHALL	75	85.20	(6.4)	109.50	(8.2)
EN	60	127.60	(41.0)	90.00	(12.1)
FAR	61	76.83	(9.4)	85.75	(2.6)
HOL	63	85.18	(10.7)	99.25	(7.5)
KEL	65	104.43	(22.4)	92.00	(8.6)
KIR	23	28.60	(5.4)	35.00	(3.2)
LAM	61	101.33	(24.6)	91.00	(4.4)
LW	63	80.10	(10.4)	90.00	(6.1)
ST	75	98.00	(12.5)	107.25	(6.4)
SUL	61	101.33	(24.6)	87.25	(3.1)
UP	73	89.96	(9.7)	106.00	(8.4)
WAD	53	76.10	(13.2)	77.00	(8.2)
WR	66	95.08	(14.2)	100.25	(4.3)
Mean (SD)	61.59 (12.1)	89.89	(20.52)	89.90	(17.17)
All properties combined (SE)	174	228.24	(18.4)	241.41	(10.5)
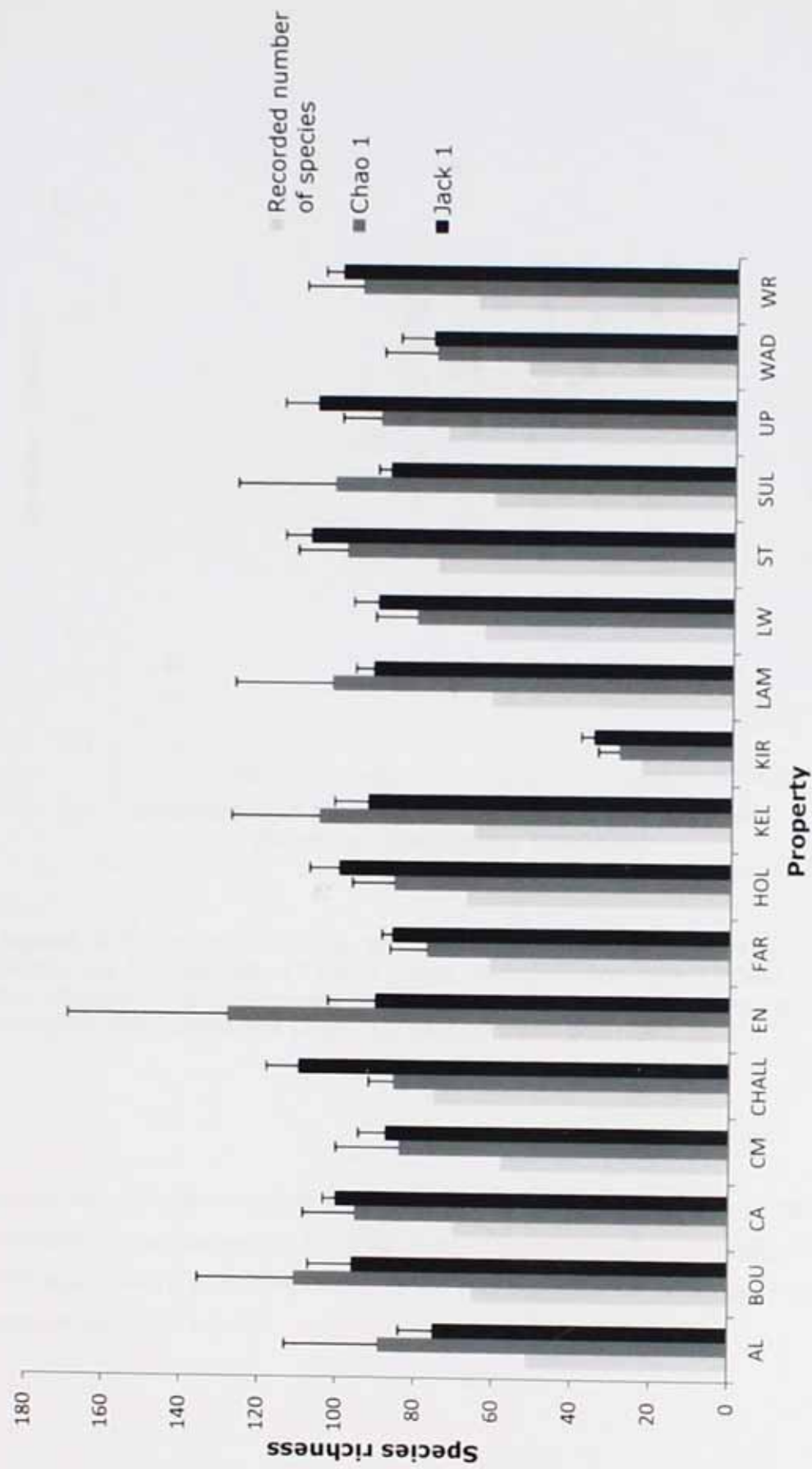
Figure 3.2 Recorded species richness and the richness estimators Chao 1 and Jack 1. Error bars = 1SD.
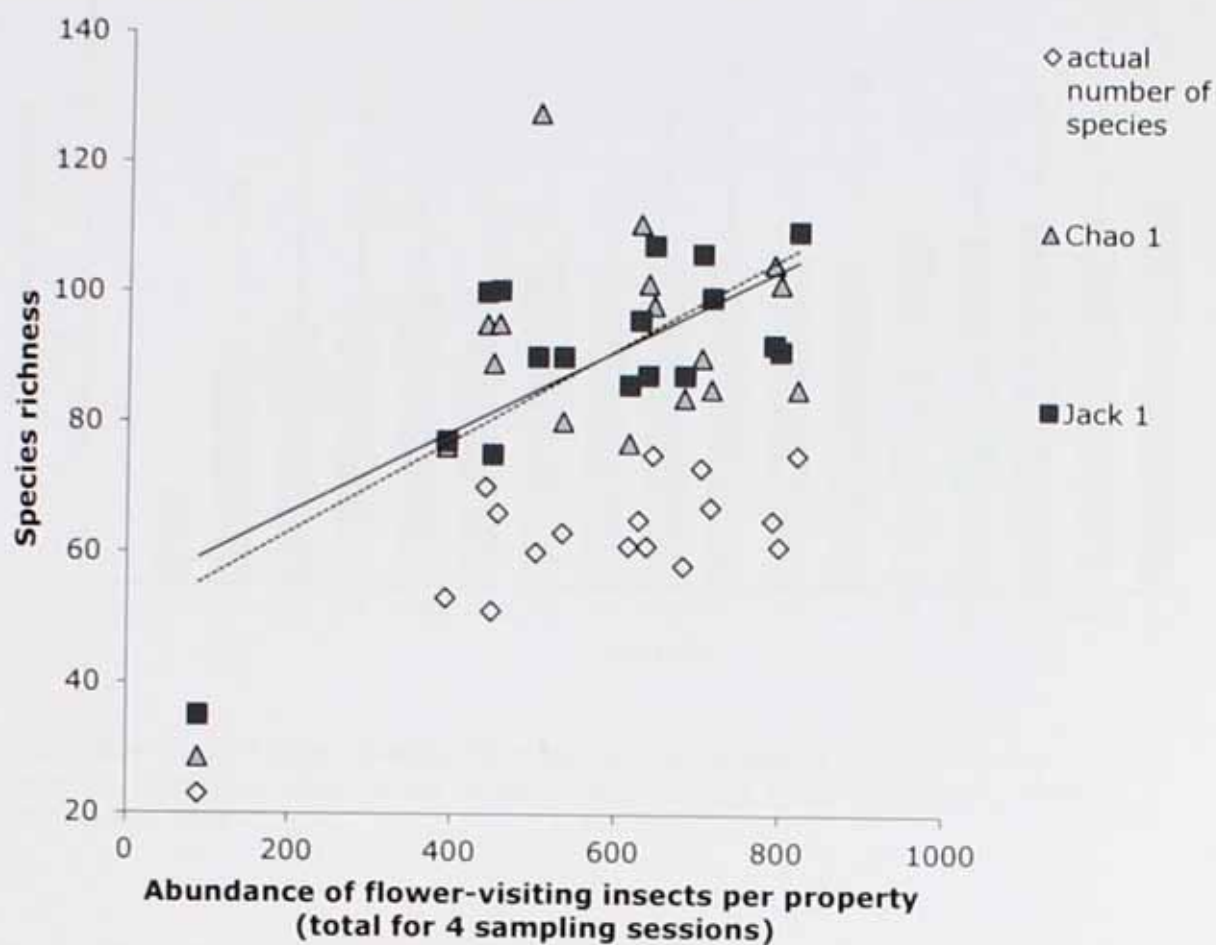
Figure 3.3 Species richness for the actual number of species recorded (open diamonds) the estimators Chao 1 (filled triangles) and Jack 1 (filled squares) against the abundance of individuals per property. Each symbol represents four sampling sessions. Solid trend line (Chao 1), dashed trend line (Jack 1).

A one-way ANOVA revealed a significant difference in mean actual species richness between properties across the four sampling sessions, $F_{16,51} = 2.88$, $P = 0.002$. *Post hoc* tests (REGWQ) showed Kirby (KIR) was significantly different to thirteen other properties (Figure 3.4).
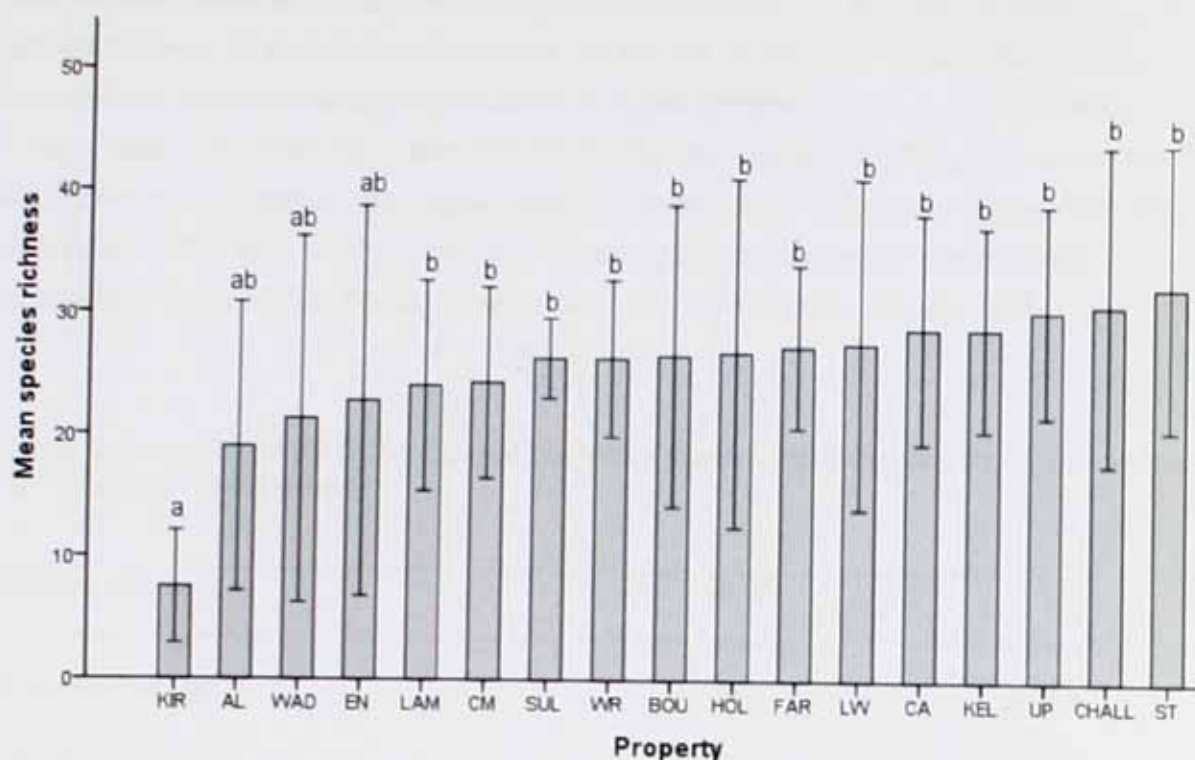
Figure 3.4 Ranked mean species richness for each property (four sampling sessions). Identical letters show homogeneous groups (REGWQ *post hoc* tests). Error bars = 95% CI.

The species richness and estimators for each of the four insect groups is given in Table 3.2. Hoverflies were the most species-rich group, followed by solitary bees.

Table 3.2 Species richness estimates for the four most speciose flower-visitor groups.

Groups for species richness estimates	Species recorded	Chao 1	(SD)	Jack 1	(SD)
Bumblebees	14	15.00	(0.3)	15.94	(0.9)
Solitary bees	50	72.13	(16.4)	68.88	(5.3)
Butterflies and day-flying moths	31	36.60	(3.9)	43.35	(3.9)
Hoverflies	59	85.33	(14.5)	85.65	(4.1)

Comparisons between properties for species richness of the four flower-visiting groups showed no significant difference for BB, SB or BDM ($P > 0.05$, Table 3.3). However HF richness varied significantly between properties ($F_{16, 51} = 5.04$, $P < 0.001$, Table 3.3). *Post hoc* tests (REGWQ) showed that Kirby (KIR), which had the lowest hoverfly richness, was significantly different to 12 properties. Kelmarsh (KEL) and Upton (UP), with the highest hoverfly species richness, were significantly different to Kirby (KIR), Easton Neston (EN) and Wrest (WR) (Figure 3.5).

Table 3.3 Results of ANOVAs comparing mean species richness across 17 properties for individual insect groups.

Species richness	F	d.f.	P
Bumblebees (BB)	1.065	16,51	0.411
Solitary bees (SB)	0.831	16,51	0.646
Butterflies and day-flying moths (BDM)	1.327	16,51	0.218
Hoverflies (HF)	5.044	16,51	<0.001
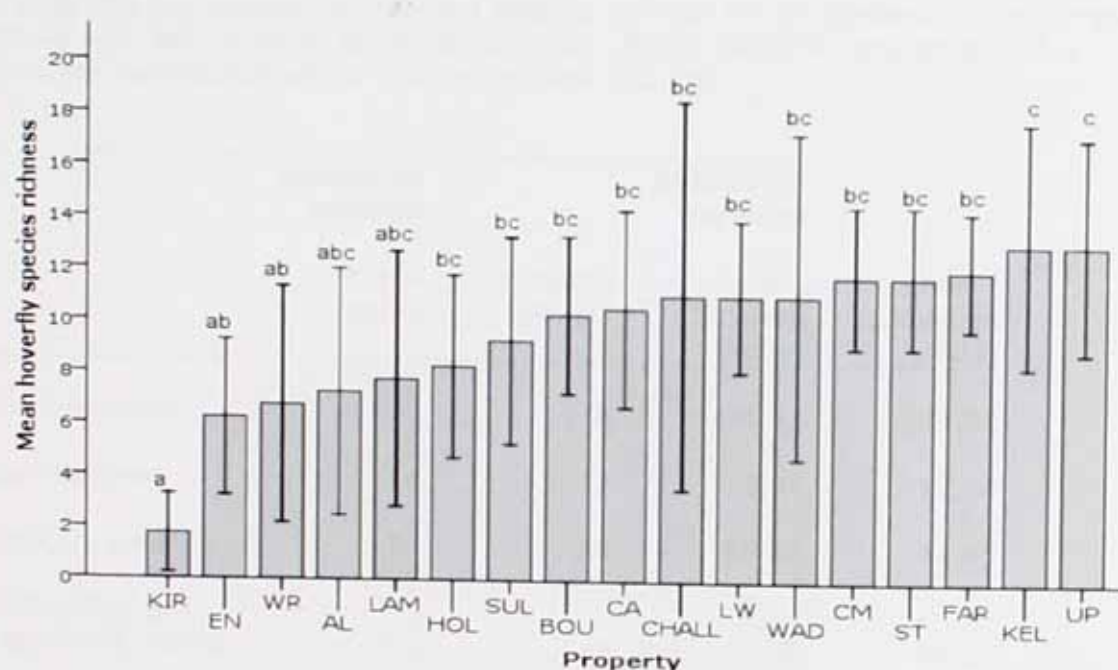
Figure 3.5 Mean hoverfly species richness for each property (four sampling sessions). Identical letters show homogeneous groups (REQWQ *post hoc* tests). Error bars = 95% CI.

Species richness: Comparison with other locations

The recorded species richness (together with species richness estimates) for the 20 NT gardens sampled by Edwards (2003) is given in Table 3.4. The data presented are for all properties combined and for the four insect groups. For comparison, the datasets from the current study and that of Edwards are presented together in Table 3.5.

Table 3.4 Species richness (actual and estimates) for the 20 NT gardens sampled by Edwards (2003). Note, no standard deviation values are provided by the EstimateS software for Boot.

Groups for species richness estimates	Species recorded	Chao 2 (SD)	Boot
All 20 properties	178	269.88 (29.08)	208.73
Bumblebees	12	12.24 (0.71)	13.08
Solitary bees	34	44.45 (8.09)	39.18
Butterflies and day-flying moths	25	45.25 (20.19)	28.64
Hoverflies	54	83.39 (16.6)	63.63

Table 3.5 Comparison of recorded species richness for 17 gardens in the current study with that of 20 NT gardens (Edwards, 2003). Note 'All properties' value includes species not within the four groups detailed.

	Recorded species		Estimated species	
	Present study	Edwards (2003)	Jack 1 (Present study)	Chao 2 (Edwards 2003)
All properties	174	178	241.41	269.88
Bumblebees	14	12	15.94	12.24
Solitary bees	50	34	68.88	44.45
Butterflies and day-flying moths	31	25	43.35	45.25
Hoverflies	59	54	85.65	83.39

Comparing species richness across gardens

Extending the comparison of the current study to that of a separate large garden (Buckingham Palace Garden - BPG), and also vice-county data, permitted the inclusion of two additional insect groups; social and solitary wasps (SOCW and SOLW). The four vice-counties listed in Table 3.6 correspond to those visited in the course of the present study.

Table 3.6 Recorded species richness for five insect groups. Data are from the current study, Edwards (2003), the species lists for BPG (Harvey, 2001 and Plant, 2001) and vice-county (VC) records. The latter are from BWARS for bees and wasps (1939 – 2012) and the Hoverfly Recording Scheme for hoverflies (1975 – 2012). Values in brackets represent (where available) the number of records contributing to the species richness figures. Nhants. = Northamptonshire, Beds. = Bedfordshire, Bucks. = Buckinghamshire and Warks. = Warwickshire.

	Present study (n = 17)		Edwards (n = 20)	BPG		VC data Nhants.		Beds.		Bucks.		Warks.	
BB	14	(2,870)	12	6[1]	(155)	14	(3,967)	17	(1,719)	15	(605)	17	(3,969)
SB	50	(674)	34	33[1]	(199)	61	(390)	72	(300)	93	(569)	117	(5,683)
SOLW	9	(35)	43	40[1]	(356)	88	(1,957)	62	(159)	80	(179)	123	(2,079)
SOCW	6	(292)	7	6[1]	(13)	7	(841)	5	(38)	8	(84)	8	(841)
HF	59	(4,430)	54	37[2]	(1,599)	182	(12,200)	179	(4,168)	168	(3,633)	193	(9,927)

[1] Species recorded using malaise and pitfall traps with limited active field work Apr. 1995 – Aug. 1997 (Harvey, 2001)
[2] Species recorded using a malaise trap. Continuous recording from Apr. 1995 – Aug. 1997 (Plant, 2001)

Sampling effort

The relationship between the number of species recorded for each insect group and the number of records on which each value is based (the sampling effort) is shown in Figure 3.6. The data points for the current study are in red.

With the exception of SOLW, the data points from the current study are within (or close to) the range of the other two studies and that of the vice-county data.
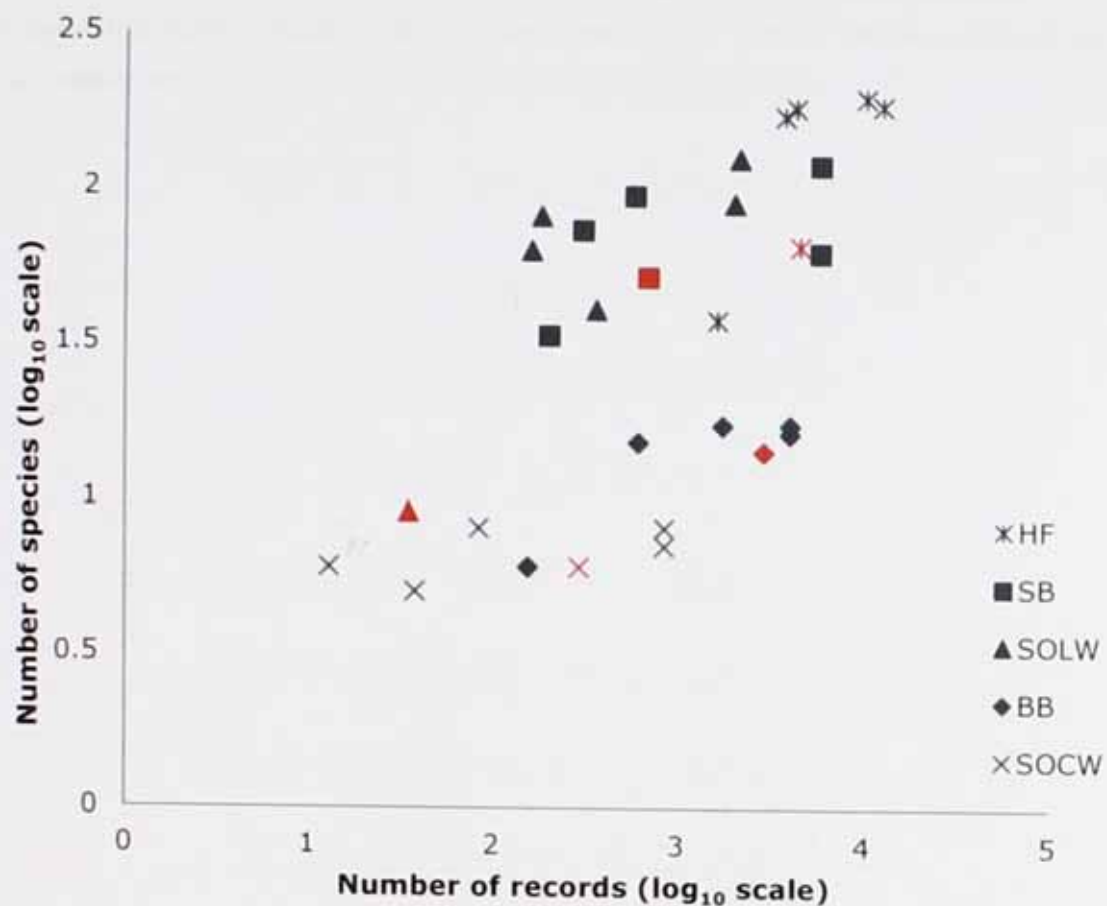
Figure 3.6 Relationship between the number of species recorded and the number of records for five insect groups using data from two studies: the current work and BPG (Plant, 2001 and Harvey, 2001) plus data for four vice-counties. Data are presented using log scales. Red data points show the position of the current study within the context of the others.

Species diversity

The Shannon diversity index values for each of the 17 properties are given in Figure 3.7. The diversity value for Kirby (KIR) is significantly lower than eight other properties. The overall Shannon diversity for all properties combined is 3.06 ± 0.18.

In addition, Shannon diversity values were calculated for the four insect groups (Figure 3.8). The hoverfly (HF) group was strongly dominated by a single species, *Episyrphus balteatus* and a second compound-species, *Syrphus* spp. (see Chapter 2, Methods). Together these accounted for 61% of the 4,474 hoverfly records. As a result the hoverfly diversity values were re-calculated to exclude these. For comparison purposes Figure 3.8 includes hoverflies (i) in their entirety, (ii) without *E. balteatus*, and (iii) without *E. balteatus* and *Syrphus* spp.
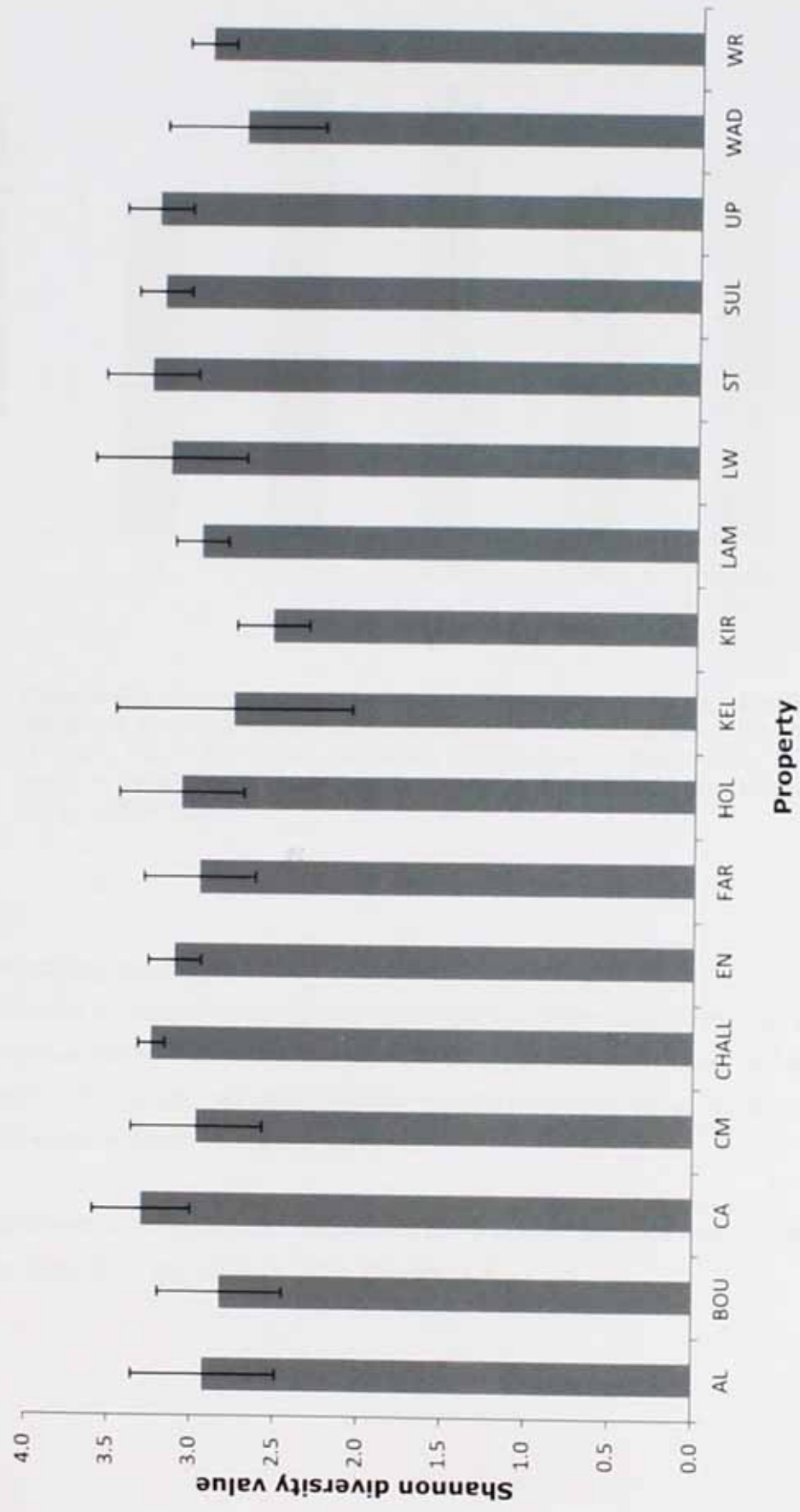
Figure 3.7 Shannon diversity values for each of the 17 properties (four sampling sessions, all species). Error bars = 95% CI.
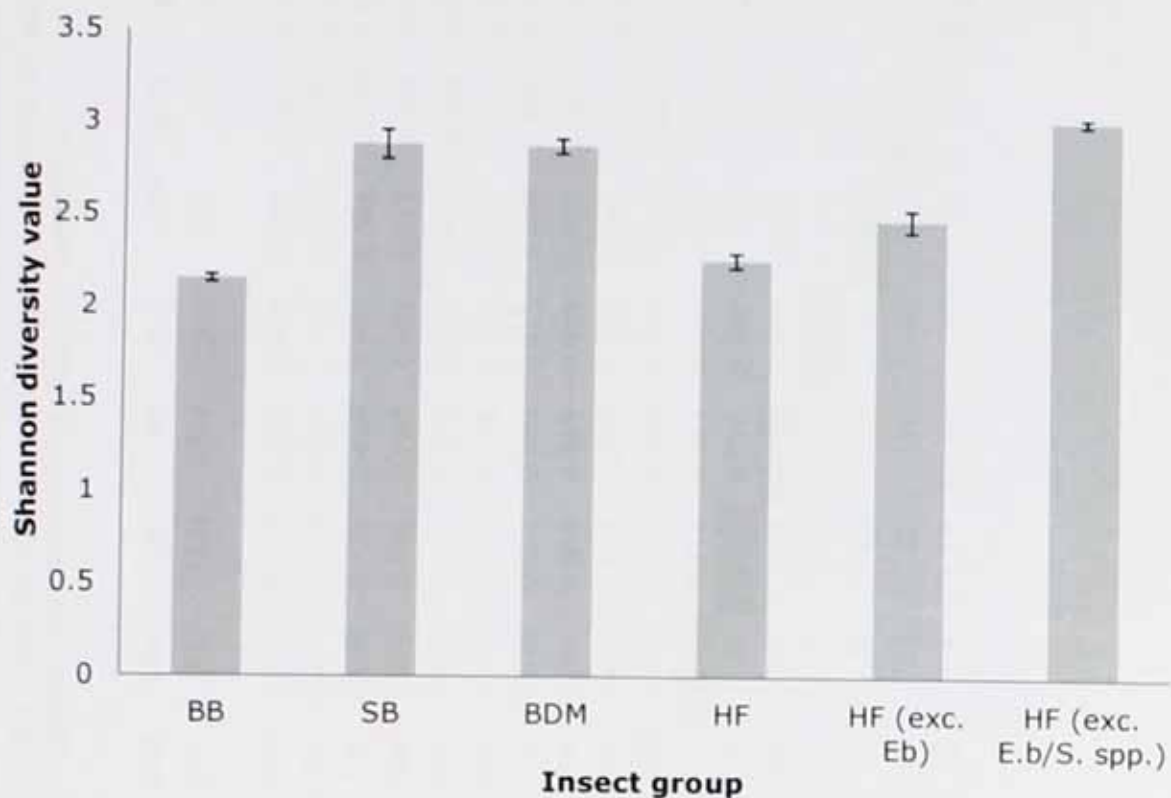
Figure 3.8 Shannon diversity for four insect groups (17 properties, all sampling sessions combined) and the recalculated values for hoverflies (HF). HF (exc. Eb) = hoverflies excluding *Episyrphus balteatus* only. HF (exc. E.b/S spp.) = hoverflies excluding *E. balteatus* and *Syrphus* spp. combined. Error bars = 95% CI.

Community similarity

The results of the pair-wise similarity comparisons (Morisita-Horn and Chao's Abundance-based Estimated Sørensen indices) are given in Table 3.7 and Table 3.8. In each case the top half of the matrix reports the index value, with the lower half showing the number of shared species.

A dendrogram using nearest neighbour hierarchical classification techniques shows Kirby (KIR) as a significant outlier (Figure 3.9).

Table 3.7 Results of Morisita-Horn pair-wise comparisons for community similarity. The top half of the matrix represents the Morisita-Horn values, with the lower half detailing the number of shared species. The values in brackets show the total number of species recorded for each property. Values in red are the seven lowest values (lowest 5%). Values in bold red highlight comparisons that relate to Kirby (KIR).

	AL (51)	BOU (65)	CA (70)	CM (58)	CHALL (75)	EN (60)	FAR (61)	HOL (63)	KEL (65)	KIR (23)	LAM (61)	LW (63)	ST (75)	SUL (61)	UP (73)	WAD (53)	WR (66)
AL		0.564	0.526	0.695	0.778	0.671	0.874	0.849	0.833	0.583	0.727	0.820	0.797	0.498	0.500	0.685	0.713
BOU	31		0.436	0.834	0.771	0.603	0.572	0.546	0.563	0.378	0.873	0.732	0.532	0.403	0.893	0.328	0.512
CA	33	36		0.479	0.675	0.387	0.494	0.373	0.412	0.335	0.438	0.430	0.459	0.807	0.591	0.328	0.853
CM	32	32	37		0.854	0.571	0.790	0.770	0.811	0.306	0.939	0.898	0.783	0.405	0.815	0.655	0.594
CHALL	36	39	46	38		0.671	0.800	0.745	0.741	0.411	0.862	0.875	0.860	0.649	0.833	0.586	0.732
EN	24	32	40	30	38		0.597	0.583	0.506	0.406	0.588	0.672	0.646	0.443	0.559	0.418	0.435
FAR	33	35	35	38	41	32		0.947	0.941	0.322	0.821	0.877	0.880	0.415	0.494	0.856	0.663
HOL	34	36	38	37	46	34	39		0.930	0.284	0.801	0.864	0.865	0.335	0.457	0.863	0.544
KEL	34	35	37	45	43	35	41	42		0.287	0.815	0.863	0.835	0.292	0.484	0.897	0.632
KIR	19	18	21	17	20	17	17	18	19		0.335	0.347	0.313	0.374	0.330	0.162	0.408
LAM	34	39	41	36	47	38	36	43	41	20		0.911	0.783	0.407	0.787	0.615	0.558
LW	31	35	36	40	47	33	43	43	42	17	39		0.876	0.438	0.699	0.694	0.543
ST	34	43	43	41	49	40	45	42	48	22	46	46		0.446	0.550	0.779	0.580
SUL	32	37	41	37	45	36	35	42	41	19	43	39	45		0.546	0.205	0.635
UP	33	41	44	45	50	39	41	46	52	21	45	49	53	46		0.282	0.559
WAD	28	31	33	33	35	27	29	35	34	16	33	31	34	30	41		0.521
WR	32	33	35	32	46	34	38	40	36	16	36	40	41	34	38	28	

Table 3.8 Results of Chao Abundance-based Estimated Sørensen pair-wise comparisons for community similarity. The top half of the matrix represents the Chao Abundance-based Estimated Sørensen values, with the lower half detailing the number of shared species. Values in red are the seven lowest values (lowest 5%). Values in bold red highlight comparisons that relate to Kirby (KIR).

	AL	BOU	CA	CM	CHALL	EN	FAR	HOL	KEL	KIR	LAM	LW	ST	SUL	UP	WAD	WR
AL		0.910	0.915	0.924	0.926	0.888	0.968	0.929	0.969	0.894	0.954	0.890	0.932	0.924	0.886	0.963	0.987
BOU	40		0.959	0.892	0.921	0.956	0.910	0.930	0.939	0.809	0.961	0.914	0.935	0.984	0.894	0.854	0.896
CA	47	66		0.967	0.936	0.976	0.869	0.895	0.896	0.753	0.964	0.920	0.873	0.950	0.925	0.841	0.868
CM	37	39	55		0.910	0.889	0.924	0.910	0.987	0.867	0.980	0.971	0.924	0.966	0.975	0.955	0.894
CHALL	45	69	64	43		0.959	0.930	0.937	0.943	0.949	0.988	0.957	0.938	0.983	0.948	0.936	0.916
EN	31	41	74	38	55		0.928	0.911	0.966	0.854	1.000	0.986	0.996	0.882	0.905	0.751	0.954
FAR	38	41	49	46	45	48		0.938	0.962	0.739	0.967	0.948	0.946	0.962	0.880	0.818	0.911
HOL	38	47	48	48	63	45	48		0.963	0.767	0.964	0.945	0.905	0.983	0.893	0.90	0.897
KEL	40	44	52	83	52	72	56	61		0.924	0.984	0.960	0.989	0.984	0.975	0.947	0.915
KIR	31	44	25	22	24	23	37	26	27		0.923	0.752	0.980	0.786	0.890	0.695	0.794
LAM	39	64	67	45	68	66	45	61	59	28		0.981	0.993	0.996	0.952	0.913	0.950
LW	35	61	47	50	64	55	54	53	56	22	58		0.982	0.952	0.972	0.887	0.907
ST	39	56	54	56	63	75	60	54	74	30	62	65		0.997	0.951	0.895	0.892
SUL	74	108	75	68	66	106	118	90	133	25	97	58	61		0.989	0.831	0.915
UP	39	51	59	69	63	62	47	63	75	24	66	71	74	172		0.952	0.877
WAD	46	44	94	64	60	46	49	60	63	27	68	62	55	63	78		0.921
WR	50	45	51	46	72	53	58	62	55	19	71	58	60	90	47	41	
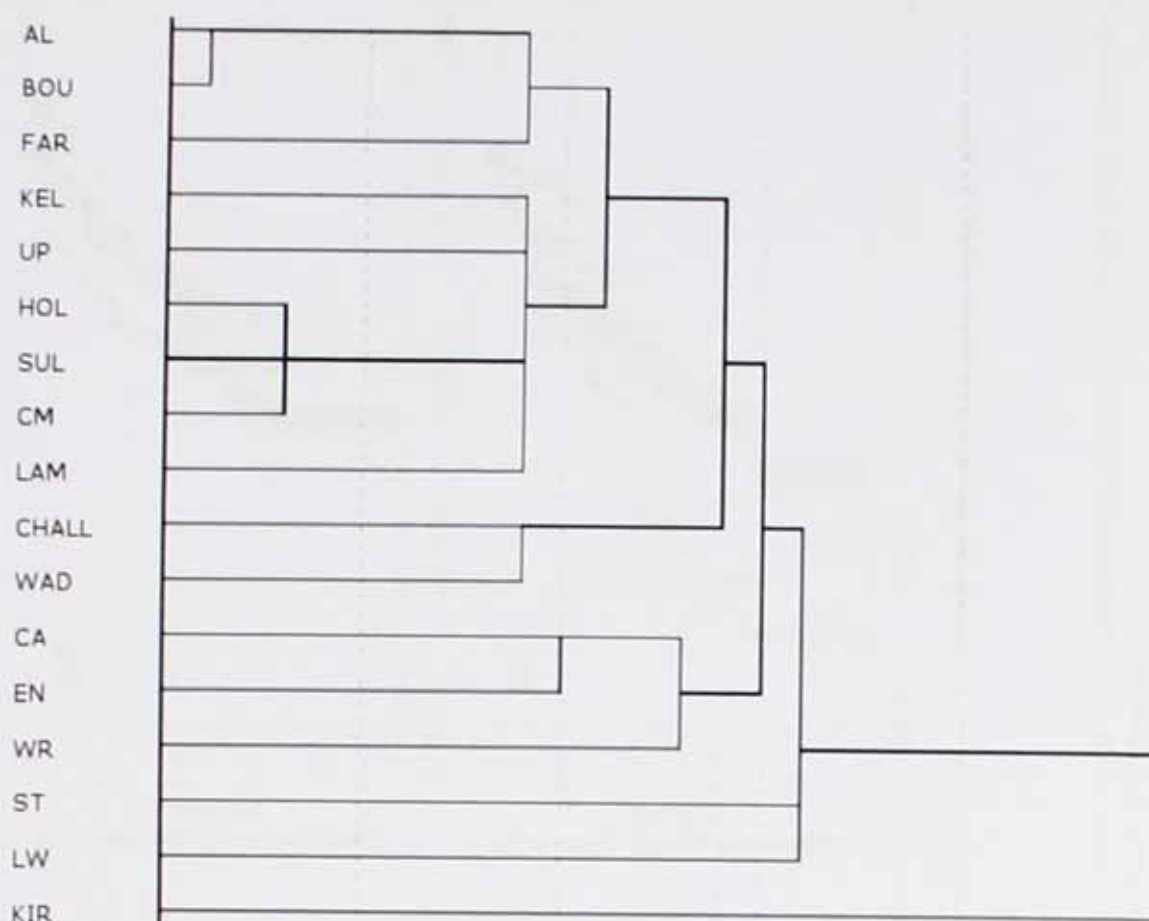
Figure 3.9 Dendrogram showing nearest neighbour linkage between 17 sites based on incidence data for species present (Jaccard method).

Species abundance distribution (ECDFs)

The ECDFs for each of the four insect groups are given in Figure 3.10. The plots show the distributions according to each of the four sampling sessions. The results of Kolmogorov-Smirnov tests for differences between sampling sessions within individual groups are provided in Table 3.9.
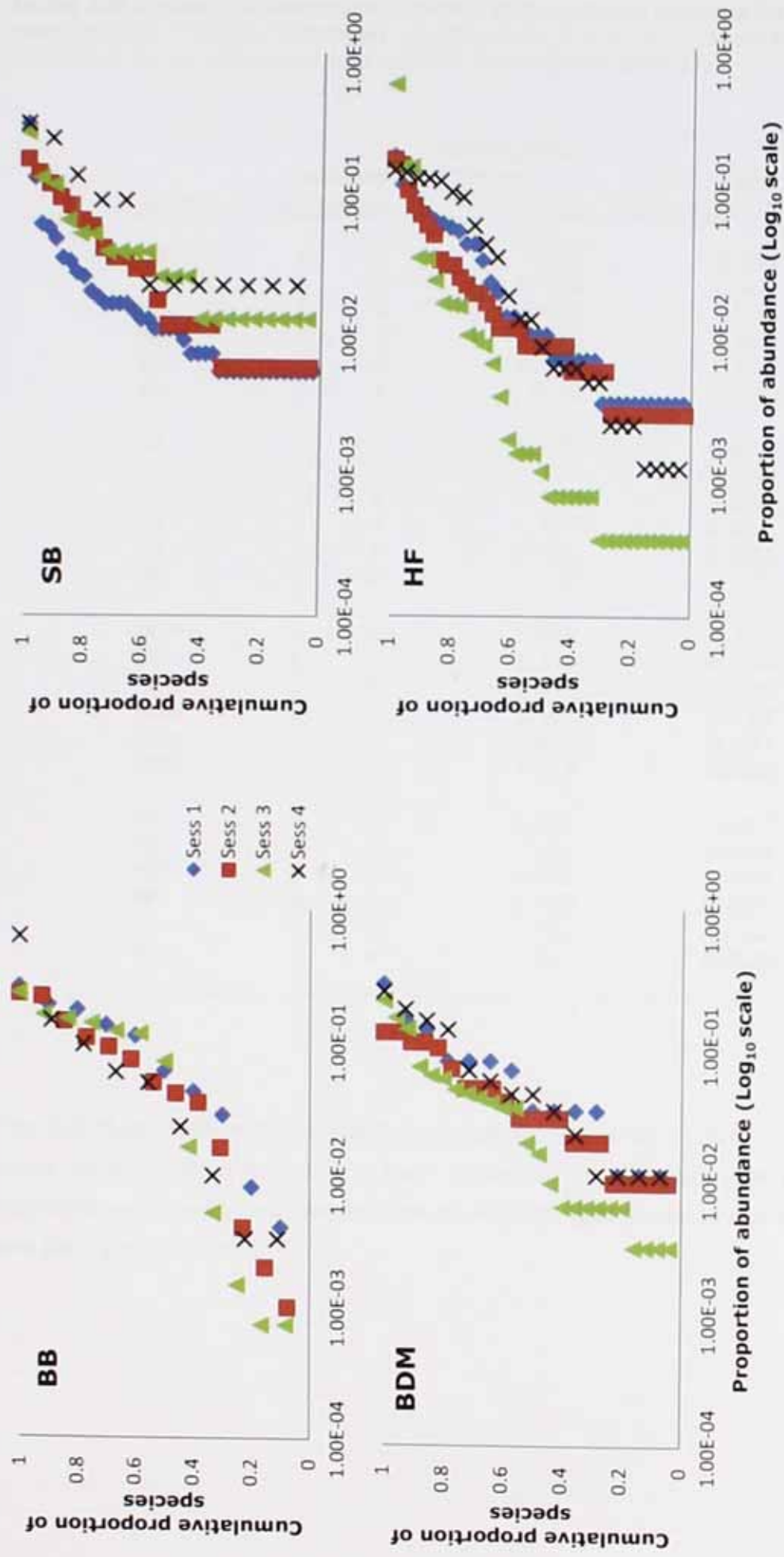
Figure 3.10 Empirical cumulative distribution frequency (ECDF) plots for four insect groups: bumblebees (BB), solitary bees (SB), butterfly and day-flying moths (BDM) and hoverflies (HF). Each set of symbols represents a sampling session.

Table 3.9 Results of Kolmogorov-Smirnov tests between sessions for each of four insect groups. _P_ values in bold are significant for _P_ ≤ 0.05. _P_ values in bold red are significant for an adjusted _P_ of ≤ 0.0085 (Dunn-Šidák method).

Group	sessions compared		Kolmogorov-Smirnov _Z_ value	Monte Carlo significance (_P_)
BB	1	2	0.64	0.704
BB	1	3	0.584	0.801
BB	1	4	0.605	0.741
BB	2	3	0.673	0.659
BB	2	4	0.355	0.996
BB	3	4	0.63	0.727
SB	1	2	1.378	**0.022**
SB	1	3	2.307	**0.000**
SB	1	4	2.378	**0.000**
SB	2	3	1.805	**0.001**
SB	2	4	1.601	**0.005**
SB	3	4	1.14	0.072
BDM	1	2	0.969	0.184
BDM	1	3	1.318	**0.038**
BDM	1	4	0.378	0.979
BDM	2	3	1.505	**0.010**
BDM	2	4	0.836	0.333
BDM	3	4	1.318	**0.035**
HF	1	2	1.202	0.062
HF	1	3	2.61	**0.000**
HF	1	4	1.052	0.129
HF	2	3	2.733	**0.000**
HF	2	4	1.093	0.102
HF	3	4	1.943	**0.000**

The ECDFs for each of the four sampling sessions are given in Figure 3.11. The plots show the distribution according to each of the four insect groups. The results of the Kolmogorov-Smirnov tests for differences between groups within the same session are provided in Table 3.10.
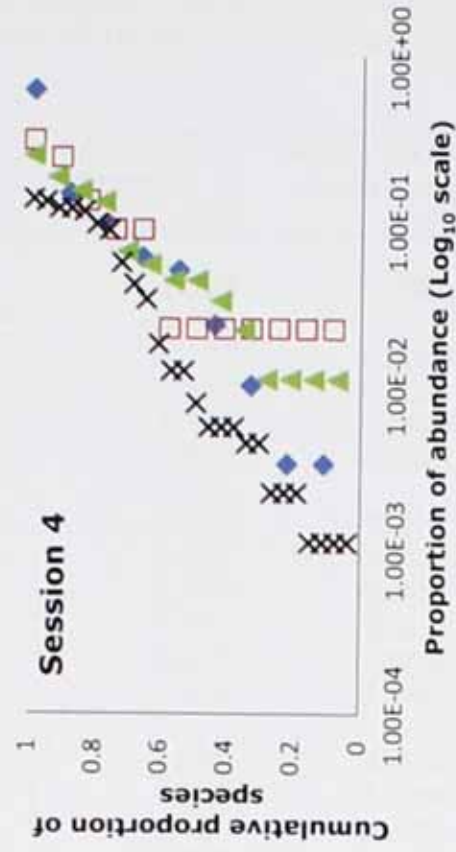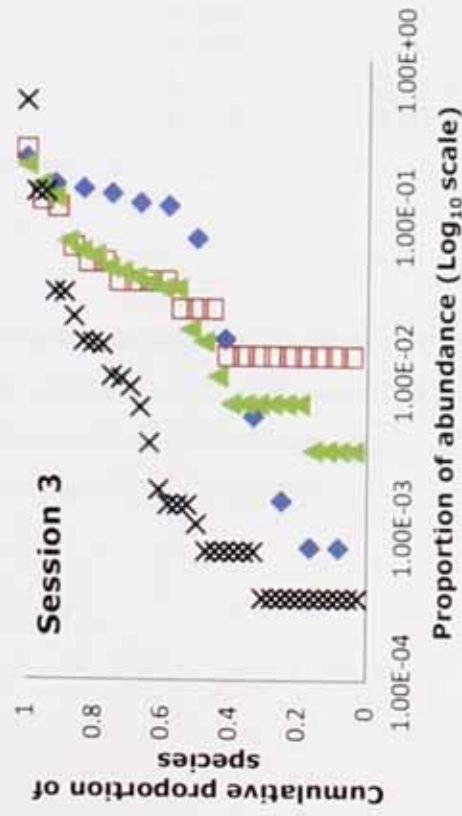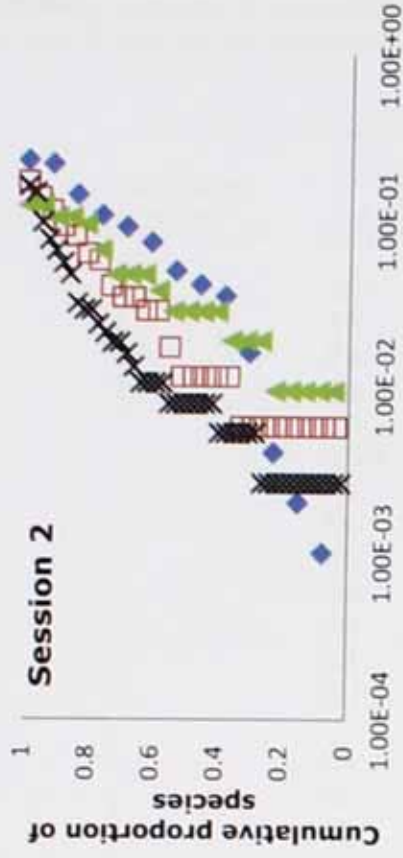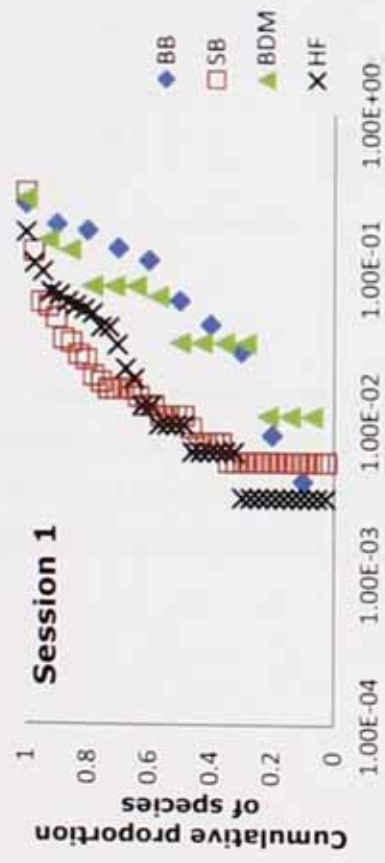
Figure 3.11 Empirical cumulative distribution frequency (ECDF) plots for the four sampling sessions. Each set of symbols represents a different insect group.

Table 3.10 Results of Kolmogorov-Smirnov tests between groups for each of four sampling sessions. *P* values in bold are significant for *P* ≤ 0.05. *P* values in bold red are significant for an adjusted *P* of ≤ 0.0085 (Dunn-Šidák method).

Sampling session	Groups compared		Kolmogorov-Smirnov *Z* value	Monte Carlo significance (*P*)
1	BB	SB	1.784	**0.002**
1	BB	BDM	0.690	0.515
1	BB	HF	1.335	**0.030**
1	SB	BDM	1.987	**0.000**
1	SB	HF	1.311	**0.036**
1	BDM	HF	0.809	**0.000**
2	BB	SB	1.173	0.081
2	BB	BDM	0.760	0.425
2	BB	HF	0.705	**0.002**
2	SB	BDM	1.161	0.070
2	SB	HF	1.643	**0.004**
2	BDM	HF	2.136	**0.000**
3	BB	SB	1.245	**0.036**
3	BB	BDM	1.319	**0.038**
3	BB	HF	1.500	**0.012**
3	SB	BDM	1.505	**0.009**
3	SB	HF	2.771	**0.000**
3	BDM	HF	2.347	**0.000**
4	BB	SB	0.756	0.434
4	BB	BDM	0.780	0.459
4	BB	HF	0.729	0.510
4	SB	BDM	0.908	0.222
4	SB	HF	1.763	**0.001**
4	BDM	HF	1.508	**0.011**

The number of honey bees recorded in each garden during each of the four sampling sessions is provided in Table 3.11. The results of Wilcoxon signed ranks tests showed that a significant difference in honey bee abundance was found between sessions three and four and sessions two and four (Table 3.12).

Table 3.11 Honey bee abundance at each garden in each of the four sessions.

	Session 1	Session 2	Session 3	Session 4	Total per property
AL	7	7	16	1	31
BOU	1	2	30	10	43
CA	15	3	8	74	100
CM	3	10	7	27	47
CHALL	5	19	13	42	79
EN	3	1	0	1	5
FAR	30	3	6	7	46
HOL	1	4	5	9	19
KEL	0	7	14	32	53
KIR	4	0	0	0	4
LAM	1	0	6	32	39
LW	4	3	0	3	10
ST	4	13	7	3	27
SUL	2	6	29	52	89
UP	2	6	1	54	63
WAD	4	6	10	2	22
WR	61	21	6	36	124
Total honey bees per session	147	111	158	385	801
Median value	4	6	7	10	
25th percentile	1.5	2.5	3.0	2.5	
75th percentile	6.0	8.5	13.5	39.0	

Table 3.12 Results of Wilcoxon signed ranks tests for honey bee abundance between sessions ($n = 17$ in all cases). Significant results ($P \leq 0.05$) highlighted in bold.

Paired sessions	1 - 2	2 - 3	3 - 4	2 - 4	1 - 4	1 - 3
Z value (based on negative ranks)	-0.388	-0.881	-2.121	-2.574	-1.681	-0.996
P values	0.698	0.379	**0.034**	**0.010**	0.093	0.319

Discussion

Species richness of the 17 properties

Despite the acknowledged species richness of flower-visitors in gardens (Smith *et al.*, 2006c, Pawelek *et al.*, 2009, Owen, 2010), little is known about the richness of gardens beyond urban matrices. Urban areas represent a mosaic of flower patches comprised of individual gardens and municipal parks which mobile insects may view as a contiguous food resource (Goddard *et al.*, 2010). For this reason, species richness totals for individual urban gardens should be viewed with caution. Rural gardens, on the other hand, are often more geographically isolated from other similar-sized flower-rich patches. In the past, these gardens would also have been part of a wider mosaic of flower-rich areas; however the dramatic decline in unimproved grassland, in particular those areas described as wildflower meadows (King, 2011), means this is no longer the case. Whilst insects move between patches within the landscape as they do in urban areas, the connectivity between such patches (or the lack of it) plays an increasingly important role in rural environments (Taylor, 1993). In accepting that these gardens are likely to be more distant from similar-sized resource patches than those in urban areas, quantifying the species richness of flower-visiting insects can be seen as a valuable activity that establishes important baseline data for sites within the UK's largely agricultural landscape.

The absolute species richness values across the 17 sites (mean 61.6 ± 12.1 per property), and for all properties taken together (174) (Table 3.1), show that rural gardens contain a wide variety of species. As a result of the sampling methods used in 2010 (only insects in contact with flowers were recorded), these results suggest that rural gardens act as important feeding locations for a range of species, in spite of the fact that many of the plants available may be non-native cultivars. The composition of flower resources in rural gardens will be explored further in Chapter 4.

Whilst the actual species richness data allow sites to be compared, it is the more informative species richness estimators such as Chao 1 and Jack 1 that provide the greatest insight into the potential richness of flower visitors in rural gardens. Although both Chao 1 and Jack 1 produced almost identical mean species richness values of 90 per property (Table 3.1), it was the latter that gave the most reliable measure based on the spread of data points (Figure 3.3). Palmer (1990) also found the Jack 1 metric to be the least biased and most precise of all the non-parametric estimators, although he noted the values generated were still likely to be an underestimate of the true species richness present. Whilst underestimation may have implications if whole regions are being assessed, calculations based on small

sub-units such as rural gardens are unlikely to be grossly affected, thereby permitting robust comparisons between sites (Palmer, 1990). Overall, the results from the current study suggest that despite a high number of species being recorded in the gardens (174), many species remain undetected (Jack 1 value of 241, Table 3.1).

Differences in species richness between properties

Comparing the actual species richness recorded at individual properties reveals that, for the most part, this richness is broadly similar at all sites. An exception to this is Kirby (KIR) which emerged as a clear outlier. Kirby's species richness was significantly lower than thirteen other gardens ($P = 0.002$). Three additional gardens: Althorp (AL), Waddesdon (WAD) and Easton Neston (EN) were also less species-rich, although not significantly so (Figure 3.4).

Species richness values are known to be affected by both sampling effort and the size of the area sampled. As both the sampling time and the area were standardised across all properties, the observed differences can therefore be assumed to relate to genuine differences in site or landscape-specific factors. The former will be explored in greater detail in the following chapter, when measures of floral richness are considered.

Differences in species richness between insect groups

Hoverflies were the most species rich of the four groups examined, with 59 species recorded in total across the seventeen gardens (Jack 1 estimate 85.7 ± 4.1). Solitary bees had the second highest species richness with 50 species (Jack 1 estimate 68.9 ± 5.3), followed by butterflies and day-flying moths and bumblebees (Table 3.2). The high richness of hoverflies agrees with that of Owen (2010) who recorded 94 species of hoverfly in her Leicester garden over thirty years.

The diverse array of hoverfly species that occurs in both gardens and semi-natural areas is often explained by the range of feeding habitats used at the larval stage (Rotheray and Gilbert, 2011, Hoverfly Recording Scheme, 2012). This is in direct contrast to the generalised feeding preferences of adult hoverflies that use pollen, nectar or aphid excretions (Rotheray and Gilbert, 2011). Hoverfly larvae range from primary and secondary consumers to primary, secondary or higher order decomposers depending on their phylogenetic classifications (Owen, 2010, Rotheray and Gilbert, 2011).

Although Owen (2010) found adults representing all four larval trophic groups during her thirty-year study, more than 81% of the 60,736 individuals caught were from species whose larvae used plants infested with aphids as their preferred feeding

sites. Despite the number of hoverflies recorded in the current study being only 7% of those found by Owen, a remarkably similar percentage had aphid-feeding larvae (79.9%, Table 3.13).

The awareness that predation by hoverfly larvae (zoophagy) allows aphid pests to be controlled is one that generated interest as far back as 1800 when Charles Darwin's grandfather, Erasmus Darwin, championed their use (Rotheray and Gilbert, 2011). This interest continues today through the investigation of specialist and generalist aphid feeders as suitable agents for biological control of fruit and cereal crops (Cowgill et al., 1993, Bergh and Short, 2008, Haenke et al., 2009, Leroy et al., 2010). Further work to establish whether the ratios observed for hoverfly larval types also occur in non-garden flower-rich patches in the landscape would be useful. The results could allow consideration of whether some hoverfly species 'spill over' from gardens into agricultural fields, thus benefiting crops that might otherwise suffer reduced yields.

In addition to being the most species rich group, hoverflies were the only taxa to show significant differences in species richness across the 17 properties ($P < 0.001$, Table 3.3). Kirby (KIR) had the lowest hoverfly species richness (mean 1.75 ± 0.96) and was significantly different to twelve other properties. Both Kelmarsh (KEL) and Upton (UP) (mean 13 ± 2.94, and 13 ± 2.58 respectively) had significantly higher hoverfly species richness than Kirby, Easton Neston (EN) and Wrest (WR) (Figure 3.5).

Table 3.13 Comparison of hoverfly species according to four larval trophic levels. [1] Adult hoverflies caught in malaise traps between 1972 - 2001 in Owen's Leicester garden (Owen, 2010), [2] Data from 17 large rural gardens (the current study). The separation of trophic groups follows Owen (2010) and is based on the system of Wiegert and Owen (1971).

Trophic group	Feeding site	Trophic level	Species[1]	Abundance[1]	% of total[1]	Species[2]	Abundance[2]	% of total[2]
A	Stems, roots, bulbs and tree sap	Primary consumers	12	4,210	6.9	9	126	2.8
B	Plants infested with aphids	Secondary consumers	57	49,384	81.3	31	3,539	79.9
C	Decaying organic material and rotting wood	Primary to n^{th} order decomposers	23	7,088	11.7	16	711	16.0
D	Nests of wasps and bumblebees	2nd to n^{th} order decomposers	2	54	0.1	3	54	1.2
Total abundance				60,736			4,430	

Comparison with other gardens

By using a repeated sampling strategy encompassing 17 properties, the current study has found that, in general, these rural gardens are homogeneous in terms of flower-visitor species richness. A potential downside is that their proximity means interpretation beyond the counties studied could be considered limited. By comparing these to gardens from a wider geographical range, e.g. those assessed by Edwards (2003), and others such as Buckingham Palace Garden (Harvey, 2001, Plant, 2001), a fuller interpretation of the value of these sites can be made.

Although the data from the 20 NT gardens (Edwards, 2003) only come from single-site visits, they compare well to those of the present work. Despite different species richness estimators being used (see Methods), the Jack 1 values from the current study and the Chao 2 values derived from the Edwards data show surprising similarities (Table 3.5). Overall, the estimate for all species for the 17 gardens is 241.4, whilst that for the 20 gardens is 269.9. Notwithstanding that these are likely to be underestimates for the true species richness for the combined sites (Gotelli and Colwell, 2011, Magurran and McGill, 2011), they highlight remarkably high species richness for areas that are human constructs.

Hoverfly species richness estimates were similar between the two studies, with 85.7 species predicted for the 17 gardens and 83.4 species for the 20 NT gardens (Table 3.5). A possible explanation for this is the timing of the Edwards study relative to Session 3 of the current study. All but three of the NT surveys took place within the dates covering Session 3 of the present work, i.e. the time when the highest abundance of hoverflies was recorded (Figures 3.10 and 3.11). With a greater relative abundance of hoverflies on the wing in July and August, the opportunity to encounter these highly mobile insects increases. As the species richness estimators focus on rarity, i.e. the presence of singletons and doubletons (for abundance data) and uniques and duplicates (for incidence data) (Colwell, 2012), fewer 'rare' species are likely to be recorded during times of high abundance. This may explain why the estimates stabilised at similar levels for both studies.

The effect of rarity may also help to explain the difference in bumblebee estimates (Table 3.5). In the current study, 14 species were recorded against 12 by Edwards (2003). The estimators take these actual values and suggest likely species richness as 15.9 and 12.2 respectively, a difference of almost four species between the two studies. The higher estimated value for the current study is probably explained by the occasional observation of two 'rare' species, *Bombus campestris* and *B. ruderatus*. Individuals of *B. campestris* were observed only twice, once at

Farnborough (FAR) and once at Waddesdon (WAD). This cuckoo species is associated with nests of *B. pascuorum*, although other carder bee nests may also be targeted (BWARS, 2012). Being a cuckoo species there is no worker caste and no pollen reserves are collected. For this reason visits to flowers are limited to those made by queens and males foraging for their own energy needs. The second species, *B. ruderatus*, was observed only once during the 68 site visits, (a single individual at Canons Ashby - CA). This long-tongued bumblebee is noted as a Nationally Scarce and BAP Priority Species (BWARS, 2012) and frequent encounters with this species would not be expected.

The higher number of sampling events in the current study (68 versus 20) that occurred throughout the season may have increased the chances for these less abundant species to be recorded. In turn these 'rarer' species push species richness estimates upwards. The fact these two bumblebee species were not recorded at the NT properties may have more to do with differences in seasons covered, methods used and the time spent sampling, rather than the true distribution status of the species themselves.

The greatest discrepancy between the current study and that of Edwards is for solitary bees, with 50 species recorded from the current study versus 34 by Edwards, i.e. almost 50% more for the 17 properties than the 20 NT sites. The Jack 1 and Chao 2 estimates for solitary bees reveal a similar picture, (68.9 and 44.5 respectively, Table 3.5). The timing of the surveys offers the best explanation for this difference. Where the current study encompasses four visits from early spring to late summer, the brief of the NT study was for a single site visit in summer. Oertli *et al.* (2005) note that the sampling of only a proportion of a season can grossly underestimate bee diversity. Edwards himself comments on the depauperate nature of solitary bee sightings and suggests further surveys spanning all seasons. Early spring is a particularly important time for recording solitary bee species as highlighted by the SB plot in Figure 3.10.

Other authors have also noted that spring and early summer is characterised by high solitary bee species richness. Tommasi *et al.* (2004) sampled solitary bees, bumblebees and honey bees in urban gardens and parks throughout the year in Vancouver, Canada, and found strong seasonal variability between wild bees and honey bees. Wild bees (47 solitary bee and 8 bumblebee species) were most abundant in late spring, and were synchronous with the native flowers in the area, whilst honey bees were more abundant in late summer (Tommasi *et al.*, 2004).

Data from Buckingham Palace Garden serve as additional information for comparison purposes. Differences in the duration of the study (three years), the location (an urban context) and collecting methods (predominantly malaise traps) mean care needs to be taken when interpreting any observed variation.

Notwithstanding the differences highlighted above, the species richness of social wasps was similar across all three studies (6, 7 and 6 species for the present study, Edwards' data and BPG respectively, Table 3.6). This congruence reflects the fact that few species of social wasp occur in the UK (currently eight, BWARS, 2012) and their relatively large colony size means encounters are frequent (BWARS, 2012).

The number of hoverfly species recorded from BPG was considerably lower than that of the other two studies (37 species versus 59 and 54 for the current study and that of Edwards). In terms of abundance, however, hoverflies represented the highest number of individuals (1599) and accounted for 68.9% of the combined total of hoverfly and aculeate (minus ants) individuals. In the current study, hoverflies were also the most abundant group, however they accounted for 53% of hoverfly and aculeate individuals (Table 3.6).

Solitary bee species richness at BPG was almost identical to that of Edwards (33 for BPG against 34 recorded in the twenty NT gardens), although lower than the 50 recorded in the current study (Table 3.6). Harvey (2001) notes that the paucity of active sampling and the use of malaise traps may have contributed to this low species richness.

Several authors report successful use of pan and malaise traps to census solitary bees; however unless a detailed examination of the pollen present on the bodies of trapped insects is made, these methods fails to return information on the types of flowers visited. Additionally, time must be allocated to process specimens that have become wet during the collection process (Grundel *et al.*, 2011). Ideally a combination of capture methods should be used to comprehensively sample solitary bees.

The relatively high bumblebee species richness shared by the current study and that of Edwards is not reflected in the BPG data (Table 3.6). The six species recorded at BPG are the suite of bumblebees classed as the 'big six'. These species are the most abundant and widespread in lowland UK (NHM, 2012) and are cited as bumblebees typically encountered in urban gardens (BBCT, 2012).

Few studies of pollinator communities provide full species lists. Of those that do, e.g. Herrera (1988), Frankie *et al.* (2005), Oertli *et al.* (2005) and Kearns and Oliveras (2009), few comparisons can usually be made with UK studies as the species differ, but see Ahrné *et al.* (2009). An exception to this is the UK study by Bates *et al.* (2011b). In this work, the authors recorded thirteen species of bumblebee, a figure much closer to that of the current study and the Edwards report. Bates *et al.* found that, of the seven species present in addition to the 'big six', five had higher mean numbers of individuals in suburban and rural areas than in exclusively urban areas. This finding, along with similar results from Sweden (Ahrné *et al.*, 2009), suggests that regardless of the size of a garden, its location within the wider landscape acts as a driver for the variety of bumblebee species present. As a group, bumblebees contain species that have undergone major range contractions in the recent past (Goulson *et al.*, 2008). The fact that so many species are recorded in large rural gardens points to these sites being important locations.

The solitary wasp species richness figure in the current study (9) shows the greatest anomaly when considering the data from Edwards and BPG (43 and 40 respectively), Table 3.6. In fact, solitary wasp richness and abundance was so patchy in the current study it was not feasible to include this group in the earlier comparisons and estimates. The disparity is likely to have arisen because of two factors: (a) the food preferences of solitary wasps, and (b) differences in sampling criteria between the studies. The majority of solitary wasps (except cuckoo species) collect insect prey as food for their offspring and only visit flowers for their own energy needs (Chapter 2). As a consequence, the chance of encountering them on flowers may be lower than for other groups that collect pollen or nectar reserves. As one of the main criteria for the sampling for this project was that insects should be in contact with flowers, any solitary wasps observed moving over plants but not directly on flowers were discounted. Although using the same capture method as the current study (hand-netting) Edwards recorded all insects, regardless of location. It must therefore be assumed that the species richness totals for the seventeen gardens studied are an underestimate of the solitary wasp species that are actually present there.

Overall, the species richness totals (both actual and estimates) suggest that large gardens are places that support a diverse array of flower-visiting insects. The findings presented here support the observation by Head (2012, p. 68) that gardens are 'intrinsically good places for wildlife', regardless of any active attempts to manage them to attract species.

Comparison with vice-county data

One of the limitations of the current study is that flower-visitor species richness data were not collected in non-garden sites around the areas of interest. This makes it difficult to be sure gardens are, indeed, rich in flower-visitors compared to other nearby areas. One of the reasons for using the sampling regime outlined in Chapter 2 was to ensure that a sufficient number of garden sites were replicated. In the event that gardens *had* been paired with non-garden environments (such as neighbouring agricultural fields), this would have necessitated halving the sample size, and in doing so introduced many new variables, including crop type, differing pesticide and herbicide use, and the presence and management of linear features such as hedges.

The inclusion of vice-county (VC) data is a means of ameliorating one of the limitations of this study and allows the species richness of the 17 gardens to be considered in a wider regional context. As with the earlier comparisons (the Edwards and BPG data), differences in sampling methods and the time spent collecting data make a true comparison with the VC data difficult. Additionally, VC totals may be inflated when counties are the 'home-turf' for some of the main specialists for the groups of interest. Examples include Stuart Ball, Roger Morris and Alan Stubbs (three acknowledged UK hoverfly experts who have sampled extensively in Northamptonshire), and Steven Falk in Warwickshire, who has worked with aculeate and hoverfly recording and conservation. Notable are the 11,643 aculeate records contributed by Falk in 17 years, out of a total of 12,731 records (spanning 114 years) for the county. Also of relevance is that records sent in to national recording schemes often reflect the interests of the keenest recorders in the area and that rare, unusual and even migrant species records are more likely to be submitted than ubiquitous generalists. The inclusion of all habitat types (ranging from woodlands, marshes and SSSIs to urban centres and brown field sites) in VC data is both a strength and a weakness when comparing the data with gardens; it highlights how species-rich gardens are, but does not permit like-for-like comparisons.

Despite these acknowledged limitations, comparisons with VC data can still be informative. Jennifer Owen compared the species richness of her Leicester garden with that of the VC of Leicestershire and noted that, in spite of the small area studied ($741m^2$), half of the aculeates recorded in the county appeared in her garden at some point during the 30-year period (Owen, 2010).

The data in Table 3.6 suggest that the gardens in the current study compare well to county data for certain groups, but that others are noticeably different. In Table 3.6 the species richness for the 17 gardens is bulked to give a single value. To make

comparisons more robust, the following refers only to the 13 properties in Northants; bumblebees (BB) = 13, solitary bees (SB) = 46 and hoverflies (HF) = 56). When comparing these totals to the Northants VC species richness values, they reveal that 93% of the bumblebee species recorded in Northants appeared in the 13 gardens, as did 75% of the county's solitary bee species, 86% of the social wasp species and 31% of the hoverfly species.

The hoverfly species richness for the gardens is noticeably lower than that of the VC data. A possible explanation for this is that the 2010 records relate to just a single sampling year and that a wide variation in pollinator numbers from year to year is common (Herrera, 1988, Oertli et al., 2005, Owen, 2010). Additionally, records from the 17 gardens were only made where insects were in contact with flowers (whereas the VC data are for hoverflies taken on flowers, in flight and at rest). Also, gardens represent one broad habitat type, whereas the VC data incorporate (amongst others) woodlands and reservoirs; both of which support specific hoverfly species (Stubbs and Falk, 2002).

As with the comparisons with the Edwards and BPG data, it is the solitary wasp species richness figure that is most different to the VC records. In addition to the causes mentioned earlier, i.e. the different sampling protocol used in the current study and the foraging habits of this group, the greater range of habitats visited by VC recorders compared to those present in gardens is likely to offer the best explanation for this disparity.

Sampling effort

The above comparisons with the VC data establish that certain insect groups are well represented in the gardens. The robustness of this claim is tested by plotting the sampling effort of the current study alongside that of the other studies and the VC data. In showing the number of species observed against the number of records (Figure 3.6) the current study appears to sit well amongst data collected using a considerably greater sampling effort. As expected, the exception to this is the number of solitary wasp species recorded.

Species diversity

The use of species diversity metrics removes one of the problems associated with species richness, i.e. all species (both rare and common) are treated with equal importance (Maurer and McGill, 2011).

The Shannon diversity values generated for the 17 properties ranged between 2.51 and 3.29, and was 3.06 for all properties combined (Figure 3.7).
These figures are broadly similar to those found by Kearns and Oliveras (2009) who considered bee diversity in urban and remote grasslands in the USA (Shannon values ranging between 2.68 – 2.80).

When considering diversity on a property-by-property basis, Kirby (KIR) was found to be significantly lower than eight other gardens (Figure 3.7). This is in contrast to the differences observed when species richness was used as a discriminator (without recourse to an estimate of evenness). In this case, Kirby returned lower species richness than 13 gardens (Figure 3.4).

Differences in Shannon diversity values emerged for the individual insect groups with the exception of solitary bees and butterfly and day-flying moths (Figure 3.8). Bumblebees exhibited the lowest diversity value due to the high abundance of certain ubiquitous species such as *Bombus pascuorum* (651 individuals recorded across all gardens), *B. hortorum* (483) and *B. lapidarius* (387). This contrasted sharply with species with few individuals; *B. rupestris* (5), *B. campestris* (2) and *B. ruderatus* (1).

Removing the two high-abundance groups from the hoverfly Shannon value revealed that the diversity of this group was more in line with SB and BDM, although still significantly different when confidence intervals were considered (Figure 3.8).

The importance of flower-visitor diversity has consequences beyond gardens. The economic importance of diverse pollinator communities for the agricultural sector was demonstrated by Klein *et al.* (2003), who found that solitary bee diversity (as opposed to abundance) played a significant role in explaining variation in the fruit-set of highland coffee. The authors found that the collective role played by a pollinating community was important for pollination success. Klein and co-authors further suggested that the conservation of areas proximal to coffee plantations was crucial in helping to encourage and maintain bee diversity. Holzschuh *et al.* (2012) highlighted a similar situation and called for bee habitat to be protected and enhanced because yields of sweet cherry increased in the presence of wild bees. They found that the deployment of honey bee hives by farmers was unlikely to increase fruit-set or yield, but that promoting high-diversity wild bee habitats close to orchards brought enhanced financial returns. More work is needed to establish whether flower-visitor populations that thrive in rural gardens can bring economic benefits to nearby agricultural crops.

Community composition

The main purpose in considering the similarity in community composition across the gardens was to identify sites that were notably different, with a view to exploring potential causes (Chapter 4).

The two indices of community similarity that were calculated (Morisita-Horn and Chao's Abundance-based Estimated Sørensen) revealed different but complementary results. The lowest seven pairings consistently included Kirby (KIR) (Tables 3.7 and 3.8). In the Morisita-Horn analysis, Kirby occurred four times out of seven, with the remainder accounted for by SUL – KEL, SUL – WAD and WAD – UP (Table 3.7). In the second analysis, Kirby occurred six times out of seven, the seventh pairing being WAD – EN (Table 3.8). The fact that these pairings are independent of the number of species recorded, lends support to the robustness of the methods used. The results suggest that factors beyond species richness and diversity of flower-visiting insects are driving community similarity.

The alternative similarity method (cluster analysis) revealed a similar situation, with Kirby (KIR) a clear outlier on the dendrogram (Figure 3.9).

Species abundance distributions

Notwithstanding the fact that evenness is incorporated into species diversity measures, and similarity metrics benefit from the estimation of 'unseen' species, both are limited by the fact they provide only a single value. Species abundance distributions (SADs) can provide a more complete picture about a community by describing it in terms of the number of individuals observed for each species recorded. In addition to providing a strong visual representation of a community along a continuum of rare to common species, SADs possess the additional useful characteristic of being amenable to robust testing.

Although little published material exists that illustrates SADs plotted as empirical cumulative distribution frequencies (ECDFs), the benefits of using them - both visually and as a precursor to testing distributions using Kolmogorov-Smirnov procedures - is not in question (McGill *et al.*, 2007, McGill, 2011).

The results of the current study showed that two insect groups are of particular interest. These are solitary bees and hoverflies (Figure 3.10). In the case of solitary bees, Sessions 1 and 2 did not differ, nor did Sessions 3 and 4, however all other possible combinations between the sessions were significantly different (Table 3.9). As discussed in the species richness section above, the timing of emergence and reproduction by solitary bees is strongly linked to season (Tommasi *et al.*, 2004).

The results of the Kolmogorov-Smirnov tests (without comparing the exact composition of the species present or their numbers) confirmed that certain times in the year were more similar for solitary bee species abundance than others e.g. spring and early summer were similar as was mid-summer and late summer. The implication for this is that crops in flower at these times may benefit from an increased diversity of bees. One mass-flowering crop that may gain is oilseed rape (OSR). In Sweden, Bommarco et al. (2012) found that the presence of insect pollinators (including honey bees) increased seed weight, seed quality and market value of this selfing crop. Jauker et al. (2012b) also found that seed set of OSR increased with increasing solitary bee density but that seed weight did not alter.

In their study, Jauker and co-workers (Jauker et al., 2012b) considered the pollinating effects of a single species of solitary bee, Osmia bicornis (the red mason bee), by comparing its efficiency with two species of hoverfly. In the current study O. bicornis was the second most abundant solitary bee species (61 individuals across 14 properties). Jauker and co-authors found that red mason bees were more efficient pollinators on OSR than hoverflies, and that pollination could be achieved using lower bee densities than those used for honey bees (16 – 36 mason bees versus 200 honey bees, Jauker et al., 2012b). Although the study considered OSR pollination in an enclosed experiment (plants were caged), the suggestion that wild pollinators are valuable agents in the transfer of pollen in both open and closed crop systems seems reasonable. This assumption will benefit from further testing.

The difference in hoverfly abundance distributions focuses on Session 3, (Figure 3.10). Results of the Kolmogorov-Smirnov tests confirm that significant differences occur between this session and the other three (Table 3.9). The ECDF plot (Figure 3.10) for hoverflies highlights both the high number of species represented by a single individual, and also the few species possessing unusually high abundance. Whilst flower-visitor communities generally fit the description 'rare is common and common is rare' (McGill, 2011, p. 105), the hoverfly community in Session 3 is an extreme example of this.

The seasonal differences between groups are highlighted in Figure 3.11. Tests for differences reveal that Session 4 is the least different of the four, with only solitary bees and hoverflies showing significant differences (Table 3.10).

Whilst honey bees cannot be compared in the same way using ECDFs, the significant difference in their abundance in Session 4 when compared to Session 3 ($P = 0.03$) and Session 2 ($P = 0.01$, Table 3.12), highlights a pattern also observed by Tommasi et al. (2004). These authors found that wild bees (SB and BB) were most abundant

during late spring, whilst honey bee numbers peaked in late summer. They noted that honey bees were less abundant than solitary bees in early spring, a time coinciding with the majority of native flowering plants, and that, overall, honey bees were less abundant across all sites. This finding is echoed by the present study, with the combined number of SB and BB totalling 3,544 versus 801 honey bees (all properties, all seasons).

At the start of the 2010 field season all property owners were asked whether honey bee hives were present on their estates. Additionally, the county Beekeepers Association (NBKA, 2012) was approached to establish whether registered hives were located within 9km of any of the seventeen gardens. No hives were reported within the stated areas. In the absence of any managed colonies, the occurrence of honey bees in the sampled gardens is likely to have resulted from the extensive foraging range of this species (Chapter 2 Study organisms). An alternative explanation is that feral colonies were present, in particular at two properties, Canons Ashby (CA) and Lois Weedon (LW). This was evidenced by activity in nearby roof structures at the two properties, although the colony at Lois Weedon disappeared mid-season (cause unknown). The relatively high number of honey bees recorded at Canons Ashby (100) suggests that *if* a feral colony was responsible for increased observations, another may also have been present at Wrest (WR), where 124 individuals were recorded (Table 3.11).

The peak in honey bee abundance at the end of summer coincides with the peak in colony size at this time (Tommasi et al., 2004). In late summer two of the three honey bee castes (workers and males) are on the wing (Hooper, 1991). In summary, honey bees, whilst not very abundant in gardens, are regularly recorded there. It is unclear whether the drivers for low numbers in spring are alternative forage resources in the wider landscape. Could more honey bees be foraging on OSR earlier in the year and therefore not visiting gardens? Alternatively, does a spill-over into forage-rich areas such as gardens at the end of the season reflect the increased colony size at the time, a decline in wild flower and mass-flowering crop resources, or both? The answer is likely to be that a combination of factors is at play. Further experimental work placing hives near to gardens and monitoring their foraging preferences throughout the season may reveal the true state of the relationship between honey bees and rural gardens.

Conclusions

The findings of this chapter can be summarised as follows:

- Large English country-house gardens contain a high number of species from a range of important flower-visiting groups, including hoverflies, solitary bees, bumblebees and butterflies.

- The results from species estimations, based on the singletons and doubletons observed, suggest that not all species are likely to have been encountered during sampling and that many more are likely be present.

- Whilst species richness is broadly similar across all 17 gardens, the garden at Kirby emerges as a significant outlier. Possible explanations for this will be explored in future chapters.

- Hoverflies were the only flower-visiting group to show a significant difference in species richness across properties. Kirby had the lowest hoverfly species richness whilst two gardens (Kelmarsh and Upton) had significantly higher hoverfly richness than the lowest three.

- Results from the study revealed that these 17 sites compare well to other large gardens. Congruence across certain groups (including the composition of these groups) suggests that species patterns are discernable in gardens.

- The large-scale nature of the study (almost 10,000 flower-visitors recorded) and the replicated design allows confidence to be placed in the results.

- A drawback of the work is the absence of a direct comparison with non-garden sites close to the sampled locations. Comparing the work with vice-county data allows inferences to be made about the richness of gardens in a regional context. The results suggest that large rural gardens are, indeed, species-rich locations.

- Of the individual insect groups considered, bumblebees had the lowest species diversity values. This was explained by certain species being highly represented, whilst others were characterised by sightings of only one or two individuals.

- The use of two similarity indices and a cluster diagram allowed the community similarity at individual properties to be compared using different, but complementary, methods. The garden at Kirby was the least similar of the sites considered.

- ECDFs provide a robust way of plotting and testing species abundance distributions for both individual insect groups and sampling sessions. Solitary bees emerged as a group characterised by many species in spring and early summer, which may have implications for crops and wildflowers in the neighbouring landscape. Hoverfly species abundance in the third sampling session illustrated that rare is common and common is rare.

- As a single species, honey bees do not lend themselves to intra-group comparisons using species richness or diversity metrics. However comparisons of honey bee abundance across sessions showed they most frequently appeared in gardens in late summer.

Overall, the gardens of large English country-houses can be considered as important sites for flower-visiting insects. This has implications for biodiversity at a time when pollinator numbers are known to be in decline (Klein *et al.*, 2007, Wratten *et al.*, 2012), and agricultural security faces severe challenges (Bommarco *et al.*, 2012, Jauker *et al.*, 2012b).

The suggestion by Head (2012) that gardens are important areas for wildlife, independent of whether they are specifically managed for this purpose, will be explored further in the following two chapters.

Chapter 4

The structure of plant and flower-visitor communities

Chapter overview

In this chapter the diversity of flowering plants in large English gardens is explored in the context of the insects that visit them. The influence of plant communities on flower-visiting insects is considered at three taxonomic levels, as well as according to their alien or native status. The effect of plant resource availability on insect visitors is examined on both a seasonal and per-property basis. Finally, patterns in networks of flower visitors and plants are elucidated. These are discussed in the light of current theories about the meaning of nestedness between these two trophic groups.

Introduction

Pollinating insects and the flowers they visit comprise some of the most ubiquitous interactions observed on Earth (Ollerton *et al.*, 2011). Since the dramatic radiation of angiosperms in the Cretaceous, the foraging behaviour of insects within and between flowers and the subsequent response of plants over generations has driven the evolution of both groups (Kevan and Baker, 1983, Kearns and Inouye, 1997).

Highly specific interactions between pollinators and plants have been observed, predicted, and continue to be discovered (Darwin, 1862, Waser and Ollerton, 2006, Ryckewaert *et al.*, 2011). Far more common, however, are generalist interactions characterised by insects visiting flowers from a taxonomically diverse range of plants (Waser *et al.*, 1996, Kearns and Inouye, 1997).

Many researchers have observed that the diversity of plants available at a site correlates with the diversity of pollinators that occurs there (Ghazoul, 2006, Frankie *et al.*, 2009, Fründ *et al.*, 2010). Attempts to understand whether greater flower variety *per se* explains increased pollinator richness - a phenomenon described by Frankie *et al.* (2005) as 'the mall effect', or whether certain combinations of plants or the nectar and pollen resources they offer are more important, continue to generate research attention (Potts *et al.*, 2003, 2004, Cussans *et al.*, 2010). In the past, this enquiry has focussed on establishing whether abundant flower richness facilitates pollination or generates competition between plants, both of which can influence evolutionary processes (Ghazoul, 2006, Hegland *et al.*, 2009). Less attention has been paid, however, to how plant richness and composition helps to structure pollinator diversity, particularly in novel ecosystems. As overall biodiversity is declining (Natural England, 2010), and the ecosystem service of pollination is considered to be in crisis (Kremen and Ricketts, 2000), research that contributes new knowledge about plant-pollinator interactions involving whole communities is

considered vital (Memmott and Waser, 2002, Olesen *et al.*, 2007, Lazaro and Totland, 2010).

In this chapter the availability of flower resources across seventeen large gardens is tested against a series of predictions to establish how floral resources influence and structure the flower-visiting insect communities found there.

Insect-plant interactions: Research focus to date

Research on plant-flower community interactions is frequently focussed on sites dominated by native plants (Ghazoul, 2006, Fründ *et al.*, 2010, but see Frankie *et al.*, 2009) and often occurs as a result of assessing restoration programs (Carvell *et al.*, 2004, Forup *et al.*, 2008). Studies that encompass a range of insect groups and their interactions with non-native (alien) plants are noticeably sparse (Carvell *et al.*, 2004, Lazaro and Totland, 2010), with virtually nothing known about the structure of plant-insect communities in novel ecosystems such as large, rural gardens.

Native and alien plant resources in gardens

Gardens are noted for their unusually high plant species richness (Galluzzi *et al.*, 2010), with some authors commenting that many urban gardens have considerably higher plant richness than adjacent non-residential patches (Kirkpatrick *et al.*, 2009 and references therein). Understanding the composition of plant assemblages in gardens is important as it can help explain how human-created green spaces link to elements in the wider environment (Smith *et al.*, 2006b).

The biodiversity that large rural gardens support is important for the sites themselves, but also as a resource that can benefit nearby crops through enhanced pollination and pest control (Jordano, 1987, Tylianakis *et al.*, 2007). Additionally it plays a role in engaging interest in the natural world, which has positive effects on human wellbeing (Loram *et al.*, 2011). Gardens are now considered the main way that the majority of people come into contact with wildlife (Cannon *et al.*, 2005).

A common theme that emerges from gardens is that plant resources are dominated by non-native 'exotic' or 'alien' cultivars (Loram *et al.*, 2008b, Goddard *et al.*, 2010). In two separate studies, non-natives accounted for 70% of plant species recorded (Smith *et al.*, 2006a, Loram *et al.*, 2008b). A detailed analysis of garden vegetation in five cities in the UK found that, despite geographical differences, these urban gardens were remarkably homogeneous in plant species richness, diversity and composition (Loram *et al.*, 2008b). **It is predicted that the ratio of alien to**

native plants is likely to be constant across a suite of large gardens in rural locations.

Some authors have noted that alien plants in gardens are infrequently used by native pollinating insects (Corbet *et al.*, 2001, Goddard *et al.*, 2010), whilst others comment that in the wider landscape these resources are used but not necessarily preferred over native plants (Williams *et al.*, 2011). Whilst this suggests that the availability of native plants relative to aliens may help explain the insect communities observed in gardens, this is not borne out by the work of Smith *et al.* (2006c). These authors found that in 61 gardens in Sheffield, invertebrate species richness was only rarely related to the presence and abundance of native plant species. In summary, little empirical evidence exists to confirm the importance of native plants in gardens. **The prediction is that in large rural gardens the species richness of flower visitors is likely to be invariant to the proportion of native plants.**

Possibly of greater importance than the ratio of native to alien plant species is the availability of floral resources over an extended period. For some groups, such as bumblebees, the requirement for suitable forage throughout the season is well documented (Dramstad and Fry, 1995, Goulson, 2010), with urban parks and gardens seen as particularly important due to their year-round availability of pollen and nectar (Stelzer *et al.*, 2010). For others such as solitary bees, a dearth of flowers at a particular time (e.g. early spring), may be more critical than season-wide availability, with a lack of resources resulting in starvation and reproductive failure (Falk, 2011). Climate change threatens to accelerate the disassociation between insect flight periods and the flowering time of plants (Memmott *et al.*, 2007). **It is predicted that the proportion of available plants that are visited by insects will vary across the season.**

'Pollinator-friendly' plants

In recent years many books, magazine columns and web pages have been written encouraging the planting of annuals, perennials and shrubs that are favoured by bees and butterflies (Goddard *et al.*, 2010). In 2011, the promotion of 'bee-friendly' or 'butterfly-loving' horticultural plants was championed by two groups with unrelated agendas. Scientists seeking to raise awareness about the plight of pollinating insects joined forces with the horticultural industry in the hope that more pollinator-friendly plants would be bought and planted (Ollerton, 2012). Trading on the messages delivered by popular gardening presenters during their broadcasts, an increase in the prevalence of 'good' flower rewards for pollinators was seen as a win-

win situation for all (Raven, 2012, RHS, 2012a). Evaluating the results of this 'perfect for pollinators' initiative is ongoing (Ollerton and Erenler, in prep.).

Attempts to establish which native plants and horticultural variants are preferred by pollinators (based on empirical measures of nectar secretion and flower morphology) have been made, albeit on a limited scale (Comba et al., 1999a,b, Corbet et al., 2001), but little work has been done beyond experimental trials (but see Cussans et al., 2010). Collections of plants in gardens (be they native or alien, pollinator-friendly or variants bred for aesthetic purposes), form communities that are likely to structure flower visitor diversity in predictable ways, thereby mimicking processes in natural ecosystems (Smith 2006b).

Plant resource similarity in gardens

Planting decisions made by households are influenced by diverse factors including income, social class, the choice of plants available for purchase, the size of garden and the desire (or not) to demonstrate planting creativity to others (Zmyslony and Gagnon, 1998, Power, 2005, Loram et al., 2008a, 2011). The question of whether planting schemes in proximally close urban gardens are more similar than those further away has been explored, with some authors reporting a planting 'mimicry effect' (Goddard et al., 2010 and references therein), though Kirkpatrick et al. (2009) found no such 'spatial contagion'. This raises the question of whether large rural gardens share ubiquitous species favoured by flower visitors. **It is predicted that certain plant families will experience higher than expected visitation by flower-visitors.**

Use of metrics to assess flower-visitor and plant interactions

Assessing how flower visitors interact with available plant resources requires the use of a suite of network metrics which allow interactions to be described, quantified and analysed. The underlying rationale for using these is to decipher patterns within communities, the relevance of which can be extended beyond the area of study (Blüthgen et al., 2008, Dormann et al., 2009).

Networks of ecological interactions are typically described in terms of connections (links) between species (nodes) and can be represented by binary (presence/absence) or abundance data (Blüthgen et al., 2008). Five common interaction metrics (connectance, generality, vulnerability, linkage density and nestedness) are used in this study. These are now considered in turn.

Connectance

Connectance (C) is a measure of the number of actual interactions or realized links (L) between a sampled community of F flower-visitors and P plants, expressed as a fraction of all possible interactions (Jordano, 1987, Dormann et al., 2009).

$$C = L / (FP)$$

In calculating the number of realized links, a measure of the complexity of a network can be made; a useful tool when multiple sites are to be compared. Connectance has two main drawbacks however: it uses unweighted (presence/absence) data, thus giving equal importance to all species regardless of their abundance (Blüthgen et al., 2008), and secondly, it is known to be highly sensitive to sampling intensity (Banasek-Richter et al., 2009).

Generality, vulnerability and linkage density

Generality (G) and vulnerability (V) characterise the number of links associated with a particular node. In a network of F flower visitors and P plants, the mean number of plant species visited by insects is termed generality ($G = L / P$), whilst the converse, vulnerability, is the mean number of flower visitors that a plant receives ($V = L / F$) (Bersier et al., 2002, Blüthgen et al., 2008). Linkage density is the mean of these two values (Tylianakis et al., 2007). Qualitative methods for calculating these metrics have been superseded by quantitative equivalents (Bersier et al., 2002).

Nestedness

Nestedness is a measure of how communities of interacting taxa are organised (Bascompte et al., 2003). The concept originates in theories postulating how islands are colonised from a mainland source (Ulrich and Almeida-Neto, 2012). The non-random pattern proposed by Darlington (1957) suggests that for a series of islands of various sizes and distances from the mainland, the most efficient dispersers will occupy the majority of islands (including the most distant ones), whilst less mobile dispersers will only appear on closer land parcels. The result is a nested pattern of colonists arranged according to differences in species and site traits (Ulrich and Almeida-Neto, 2012).

This concept was extended to ecological networks by Jordano (1987), Bascompte et al. (2003) and others to describe mutualistic interactions such as those between plants and pollinators. Considering flowers as islands, and making pollinators analogous to Darlington's mainland biota, the nested pattern proposed in the

twentieth century to describe island colonization appears to be a common feature of pollination networks (Ollerton *et al.*, 2007, Dupont *et al.*, 2009).

These networks are frequently interpreted as exhibiting 'specialization asymmetry', that is, specialists - species with few connections, interact with generalists - species with many connections (Blüthgen *et al.*, 2008). More specifically, this leads to generalised pollinators interacting with all or many plants, with subsequent insect taxa interacting with a decreasing subset of these (Allesina, 2012; Figure 4.1).
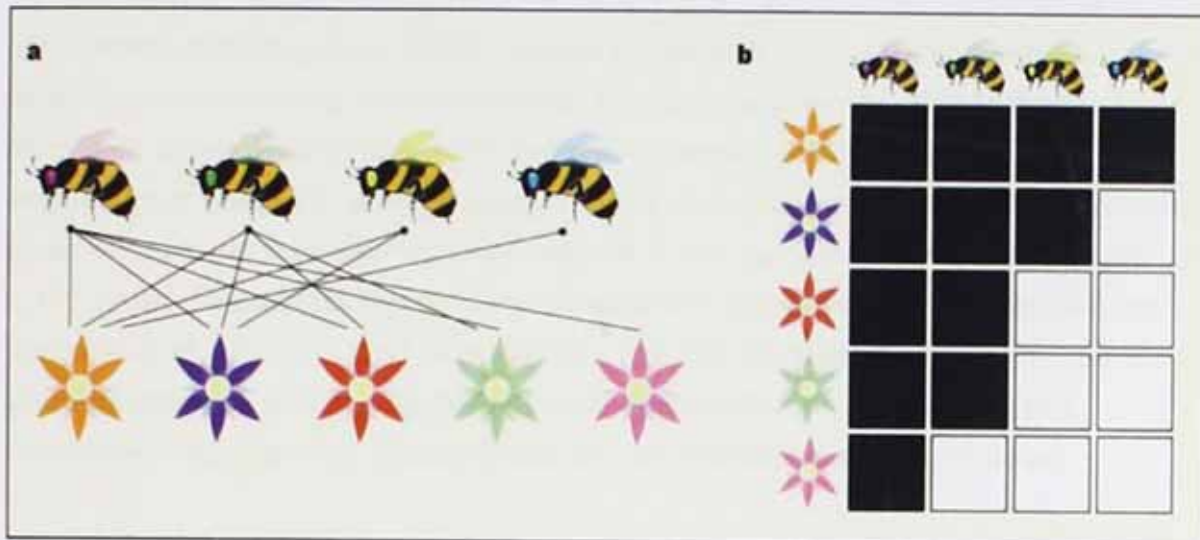
Figure 4.1 Illustration of typical interactions between pollinators and plants. **(a)** Generalist species (such as the pink-eyed bee) interact with many plants, whereas specialists have only a few or, in the case of the blue-eyed bee, a single partner. **(b)** The network shown in (a) is described as perfectly nested as all species interactions are proper sub-sets of other species interactions. As such, a triangular pattern occurs when the links (black squares) are arranged in a matrix. Reprinted by permission from Macmillan Publishers Ltd: Nature, (Allesina – 'The more the merrier', 2012). Copyright 2012.

Early calculations of nestedness between pairs of species involved the use of thermodynamic measures such as the Nestedness Temperature Calculator software of Atmar and Patterson (1993). This received criticism for overestimating the degree of nestedness in a network (Fischer and Lindenmayer, 2002) and was superseded by other programs such as NODF - Nestedness metric based on Overlap and Decreasing Fill (Ulrich and Gotelli, 2007, Ulrich *et al.*, 2009). Recently, the weakness associated with using incidence data to analyze interaction networks has received increasing attention (Ings *et al.*, 2009; Almeida-Neto and Ulrich, 2011: Ulrich and Almeida-Neto, 2012), the main criticism being that presence-absence data imply that all interactions are of equal importance, when in reality this is unlikely to be the case

(Ulrich and Almeida-Neto, 2012). In response to this, weighted metrics have been developed offering more robust assessments of whether a community exhibits a nested pattern, e.g. WINE – Weighted Interaction Nestedness Estimator (Galeano *et al.*, 2009) and WNODF – Weighted Nestedness metric based on Overlap and Decreasing Fill (Almeida-Neto and Ulrich, 2011; Ulrich, 2012). The need to test calculations of nestedness against appropriate null models is necessary if correct interpretations are to be made (Dormann *et al.*, 2009, Gibson *et al.*, 2011).

The nestedness observed in mutualistic webs has been interpreted in several, often complementary, ways. For example, Memmott *et al.* (2004) examined whether a non-random nested pattern might indicate robustness in the face of selected extinction events. Using 'attack tolerance curves' (Burgos *et al.*, 2007) they quantified the proportion of a guild that might become extinct following the elimination of species in another guild. Their findings suggested that the loss of core generalists (those that are maximally packed in the top left hand corner of Figure 4.1b) posed the greatest threat to the continuation of pollinator-plant interactions. Fontaine *et al.* (2006, p.129) extended this concept by suggesting that nestedness confers resilience, and that 'generalist pollinators buffer the loss of specialist pollinators'. Bezerra *et al.* (2009) tested this by simulating species removal.

Nestedness has also been used as a conservation tool to identify keystone species and highlight critical changes in interaction structure in advance of biodiversity losses (Benedek *et al.*, 2007, Ebeling *et al.*, 2011).

To my knowledge, network structure in gardens has not been assessed. Olesen *et al.* (2007, p.19891) noted that 'in natural communities, species and their interactions are often organised as non-random networks'. As the study sites for the present work are human constructs (and therefore likely to contain non-native plants), one of the aims of this work is to establish whether the reported non-randomness associated with natural environments also applies to novel ecosystems. **It is predicted that networks in gardens mimic those of natural settings by exhibiting a nested structure.** Furthermore, as plant populations in 'natural' settings experience quantitatively and qualitatively different visits from pollinating insects over a season (resulting in networks appearing as highly temporally dynamic - Herrera, 1988, Ollerton *et al.*, 2007, Dupont *et al.*, 2009, Alarcón, 2010), **it is predicted that some sampling sessions will have a greater proportion of nested networks than others.**

Aims

The aim of this chapter is to consider how assemblages of plants influence communities of flower-visiting insects. Specifically, the chapter seeks to answer the following questions:

1. Does the number of plant taxa available in a garden affect the richness and abundance of flower-visiting insect species that are observed?

2. What is the relationship between the availability of plants and those visited by flower-visitors, and does this differ across properties and seasons?

3. Is the proportion of native and alien plants similar across sampling sessions?

4. Are native plants in gardens preferred by flower visitors?

5. Are certain plant families that are common to a number of gardens more favoured by flower visitors than others?

6. Does connectance vary between properties across seasons where (i) only visited plants are assessed and (ii) all available plants are assessed?

7. Do generality, vulnerability and linkage density differ between properties and are seasonal patterns evident?

8. Do the observed plant and flower-visitor communities exhibit nested structures and are these consistent across the season?

Methods

Study sites and timing of sampling

17 gardens in four counties in lowland Central England were used as the basis for the study. Sampling took place between April and September 2010. Full details of the sites and methods for censusing plants and flower visitors are given in Chapter 2 (2010 field season).

Plant classification

Plants were ascribed to families according to the most recent Angiosperm Phylogeny Group publication (APG III, 2009).

Throughout this chapter the term 'plant element' is used instead of plant species. This follows the convention of Frankie et al. (2005) and reflects the difficulty in classifying ornamental garden plants according to standard taxonomic guidelines.

Here, plant element refers to any species, variety, cultivar or hybrid that is commonly used in the horticultural arena.

Due to the problems associated with reliably identifying certain plant elements, a generic grouping was sometimes used. Examples include *Lavandula* spp., *Nepeta* spp., and *Origanum* spp. This cautionary approach means overall plant species richness across gardens is likely to have been underestimated.

The classification of plant elements according to native or alien status was made with reference to Stace (1997) following the methods of Smith *et al.* (2006a) and Loram *et al.* (2008a).

Data analysis
Unless otherwise stated, each sampling session at each property was considered separately.

Relationship between plant availability and observed flower visitors
The relationship between plant family, genera or element availability and observed insect richness and abundance was explored using nonlinear regression. Power function trend lines were fitted through the data as these best represented the accumulation of flower visitors with increasing plant richness. The significance of each fit was established by performing linear regressions on log-transformed data.

Availability of plants compared to plants visited
The median number of plant elements available at each garden was compared to the number of plant elements visited using a Mann-Whitney U test. The same test was used to examine differences in availability and use of plants across the four sampling sessions.

Proportion of native and alien plants
Differences in the proportion of alien plants available across the four sessions were examined using a one-way ANOVA (the data met assumptions of normality and homogeneity). This was followed up with REGWQ *post hoc* tests.

The relationship between the proportion of native and alien plants available and those used in each of the four sessions was explored using a chi-square test of association in Excel following the methods of Dytham (2011).

Evaluating highly visited plant families
Plant elements that were common to a number of gardens within each of the four sessions (and which were visited by flower-visitors at a minimum of five properties)

were identified. Working at family level, a per-session visitation preference index (VPI) was calculated. This index incorporated two factors; (i) the number of gardens where an element was used as a proportion of the number of gardens where the element was available and (ii) the number of elements used (within a family) as a proportion of the total number of elements available within the family in the session in question. The VPI values were log transformed and plotted against the (log transformed) number of elements available within the family. A linear trend line was fitted through the points and 95% confidence intervals added to identify those families with a VPI lying beyond the upper limits of the confidence lines. Flowers within families with a high VPI were characterised according to whether they were open or tubular, following the methods of Fontaine *et al.* (2006).

Connectance

For each sampling session plant and flower-visitor data were arranged as a matrix. The available and realised links were calculated according to

$C = L / (FP)$ (see Introduction). Connectance values were calculated for two scenarios:

1. The number of links between plants that had a minimum of one visitor and the number of flower-visitor species.

2. The number of links between all available plants (see Chapter 2, 2010 field season) and the total number of flower-visitor species.

Median connection values ($n = 68$ per scenario) are presented for each property. Differences between properties were examined using the non-parametric Kruskal-Wallis test.

Generality, vulnerability and linkage density

Generality, vulnerability and linkage density values for each session were calculated in R (R Development Core Team) using the package Bipartite, Version 1.17 (Dormann *et al.*, 2008). Abundance data were arranged in matrices with flower-visitors as columns and plant elements as rows. Differences in median values between properties ($n = 4$) were examined using a Kruskal-Wallis test. Median values per session ($n = 17$) were also calculated and tested in the same way. Mann-Whitney *U* tests, with Dunn Šidák corrected critical values (Sokal and Rohlf, 1981) were used as non-parametric *post hoc* procedures.

Nestedness

To assess whether communities of flower-visitors and plants exhibited nested patterns, the data were examined using WNODF (weighted nestedness metric based on overlap and decreasing fill) software, Version 2.0 (Almeida-Neto and Ulrich, 2011). To avoid the problems associated with the non-matching of species attributes, e.g. the creation of 'forbidden interactions' (Jordano, 1987, Weiner *et al.*, 2011), whereby spring insect species appear in matrices with late summer flowering plants despite the two never co-occurring, data from each sampling session were considered separately. Matrices of interacting species (*n* = 68) were prepared in EcoSim format (space delimited columns of plant elements and rows of flower-visitors), and run in the WNODF program using the following parameters: (i) matrix sorting was by row and column species richness, with rows and columns of equal species richness further sorted according to abundance totals and (ii) null model '*rc*' was selected, whereby individuals are assigned to matrix cells proportional to the observed row and abundance column totals until total abundances for each row and column are reached. Finally, the degree of nestedness was established by comparing the actual distribution values with the scores obtained from 500 runs of the null model (Almeida-Neto and Ulrich, 2011, Ulrich, 2012). The probability of the observed network differing from random (and therefore exhibiting a nested pattern) was considered significant at $\alpha \le 0.05$. Differences between seasons were quantified by considering the proportion of significantly nested samples they contained. A chi-square test of association was used to establish whether these observed values were significantly different from expected.

Results

Plant richness

A total of 98 plant families, 409 genera and 988 plant elements were recorded across all properties for sessions one to four inclusive, constituting more than 22% of the world's total recognised plant families (APG III, 2009, Table 4.1, Appendix VII).

Relationship between plant availability and observed flower visitors

Flower-visitor species richness and abundance increased significantly as the number of plant families, genera and elements increased (Figures 4.2 and 4.3). Flower-visitor abundance was best explained by the number of plant genera available ($R^2 = 0.35$, $P < 0.001$), with the number of plant elements being the poorest predictor of plant species richness ($R^2 = 0.19$, $P = < 0.001$), (Table 4.2).

Table 4.1 Number of plant families (F), genera (G) and elements (PE) recorded for each property at each of four sampling sessions, together with the total number of distinct taxa for each property.

Session number	1			2			3			4			Total unique F, G and PE all sessions		
Taxonomic level	F	G	PE	F	G	PE	F	G	PE	F	G	PE	F	G	PE
PROPERTY															
AL	27	42	45	21	40	46	15	25	27	15	21	23	37	79	143
BOU	19	24	24	32	74	85	26	69	81	25	52	62	45	127	249
CA	15	18	19	29	47	54	34	65	77	28	51	56	51	115	206
CM	24	38	41	35	68	102	34	70	89	33	65	86	50	145	318
CHALL	18	22	23	38	64	89	27	52	67	21	35	44	51	109	223
EN	14	17	19	30	55	68	33	59	67	25	46	54	45	113	208
FAR	24	34	38	26	44	54	23	40	54	29	46	56	48	97	202
HOL	20	25	28	34	72	103	37	83	97	31	57	68	56	148	296
KEL	24	35	37	36	91	120	28	84	103	30	62	74	50	163	334
KIR	16	21	22	12	14	21	9	12	12	9	14	15	22	36	70
LAM	14	19	20	28	57	78	24	49	54	17	31	37	41	109	189
LW	19	25	26	33	64	79	29	64	76	28	56	68	49	123	250
ST	24	38	46	37	70	95	37	74	86	33	63	74	55	135	301
SUL	11	17	18	27	67	70	36	88	110	35	84	93	52	167	291
UP	19	31	32	30	73	101	32	79	87	30	65	77	52	146	297
WAD	9	10	11	21	31	35	18	26	28	11	15	16	30	45	90
WR	19	25	27	24	40	52	16	32	36	16	25	29	39	73	144
Mean	18.59	25.94	27.82	29.00	57.12	73.65	26.94	57.12	67.71	24.47	46.35	54.82			
SD	5.01	8.99	10.33	6.79	19.02	27.09	8.44	23.16	28.62	8.12	19.98	24.07			
Total unique number of F, G and PE all properties													98	409	988

103
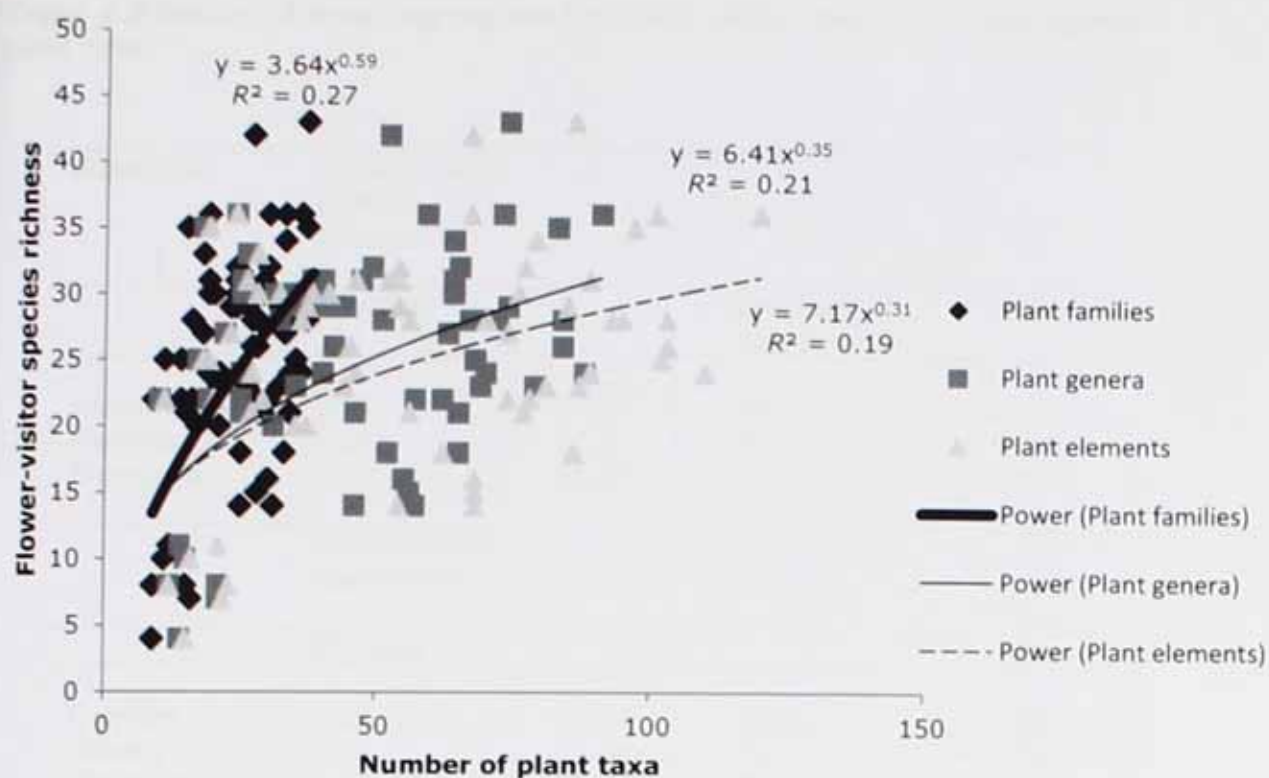
Figure 4.2 Flower-visitor species richness as a function of available plant taxa. Trend lines are power functions.
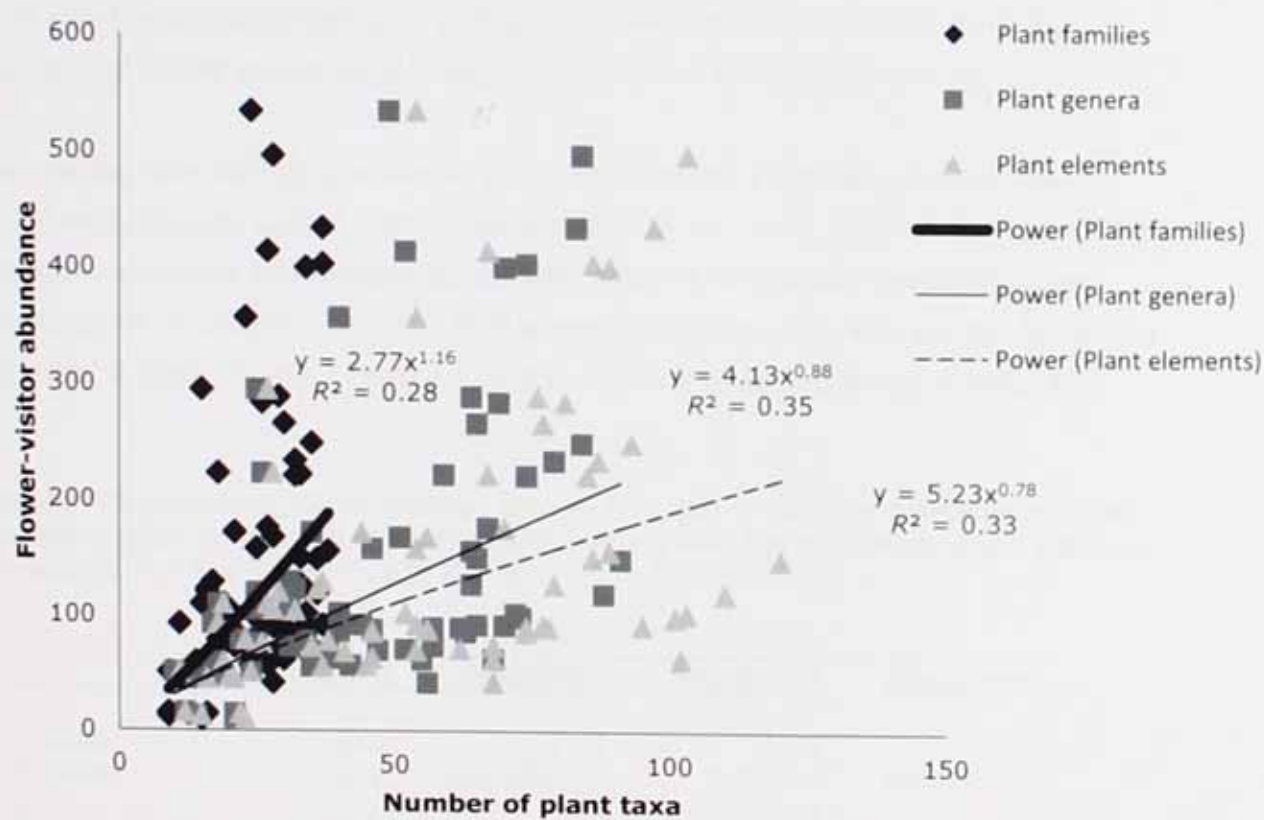
Figure 4.3 Flower-visitor abundance as a function of available plant taxa. Trend lines are power functions.

Table 4.2 Results of linear regressions for flower-visitor species richness against plant taxa.

Plant taxa	Flower visitor species richness			
	R^2 value	F	Degrees of freedom	P value
Families	0.27	24.27	66, 1	< 0.001
Genera	0.21	17.16	66, 1	< 0.001
Elements	0.19	15.45	66, 1	< 0.001
	Flower visitor abundance			
	R^2 value	F		P value
Families	0.28	25.37	66, 1	< 0.001
Genera	0.35	35.34	66, 1	< 0.001
Elements	0.33	35.53	66, 1	< 0.001

Comparing plants visited with the number of plants available

The number of plants visited in each garden was significantly lower than the number of plants available, $n = 68$, $Z = -5.97$, $P < 0.001$ (Figure 4.4).

Across the four sampling sessions, all except Session 1 had significantly lower numbers of plants visited than those available ($P = < 0.01$, Table 4.3, Figure 4.5). As some sampling events overlapped with dates in neighbouring sessions (see explanation in Chapter 2 – 2010 field season) the data were also plotted according to date. A similar pattern to that found in Figure 4.5 was observed (Figure 4.6).

Table 4.3 Results of Mann Whitney U tests for each of the four sampling sessions comparing the number of plant elements visited with the number of plant elements available. * = $P \le 0.05$, ** = $P \le 0.01$, *** = $P \le 0.001$.

	Session 1	Session 2	Session 3	Session 4
Z value	-2.09	-4.46	-2.95	-3.62
P value	0.04*	<0.001***	0.003**	<0.001***
n	17	17	17	17
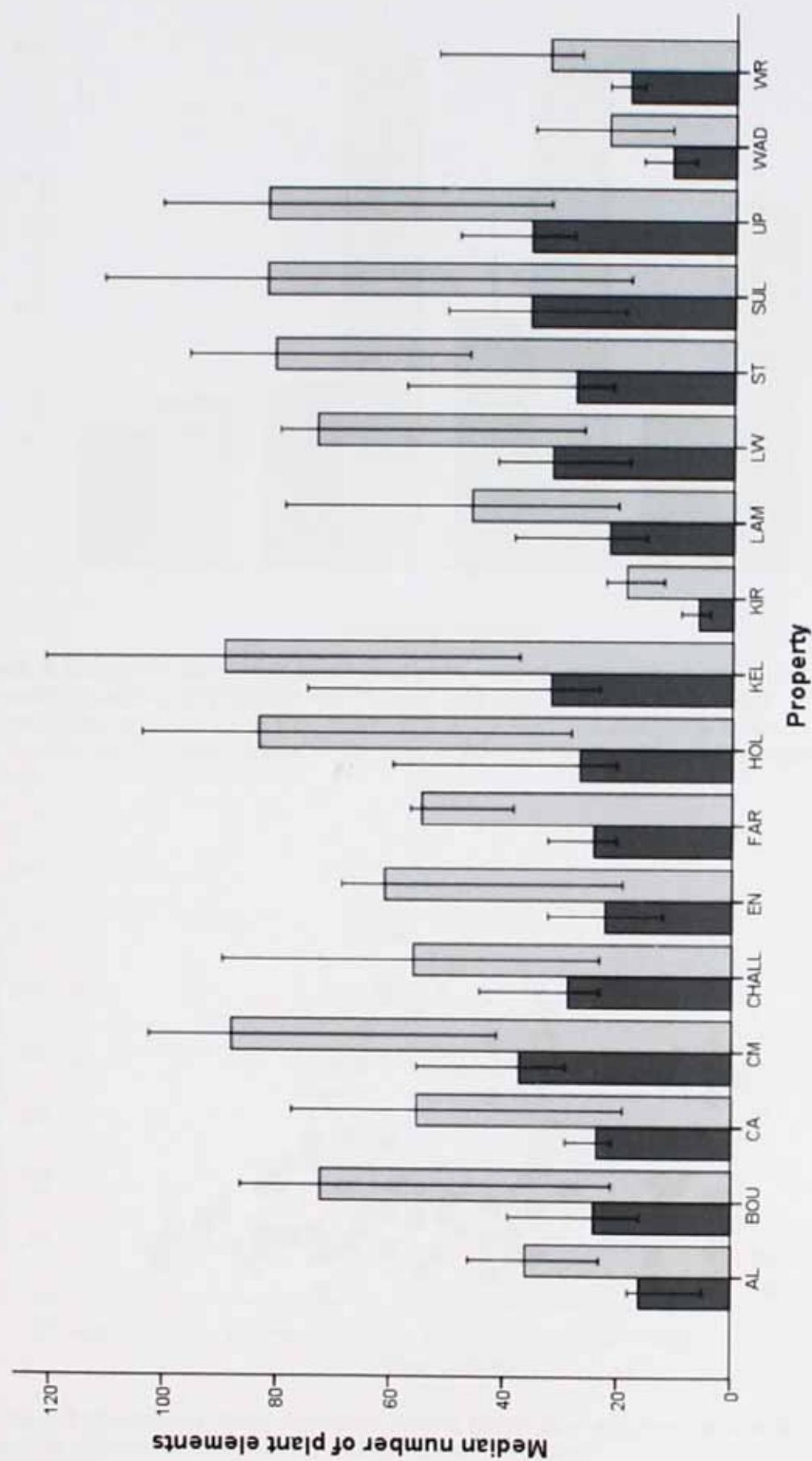
Figure 4.4 Median number of plant elements visited (dark grey bars) compared to median number of plant elements available (light grey bars) for each property ($n = 4$). Error bars = 95% confidence intervals.
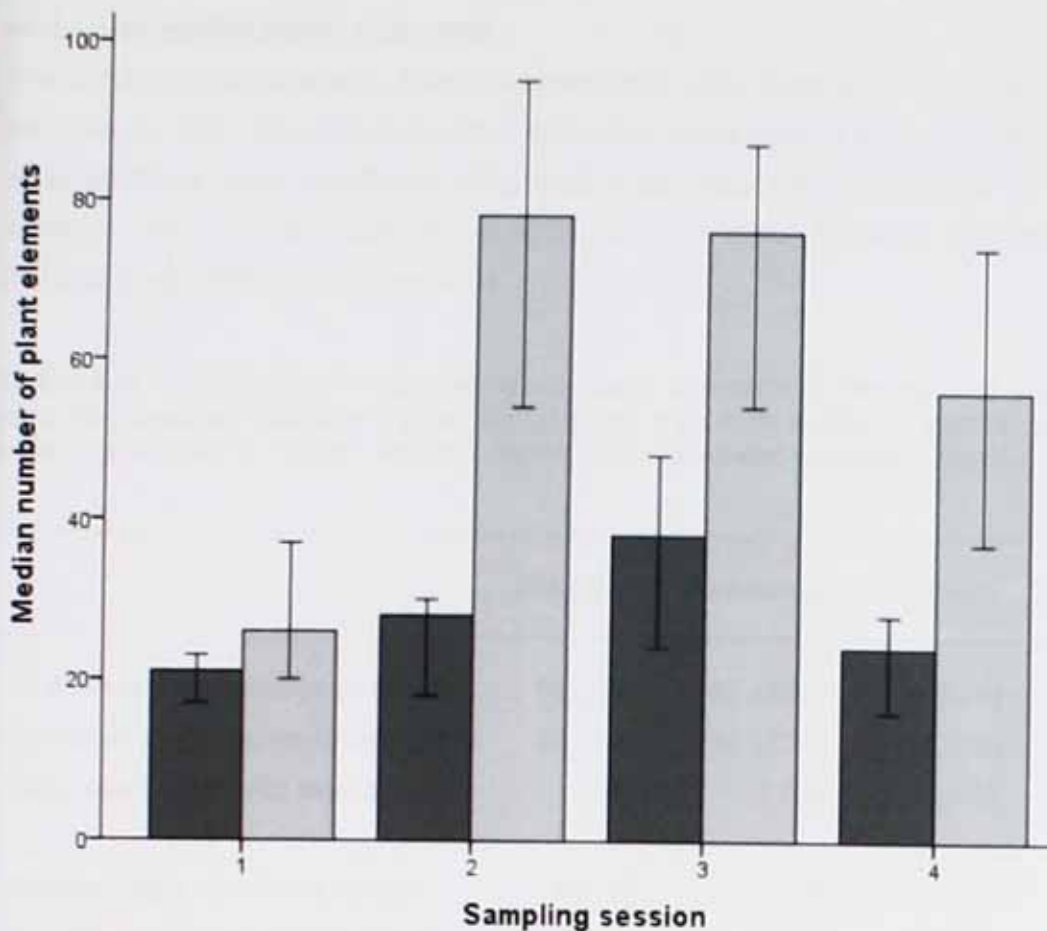
Figure 4.5 Median number of plant elements visited (dark grey bars) compared to the median number of plant elements available (light grey bars) for each of the four sampling sessions ($n = 17$). Session 1 = 22 Apr. – 5 Jun., 2 = 6 Jun. – 18 Jul., 3 = 19 Jul. – 9 Aug. and 4 = 10 Aug. – 30 Sep. Error bars = 95% confidence intervals.
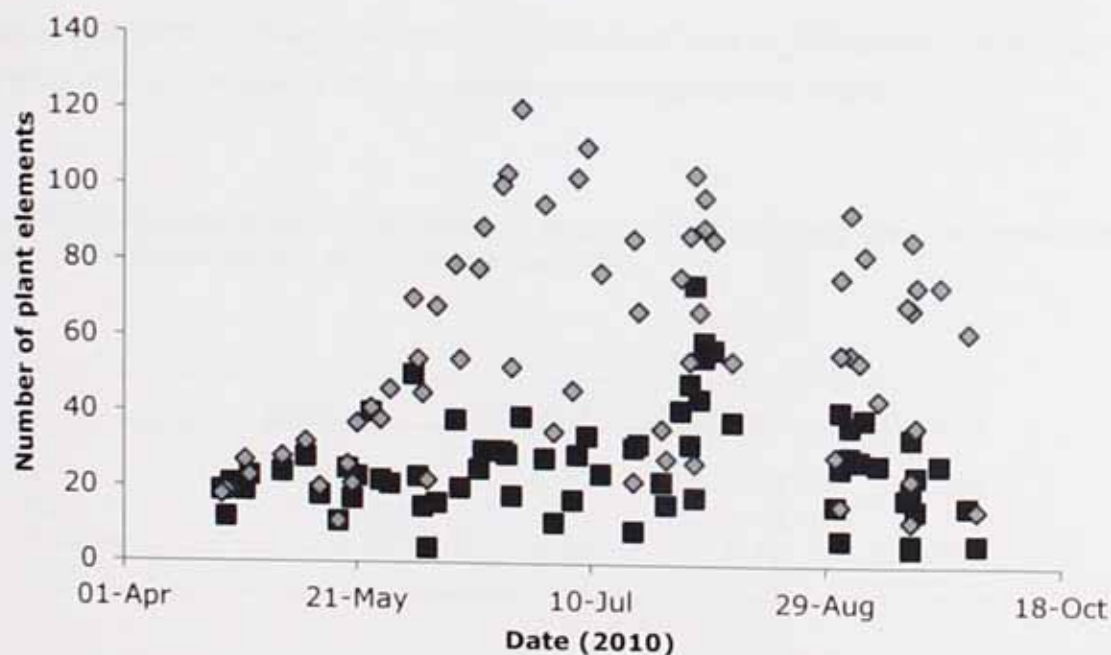
Figure 4.6 Number of plant elements visited (dark grey squares) and available (light grey diamonds) plotted according to date sampled.

Alien and native plant elements

The percentage of available plant elements that were classed as aliens ranged between 62 and 79% across the four sessions (Table 4.4). A one-way ANOVA revealed there was a significant difference in the proportion of alien plants available ($F = 5.97$, d.f. 3,64, $P = 0.001$). *Post hoc* tests (REGWQ) showed that Session 1 was different to Session 4.

Table 4.4 Percentage of alien and native plant elements across each of the four sampling sessions. Data are given for (i) plant elements available and (ii) plant elements visited by flower-visitors. Numbers in brackets represent absolute values.

	Session 1	Session 2	Session 3	Session 4
% alien plant elements available	62 (295)	69 (868)	74 (848)	79 (734)
% native plant elements available	38 (181)	31 (384)	26 (303)	21 (198)
Total plant elements available	476	1252	1151	932
% alien plant elements visited	66 (90)	71 (147)	76 (220)	77 (148)
% native plant elements visited	34 (46)	29 (59)	24 (69)	23 (45)
Total plant elements visited	136	206	289	193

Chi-square tests of association revealed that there was no difference in the number of alien and native plants visited relative to those available (Table 4.5).

Table 4.5 Results of chi-square tests of association comparing the number of alien and native plants visited versus those available.

	Session 1	Session 2	Session 3	Session 4
x^2	0.80	0.35	0.72	0.41
d.f.	1	1	1	1
P value	0.37	0.56	0.40	0.52

On a per-garden basis, the proportion of alien plants ranged from 0.45 to 0.91 across all sampling sessions, with the proportion of native plants ranging from 0.09 to 0.55 over the whole season. Overall, the mean proportion of available plants that were classed as alien was 0.68 ± 0.09 (Table 4.6).

Table 4.6 Range and mean proportion of alien and native plant elements across each of the seventeen properties (four sessions combined) plus mean proportion for all properties.

Property	Alien			Native		
	n plant elements	Range	Mean ± SD n = 4		Range	Mean ± SD n = 4
AL	143	0.49 – 0.74	0.59 ± 0.11		0.26 – 0.51	0.41 ± 0.11
BOU	249	0.67 – 0.84	0.74 ± 0.07		0.16 – 0.33	0.26 ± 0.07
CA	206	0.57 – 0.80	0.68 ± 0.12		0.20 – 0.43	0.32 ± 0.12
CM	318	0.71 – 0.89	0.83 ± 0.09		0.11 – 0.29	0.17 ± 0.09
CHALL	223	0.58 – 0.67	0.64 ± 0.04		0.33 – 0.42	0.36 ± 0.04
EN	208	0.63 – 0.74	0.68 ± 0.05		0.26 – 0.37	0.32 ± 0.05
FAR	202	0.61 – 0.66	0.64 ± 0.02		0.34 – 0.39	0.36 ± 0.02
HOL	296	0.68 – 0.79	0.74 ± 0.05		0.21 – 0.32	0.26 ± 0.05
KEL	334	0.57 – 0.91	0.74 ± 0.14		0.09 – 0.43	0.26 ± 0.14
KIR	70	0.45 – 0.53	0.50 ± 0.04		0.47 – 0.55	0.50 ± 0.04
LAM	189	0.60 – 0.83	0.76 ± 0.11		0.17 – 0.40	0.24 ± 0.11
LW	250	0.65 – 0.78	0.72 ± 0.07		0.22 – 0.35	0.28 ± 0.07
ST	301	0.71 – 0.78	0.75 ± 0.03		0.22 – 0.29	0.25 ± 0.03
SUL	291	0.56 – 0.85	0.70 ± 0.13		0.15 – 0.44	0.30 ± 0.13
UP	297	0.66 – 0.82	0.76 ± 0.07		0.18 – 0.34	0.24 ± 0.07
WAD	90	0.45 – 0.75	0.54 ± 0.14		0.25 – 0.55	0.46 ± 0.14
WR	144	0.48 – 0.64	0.60 ± 0.08		0.36 – 0.42	0.40 ± 0.08
Mean for all properties n = 68			0.68 ± 0.09			0.32 ± 0.09

Highly visited plant families

The visitation preference index for ubiquitous and highly visited families revealed that different families were preferred at different times of the year. During spring (Session 1), Asteraceae, Boraginaceae and Lamiaceae were highly favoured (Figure 4.7). In Session 2 this increased to four families: Amaryllidaceae, Apiaceae, Lamiaceae and Rosaceae (Figure 4.8). Asteraceae was again highly preferred in Session 3 together with Acanthaceae and Scrophulariaceae (Figure 4.9), whilst in Session 4 no family emerged as more highly visited than others (Figure 4.10).
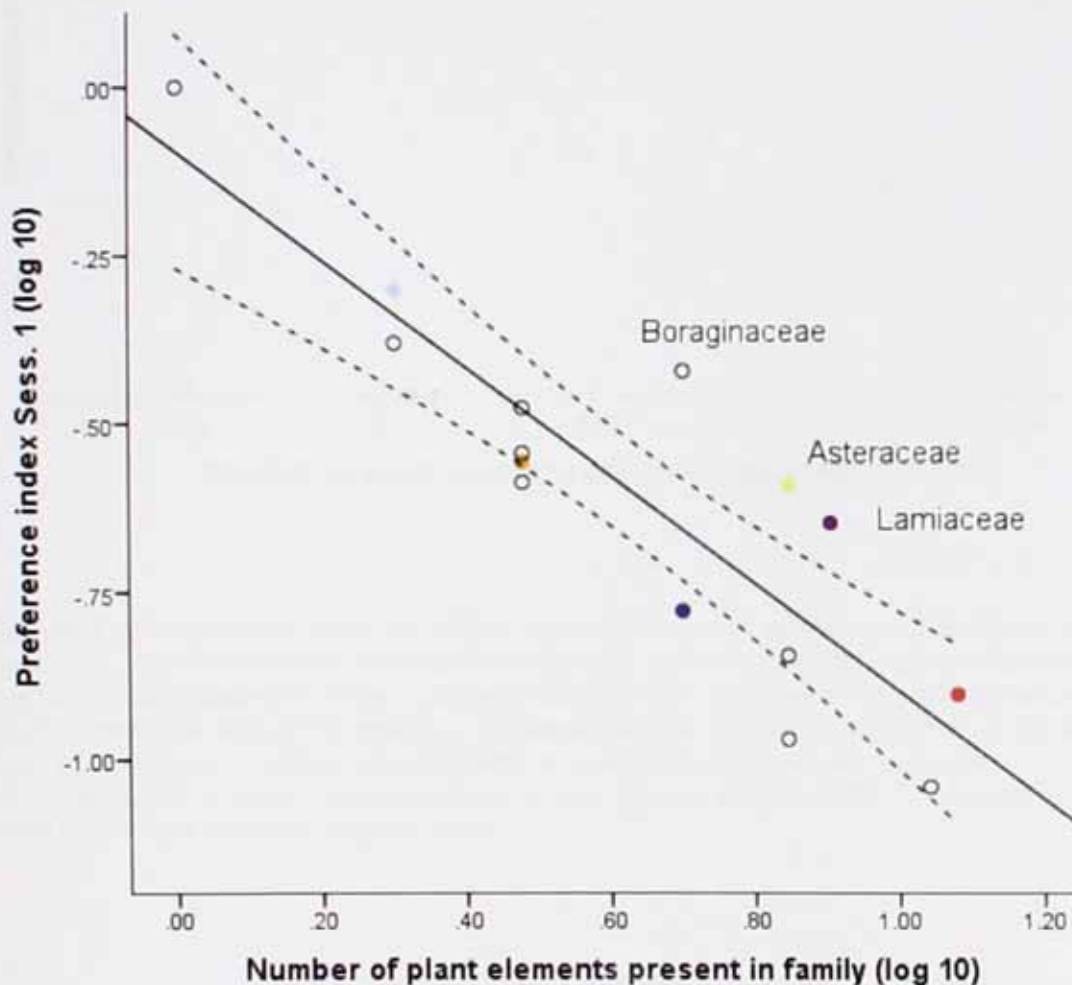
Figure 4.7 Preference index for highly represented and visited plant families in Session 1. Named families are those containing elements which experience higher than expected visitation rates. Coloured data points represent families common to three of the four sampling sessions. Amaryllidaceae = orange, Apiaceae = dark blue, Asteraceae = yellow, Geraniaceae = pale blue, Lamiaceae = purple and Rosaceae = red. Dotted lines = 95% CI around linear trend line fitted through logged data.
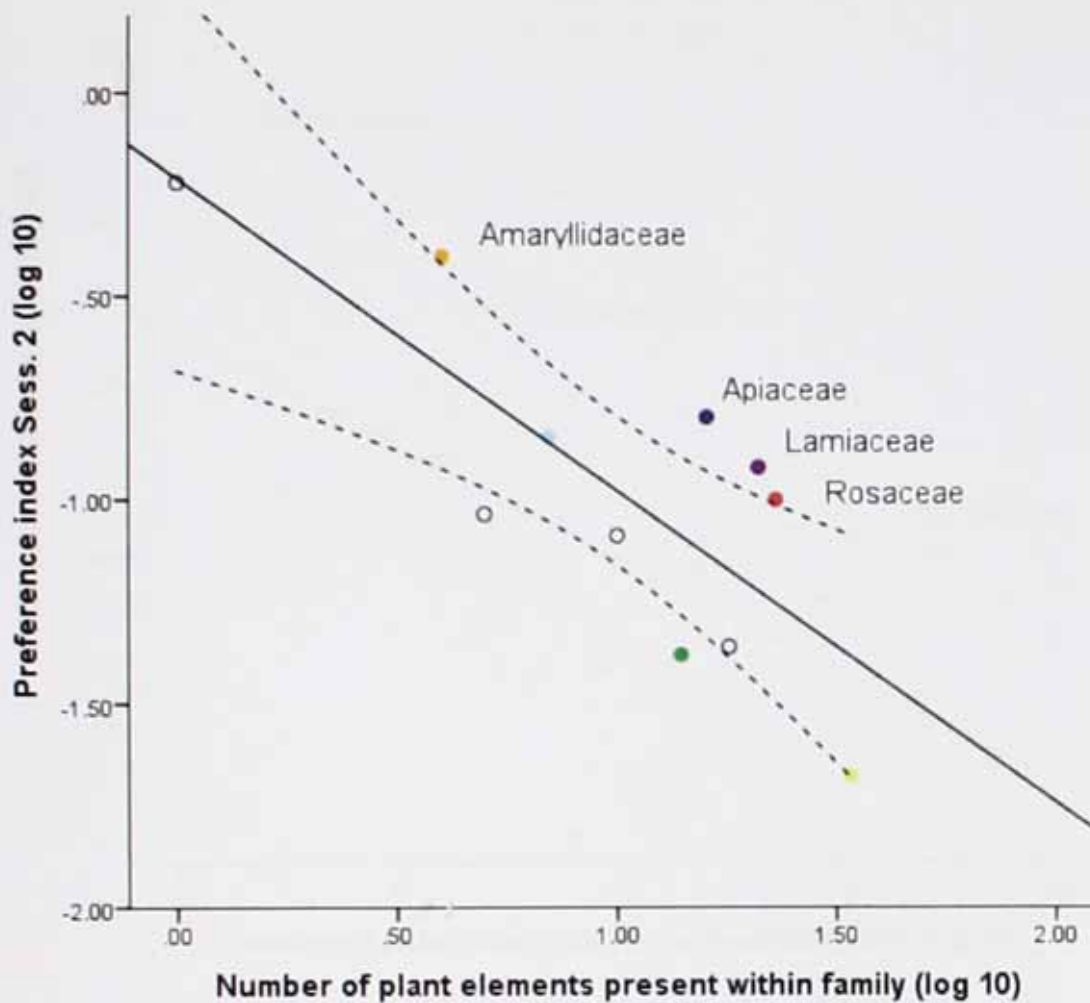
Figure 4.8 Preference index for highly represented and visited plant families in Session 2. Named families are those containing elements which experience higher than expected visitation rates. Coloured data points represent families common to three of the four sampling sessions. Amaryllidaceae = orange, Apiaceae = dark blue, Asteraceae = yellow, Geraniaceae = pale blue, Lamiaceae = purple, Ranunculaceae = green and Rosaceae = red. Dotted lines = 95% CI around linear trend line fitted through logged data.
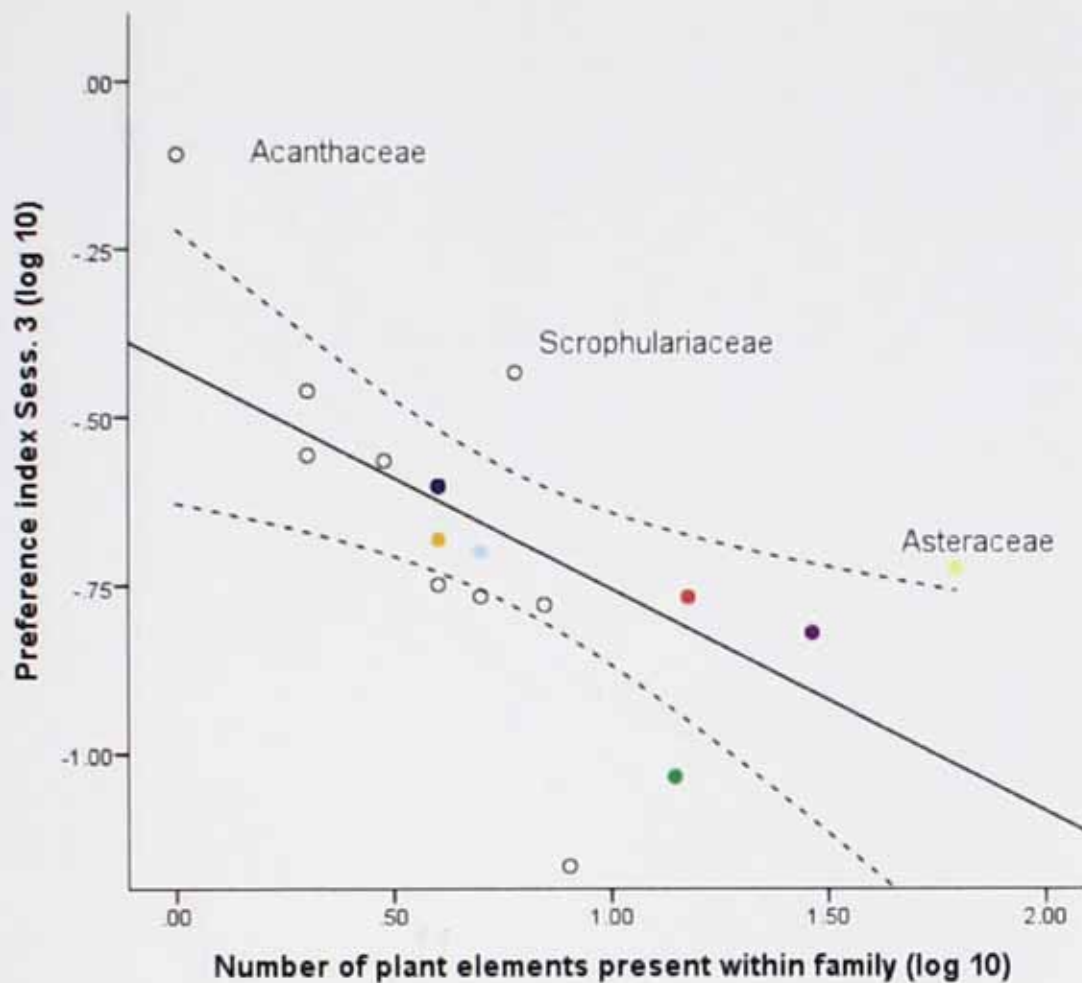
Figure 4.9 Preference index for highly represented and visited plant families in Session 3. Named families are those containing elements which experience higher than expected visitation rates. Coloured data points represent families common to three of the four sampling sessions. Amaryllidaceae = orange, Apiaceae = dark blue, Asteraceae = yellow, Geraniaceae = pale blue, Lamiaceae = purple, Ranunculaceae = green and Rosaceae = red. Dotted lines = 95% CI around linear trend line fitted through logged data.
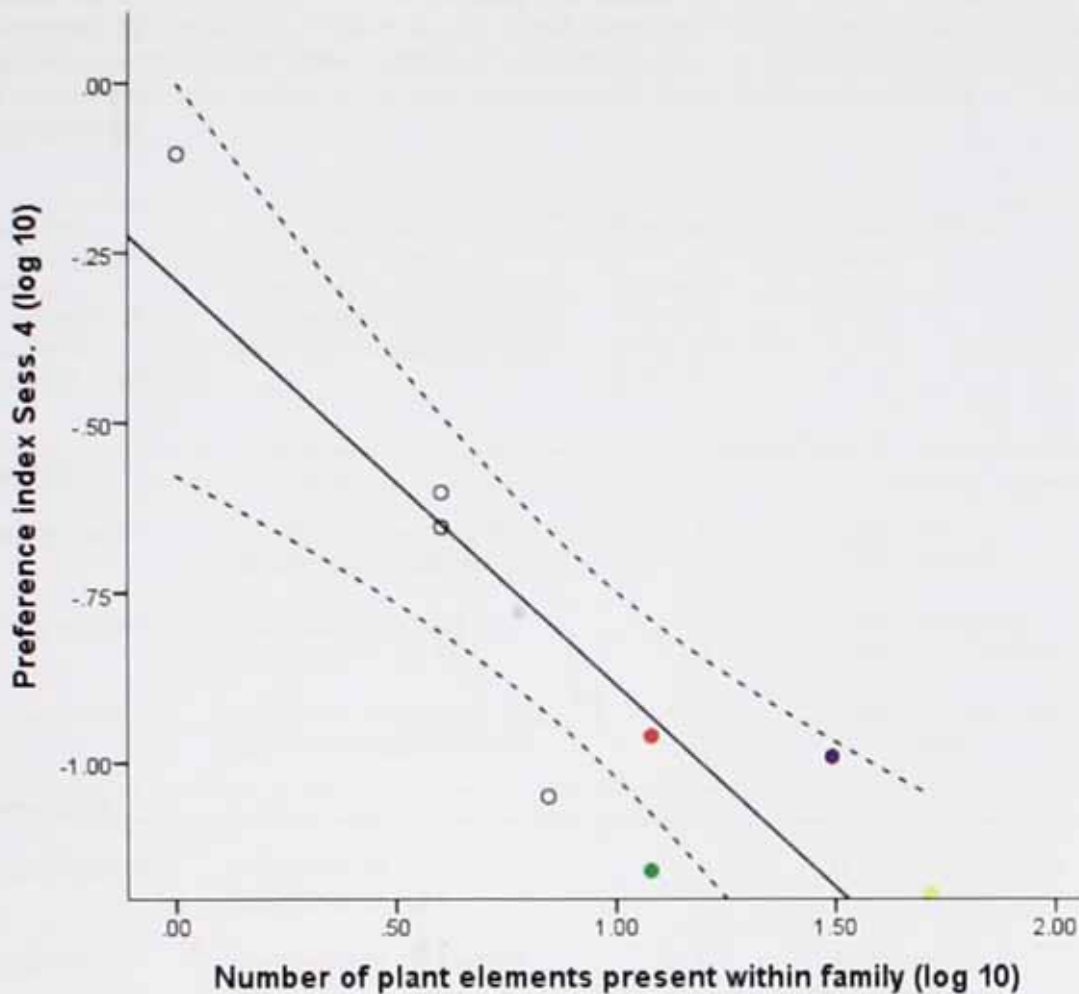
Figure 4.10 Preference index for highly represented and visited plant families in Session 4. Coloured data points represent families common to three of the four sampling sessions. Asteraceae = yellow, Geraniaceae = pale blue, Lamiaceae = purple, Ranunculaceae = green and Rosaceae = red. Dotted lines = 95% CI around linear trend line fitted through logged data.

A list of the plant elements within families identified using the visitation preference index is given in Table 4.7. A measure of the availability of these elements and the proportion of gardens where they were visited is included, as well as the colour, general overall shape of the flowers and their native or alien status.

Table 4.7 List of highly visited families per session (note, no specific families emerged for Session 4, Figure 4.10). Plant elements within each family that were visited by insects are listed, together with their alien or native status, their levels of occurrence and visitation across the gardens, their colour and flower morphology.

Families according to session. * indicates family occurs in multiple sessions	Plant elements visited within each family (N = native, A = alien) ** indicates plant element occurs in multiple sessions	Number of gardens where present (min. 5)	Proportion of gardens where visited	Colour	Flower shape T = tubular O = open
Session 1					
Asteraceae*	Centaurea montana (A)**	8	0.88	blue	O
	Taraxacum officinale (N)**	12	0.92	yellow	O
Boraginaceae	Pulmonaria sp. (A)	6	0.83	lilac/blue	T
	Symphytum sp. (N)	9	0.56	pink/lilac/blue	T
Lamiaceae*	Glechoma hederacea (N)	10	0.80	lilac/purple	T
	Lamium maculatum (A)	8	1.00	pink	T
Session 2					
Amaryllidaceae	Allium sp. (A)	8	0.88	lilac/purple	O
	Narcissus sp. (A)	7	0.71	yellow	T
Apiaceae	Aegopodium podagraria (A)	5	1.00	white	O
	Angelica archangelica (A)	5	1.00	white	O
	Astrantia major (A)	9	0.56	pink	O
Lamiaceae*	Nepeta sp. (A)	11	0.82	lilac/blue	T
	Salvia sp. (A)	8	0.88	various	T
	Thymus sp. (A)	6	0.83	pink/lilac	T
Rosaceae	Alchemilla mollis (A)	13	0.38	cream	O
	Rosa rugosa (A)	7	1.00	red	O
	Rosa sp. (A)	13	0.92	various	O
Session3					
Acanthaceae	Acanthus mollis (A)	9	0.78	purple	T
Asteraceae*	Achillea sp. (A)	9	0.67	pink/white	O
	Centaurea montana (A)**	11	0.45	blue	O
	Cirsium arvense (N)	6	0.83	pink/lilac	O
	Cosmos bipinnatus (A)	6	0.83	pink/white	O
	Echinacea sp. (A)	8	0.75	pink	O
	Echinops sp. (A)	8	0.75	blue	O
	Leucanthemum sp. (A)	11	0.64	white	O
	Taraxacum officinale (N)**	6	1.00	yellow	O
Scrophulariaceae	Buddleja davidii (N)	11	1.00	lilac	T
	Penstemon sp. (N)	7	0.71	various	T
	Verbascum sp. (A)	10	0.50	yellow	O

Connectance

Median connectance values for each of the 17 properties for each of the two scenarios (see Methods) are given in Figure 4.11. Connectivity was higher where matrices were smaller (Figure 4.12), hence Kirby (KIR), with the fewest flower-visitors and plant resources, had the highest median connectance value for both scenarios. Results of Kruskal-Wallis tests revealed a significant difference between median connectance values for properties under Scenario 1 (realised links between the number of plants that were visited at least once and the number of insect species they connected to), $H = 31.47$, d.f. $= 16$, $P = 0.012$. The median connectance value for KIR (0.26) was > 80% greater than that of the second highest connectance value (Althorp – AL, median value $= 0.14$). Under Scenario 2, no difference in median connectance values between properties was observed ($H = 17.56$, d.f. $= 16$, $P > 0.05$).
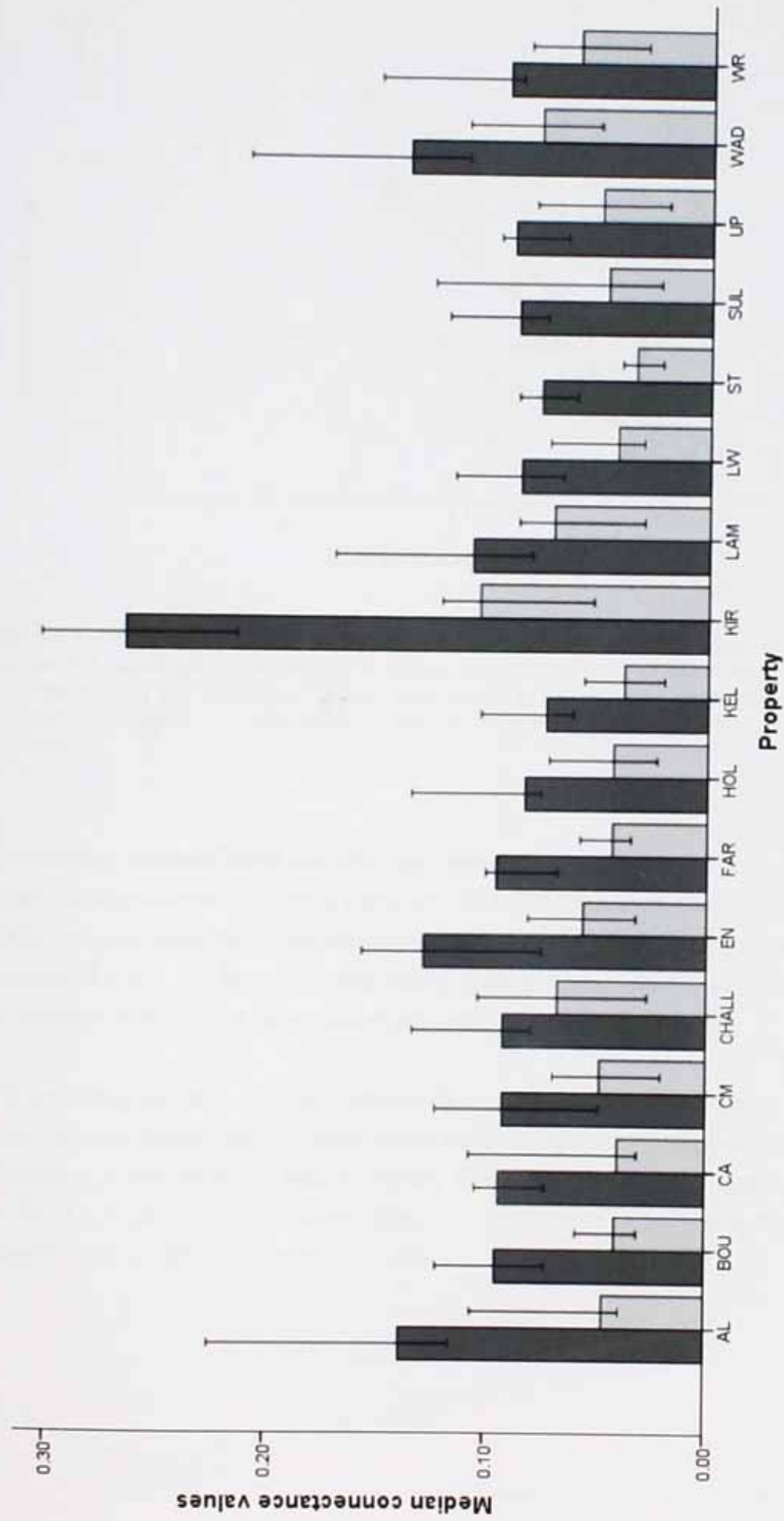
Figure 4.11 Median connectance values for each property for (i) only plant elements that were visited (dark grey bars) and (ii) all plant elements available (light grey bars), ($n = 4$). Error bars = 95% confidence intervals.
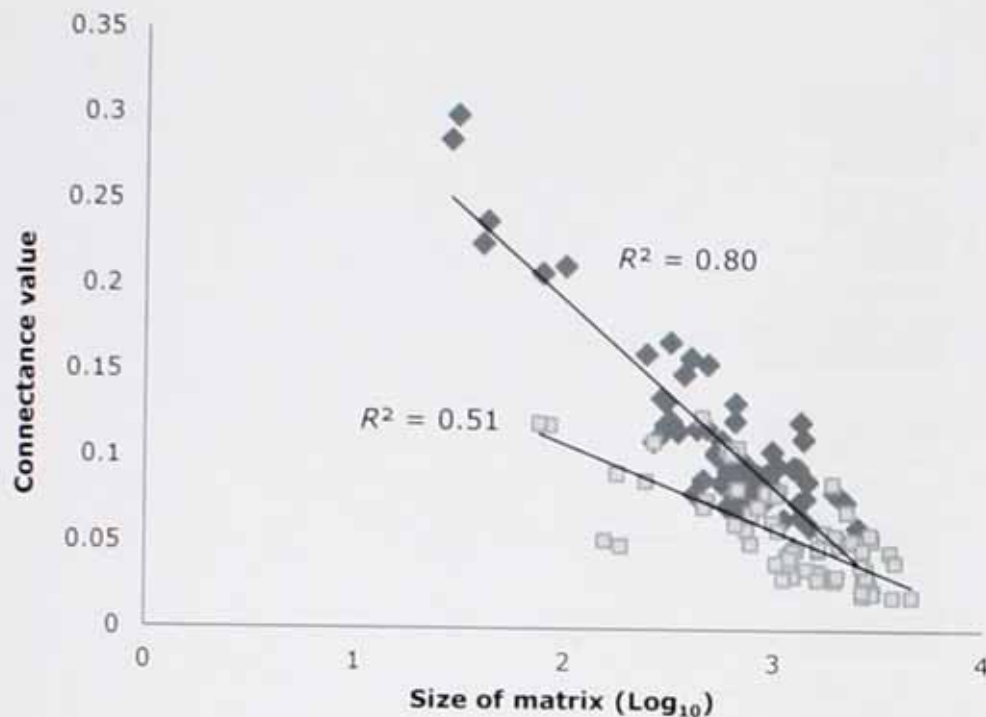
Figure 4.12 Decreasing connectivity as a function of matrix size for two scenarios. Scenario 1 (dark grey diamonds) = matrix comprised only of plant elements visited by insects, n = 68. Scenario 2 (light grey squares) = matrix comprised of all plant elements available, n = 68. Lines of best fit drawn for each scenario with R^2 values included.

Generality, vulnerability and linkage density

Flower visitors interacted with a mean of 4.5 ± 3.6 plant elements across all properties and sessions (generality) whereas plant elements interacted with an average of 3.6 ± 1.0 flower-visiting insect species (vulnerability). Overall there was an average of 4.1 ± 2.0 interactions per organism (linkage density).

The median generality and vulnerability values per property are given in Figure 4.13. Kruskal-Wallis tests revealed there were no significant differences in generality, vulnerability or linkage density values across gardens (generality: H = 18.24, d.f. = 16, P = 0.31; vulnerability: H = 24.27, d.f. = 16, P = 0.08; linkage density: H = 17.96, d.f. = 16, P = 0.33).
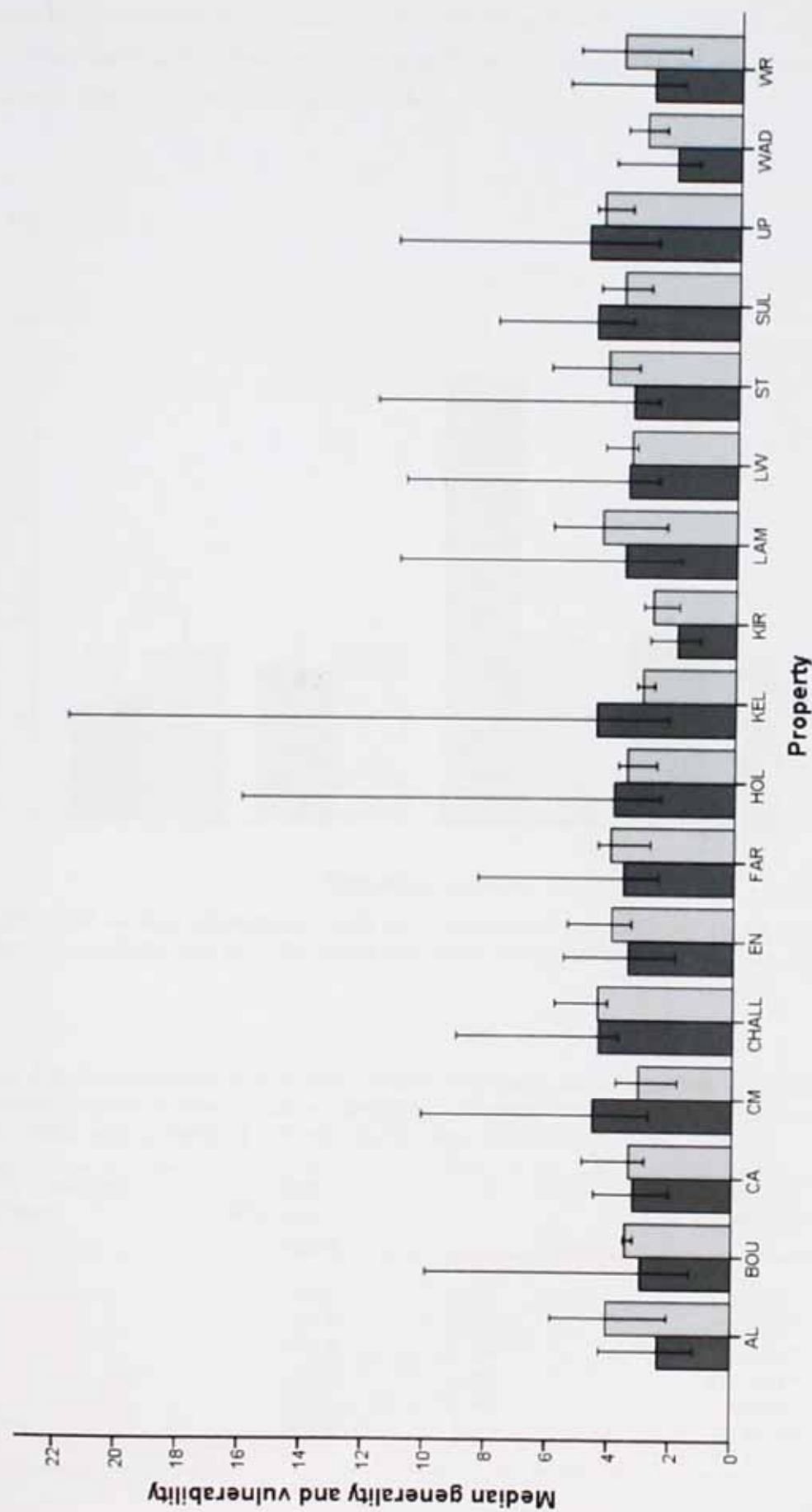
Figure 4.13 Median generality (dark grey bars) and vulnerability (light grey bars) values ($n = 4$) for each of the 17 properties. Error bars = 95% confidence intervals.

Across the four sampling periods, Session 3 exhibited the highest median
generality values (Figure 4.14). A Kruskal-Wallis test revealed that a significant
difference existed between sessions ($H = 27.82$, d.f. $= 3$, $P = <0.001$), with *post
hoc* tests showing that Session 3 was significantly different to all others, and that
Session 1 was different to Session 4 (Table 4.8).
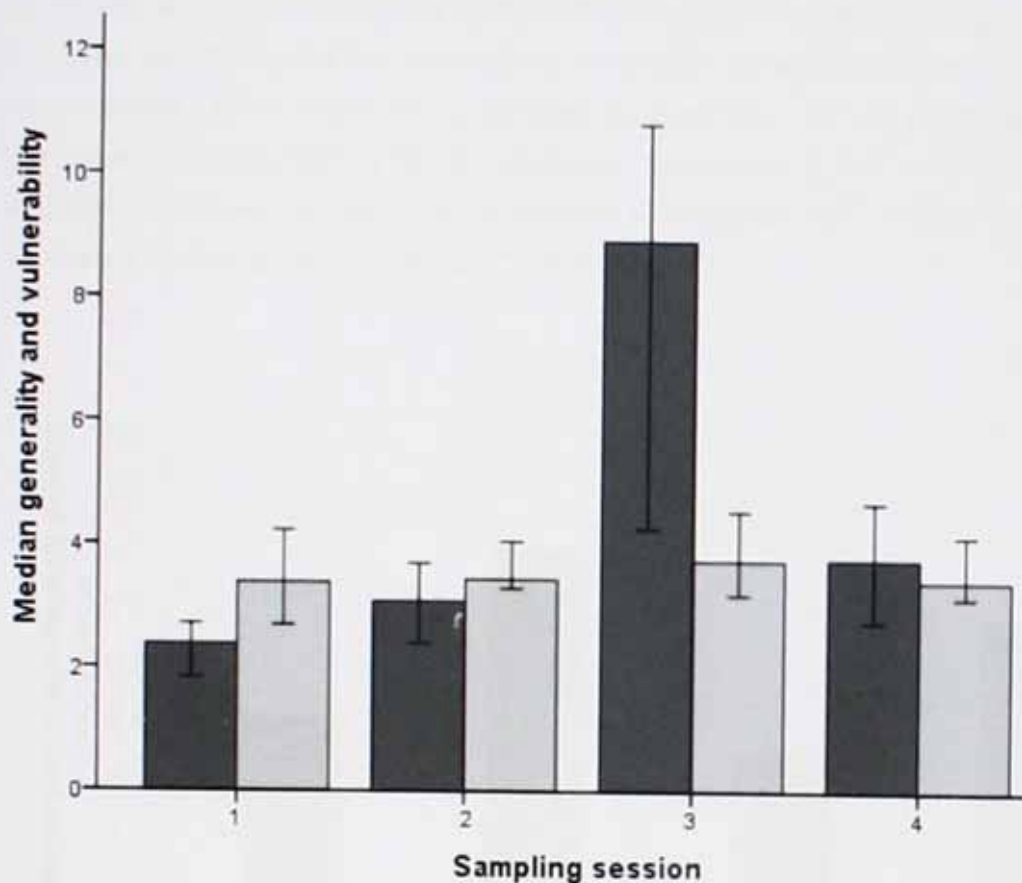
Figure 4.14 Median generality (dark grey bars) and vulnerability (light grey bars)
values ($n = 17$) for the four sampling sessions. Error bars = range.

Table 4.8 Results of *post hoc* tests (Mann Whitney) for differences in median
generality values between paired sessions. Degrees of freedom = 3 in all cases.
Dunn Šidák adjustment of critical values used (Sokal and Rohlf, 1981).

Paired sessions examined	Mann Whitney U value	Z	P (adjusted $\alpha \leq 0.009$) * = significant
1, 2	78.0	-2.29	0.022
1, 3	22.0	-4.22	<0.001*
1, 4	58.0	-2.98	0.003*
2, 3	38.0	-3.67	<0.001*
2, 4	103.0	-1.43	0.160
3, 4	56.0	-3.05	0.002*

Nestedness

The outputs of the 68 WNODF nestedness procedures (involving 34,000 null model simulations) are given in Table 4.9. All 17 properties had at least one session with a significantly nested network. On average, 2.1 ± 0.7 networks were significantly nested per property (51% were nested overall).

Assessing the results according to the different sampling sessions (Figure 4.15) revealed that Session 2 had the highest proportion of significantly nested communities (12 of 17 gardens), followed by Session 4 (10 out of 17 gardens). Less than half were nested for the remaining two sessions. A chi-square test of association showed no significant difference in observed versus expected numbers of nested networks ($X^2 = 5.36$, d.f. 3, $P = 0.15$).
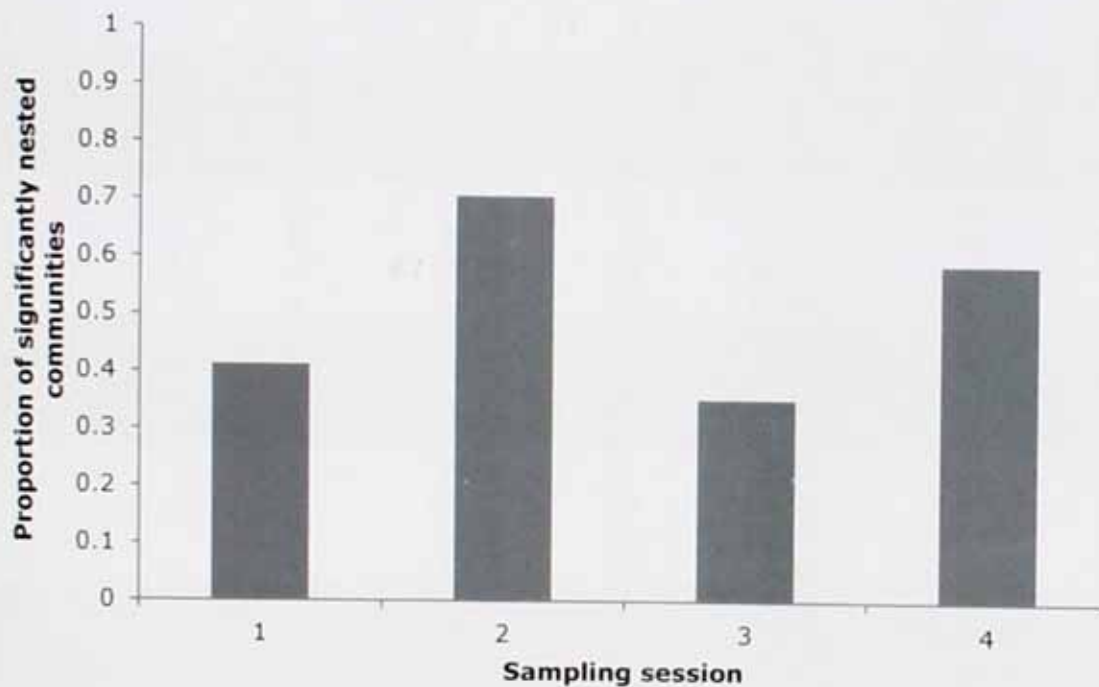
Figure 4.15 Proportion of communities within each sampling session exhibiting significantly nested interaction networks.

Table 4.9 Results of 68 tests for nestedness. *P* values of ≤ 0.05 (in red) denote matrix significantly different from random and therefore nested (Ulrich pers. comm.). Red bold ≤ 0.01.

Property	Session	Flower-visiting insect species	Plant elements	WNODF degree of nestedness	WNODF Z value	P value
AL	1	26	15	4.03	0.02	0.49
AL	2	26	17	6.65	-3.59	**<0.01**
AL	3	23	18	19.73	-3.42	**<0.01**
AL	4	8	5	n.a.	-0.05	0.48
BOU	1	36	22	0.12	-1.50	0.07
BOU	2	31	31	5.83	-4.83	**<0.01**
BOU	3	26	39	19.01	-1.38	0.08
BOU	4	20	16	6.25	-2.11	0.02
CA	1	35	21	5.43	-2.39	0.01
CA	2	35	23	1.79	-0.01	0.50
CA	3	22	24	6.52	-0.40	0.34
CA	4	29	29	8.94	-2.95	**<0.01**
CM	1	31	40	0.54	0.99	0.16
CM	2	26	29	0.93	-0.84	0.20
CM	3	25	55	14.30	-3.46	<0.01
CM	4	19	34	8.74	-2.69	<0.01
CH	1	27	23	5.10	-0.92	0.18
CH	2	33	30	6.83	-3.46	**<0.01**
CH	3	44	44	16.00	-1.18	0.12
CH	4	24	27	12.44	-1.67	<0.05
EN	1	25	12	5.95	-1.43	0.08
EN	2	18	16	3.88	-3.86	**<0.01**
EN	3	41	32	10.62	-2.05	0.02
EN	4	17	28	12.33	-2.56	**<0.01**
FAR	1	31	22	1.97	-3.66	**<0.01**
FAR	2	31	20	6.07	-1.85	0.03
FAR	3	32	32	20.84	-1.03	0.15
FAR	4	22	26	6.12	-1.32	0.09
HOL	1	30	24	4.56	-2.77	**<0.01**
HOL	2	30	29	3.83	-1.38	0.08
HOL	3	37	59	15.65	-1.46	0.07
HOL	4	15	20	9.11	-0.65	0.26
KEL	1	33	23	0.62	0.30	0.38
KEL	2	38	39	4.37	-2.59	**<0.01**
KEL	3	28	75	21.31	-2.16	0.02
KEL	4	22	24	4.87	-2.99	**<0.01**
KIR	1	7	4	n.a.	-2.28	0.01
KIR	2	11	9	13.41	-1.96	0.03
KIR	3	7	6	13.89	-0.04	0.48
KIR	4	5	6	16.00	-0.60	0.27
LAM	1	23	18	1.35	-2.16	0.02
LAM	2	26	25	5.56	-2.61	**<0.01**
LAM	3	35	38	26.40	0.58	0.28
LAM	1	23	18	1.35	-2.16	0.02

Table 4.9 continued

Property	Session	Flower-visiting insect species	Plant elements	WNODF degree of nestedness	WNODF Z value	P value
LW	1	32	25	1.49	-1.60	0.05
LW	2	37	38	2.39	-2.99	**<0.01**
LW	3	30	41	19.62	-0.57	0.28
LW	4	16	18	4.71	1.02	0.15
ST	1	31	21	2.73	0.29	0.39
ST	2	31	28	1.59	-3.43	**<0.01**
ST	3	44	57	13.82	-0.43	0.33
ST	4	27	27	4.48	0.09	0.46
SUL	1	25	19	7.41	-1.75	0.04
SUL	2	30	50	6.70	-0.53	0.30
SUL	3	24	34	4.57	-3.05	**<0.01**
SUL	4	28	37	9.19	-3.58	**<0.01**
UP	1	32	28	3.14	-0.23	0.41
UP	2	39	30	2.99	-0.50	0.31
UP	3	27	48	14.42	-3.38	**<0.01**
UP	4	35	41	10.39	-2.16	**<0.01**
WAD	1	24	11	2.47	-2.54	**<0.01**
WAD	2	22	11	5.80	-3.17	**<0.01**
WAD	3	35	16	14.10	-1.35	0.09
WAD	4	11	7	7.89	-2.77	**<0.01**
WR	1	24	19	2.35	-4.93	**<0.01**
WR	2	31	18	3.66	-4.01	**<0.01**
WR	3	29	22	15.44	0.66	0.25
WR	4	23	16	14.14	-1.91	0.03

Discussion

Relationship between plant availability and observed flower visitors

The sampled gardens contain a remarkably high diversity of plants (Table 4.1).
As only urban garden plant diversity has been considered to date (Smith *et al.*,
2006a, Loram *et al.*, 2008a,b), the results of this study provide the first insight into
how diverse estate gardens can be.

Both flower-visitor species richness and abundance were found to positively
correlate with the number of plant families, genera and elements available. Despite
all taxonomic levels of plants significantly influencing these response variables,
some were of more relevance than others. For example, the number of plant
genera within a sampled area of garden was the best predictor of insect
abundance, $P < 0.001$, $R^2 = 0.35$ (Figure 4.3). The observed relationship between
plants and flower visitors echoes the findings of Fontaine *et al.* (2008) who
considered the response of *Bombus terrestris* individuals to plants in experimental

conditions and Ebeling *et al.* (2008, 2011) who found the number of pollinating insects was 'strongly positively' affected by the number of plant species available in a grassland in Germany. Ebeling *et al.* (2008) noted that, as with the power functions used here (Figures 4.2 and 4.3), the relationship was both non-linear and saturating. Lazaro and Totland (2010) noted the effect plant richness had on specific pollinator guilds. By considering visitation rates to two plant species placed within patches of *Taraxacum officinale* (dandelion) they established that some guilds behaved differently and that in the case of bees, eusocial and solitary species did not respond in similar ways. Similarly, Hegland and Boeke (2006) found that whilst the number of hoverflies responded positively to plant species richness in a temperate grassland, bumblebees did not. Further analysis considering the response of specific guilds to plant richness in gardens will add to these findings.

Notwithstanding the association noted in the current study, plant richness explains only a proportion of the observed insect richness (Figure 4.2). Other factors will be explored in Chapter 5.

During the 2010 field season the assessment of plant abundance was not possible due to time constraints. Further work incorporating the abundance of flower resources in rural gardens into analyses will add to the knowledge gained from this study into how pollinators behave in novel habitats.

Comparing plants available with the number of plants visited

Fewer plant elements were visited than those available (Figure 4.4). In the case of Sessions 2, 3 and 4, the number visited was significantly lower than those available, $P < 0.01$, (Figure 4.5). Whilst Session 1 was also significant, it was less so than the others ($P = 0.04$). One possible explanation for this concerns the availability of flower resources in early spring. At this time flower resources are often scarce (pers. obs.). Optimal foraging theory states that the preference for patches containing high densities of flowers should be the norm for the majority of pollinators (Pyke, 1984). Therefore having arrived at a florally dense patch, foraging is maximised by visiting several (or many) flowers within the area (Hegland and Boeke, 2006). This generates the appearance of heightened use in flower patches within gardens.

A concern in treating the four sampling sessions as distinct was the fact that a small amount of field-work took place on dates a few days beyond the boundary of the previous session. As described in Chapter 2 (2010 field season), this situation arose because of visiting restrictions imposed by some property owners. To check

whether this affected the results, the number of plants available and those visited were plotted according to the date assessed. The outcome mirrored that of the session-wise tests, thus placing confidence in the results obtained (Figure 4.6).

Alien and native plant elements

The majority of plant elements available were classed as alien, ranging from 62% – 79% across the four sampling sessions (Table 4.4), with the percentage of alien plants increasing as the season progressed. A one-way ANOVA revealed that Session 4 had a significantly higher number of alien plant elements than Session 1 ($P < 0.001$). Overall, the mean percentage of alien plant elements was 68 (Table 4.6).

This is remarkably similar to results obtained for gardens in urban areas. For example Loram et al. (2008b) reported that across five UK cities (incorporating 267 gardens), the percentage was 70. Similarly, Smith et al. (2006a) reported that in 61 Sheffield gardens 70% of plants were alien, as were those in a study of home gardens in Mexico City.

Despite some variation between properties and across the seasons (Tables 4.4 and 4.6), the congruence in the overall mean proportion of aliens is a surprising result, raising questions about why this near consistent figure of 70% occurs, regardless of whether gardens are urban or rural, and located in Scotland, Ireland, lowland England or Mexico.

Several authors have noted that urbanisation tends to increase the proportion of alien plant species (Roy et al., 1999, Smith et al., 2006b), although the exact causes have rarely been explored. Whilst this 'urban = alien' rule may hold true for cities (Smith et al., 2006a, Loram et al., 2008b), the majority of the sites sampled in the present work are located many miles from the nearest towns. As such they are not subject to common urban influences and characteristics including the heat island effect and matrices of green spaces and hard surfaces. It is likely that the proportion of aliens found in the gardens surveyed occurs due to two simple factors: plant availability and planting preferences.

Brickell (1999) notes that some 15,000 plant species are available commercially to garden owners in the UK. Regional variation in soil and climate are likely to affect what grows well in an area, thus determining which plants garden centres sell, but overall, garden nurseries almost exclusively stock alien plants (pers. obs.). Many people see their gardens as highly visible extensions of their homes, and are

known to be influenced by what neighbours plant (Goddard *et al.*, 2010). Few choose to fill flower beds and borders exclusively with natives and indeed for many, native flowers only feature as a side-effect of poor weed control. Instead, garden owners can select from a wide range of nursery plants (Smith *et al*, 2006a). Gardening fashions come and go, and the composition of plant communities in the gardens of large estates is unlikely to resemble that of previous times unless an attempt at historical planting is made (e.g. certain beds within the gardens at Kirby and the small Elizabethan garden at Holdenby). Although earlier planting regimes in estate gardens were also likely to contain many aliens (early plant exploration and importation was often initiated and financially underpinned by wealthy landowners, Fisher, 1989), today head gardeners have access to broadly the same plants as those available to the general public. The increasingly common activity of opening country-house gardens to the public adds renewed vigour to the desire to conspicuously exhibit complex planting schemes containing intriguing alien elements.

Notwithstanding the high proportion of alien plants available, flower-visitors do not appear to prefer native plants over their alien neighbours in mixed planting environments. Results of a chi-square test of association revealed that the number of alien and native plants visited by insects did not depart significantly from the number of alien and native plants available (Table 4.5).

Overall, the domination of large rural gardens by alien plant species does not appear to act as a barrier for flower-visiting insects looking to feed there. For example fourteen species of bumblebee were recorded across all sites, representing 58% of the UK total and 93% of those potentially encountered according to current distribution maps (BWARS, 2012 and Appendix VI). In fact, the high richness of insects recorded suggests that the presence of aliens *elevates* the importance of these sites as rich habitats for pollinating insects.

A limitation of the 2010 fieldwork was that the relative abundance of native and alien flowers was not assessed. Also, the assignment of alien or native status to plants followed the definitions given by Stace (1997). This does not take into account plants have become naturalised or are so morphologically similar to their native counterparts that they may be indistinguishable to flower visitors. An example of this is the cultivar *Lamium maculatum* (an alien according to Stace) and the native *L. album*.

Highly visited plant families

Certain plant families emerged as more highly visited than others based on the visitation preference index. Only Session 4 did not have distinct plant families that achieved higher than expected visitation rates. There was little congruence across the seasons with only two families (Asteraceae and Lamiaceae) appearing as highly visited in more than one sampling session (Figures 4.7, 4.8, 4.9 and 4.10). Two plant elements, *Centaurea montana* and *Taraxacum officinale* (both Asteraceae), appeared in two sessions, but the general rule was for different plant elements and families to replace others in importance as the season progressed (Table 4.7). Although a long tail of singletons (plant elements occurring at only one garden in any session) was the rule, the fact that many flowering plants favoured by insects appeared in five or more gardens suggests a level of plant resource homogeneity across sites.

In categorising the elements within the most visited families according to both colour and flower morphology, a picture emerges of highly visited early spring flowers being a mixture of alien and natives that are frequently lilac or blue in colour, and tubular in shape, e.g. *Pulmonaria* sp. and *Glechoma hederacea*. As the season progresses, increasingly more open flowers are preferred from a range of colours with a greater emphasis on alien species. A likely explanation for this is the phenology of the insect visitors recorded. Bumblebees (especially long-tongued species) and solitary bees such as *Anthophora plumipes* are in flight early in the year and are able to exploit resources from a variety of tubular flowers. Both appear to favour blue/lilac plants in spring (pers. obs.). Later in the year, as the diversity and abundance of hoverflies and butterflies increases, the diet breadth of visitors expands and easily alighted flowers with open resources are preferred.

Taraxacum officinale (dandelion) is an interesting example of this 'open-flower' group. Dandelions generally appear in early-spring and are known as a 'cornucopian' flowers (Kevan and Baker, 1983) as they offer copious quantities of nectar and pollen and can attract pollinators from nearby plants (Fontaine *et al.*, 2008, Munoz and Cavieres, 2008, Lazaro and Totland, 2010). They are cosmopolitan weeds that are little tolerated by gardeners who frequently eliminate them with systemic herbicides (pers. obs). Despite their ongoing removal, the current study found that where dandelions were allowed to persist, they were a much visited plant. In the 2010 field season 15 hoverfly, five bumblebee, nine solitary bee and eight butterfly and day-flying moth species, as well as the common honey bee, were recorded visiting them. Across the two sampling years (2010 and 2011) 41 flower-visitor species were recorded visiting this plant element (data not presented). The flowers appeared to be particularly favoured both early

and late in the year (Table 4.7) when forage quantity and quality elsewhere in the gardens may have been at a premium. In Session 4 they were visited at more than 50% of the properties where they occurred (data not presented). In gardens that are routinely managed to a high level, e.g. Coton Manor, *T. officinale* was conspicuous by its absence.

A recommendation arising from this work is that, balanced with the functional needs of a garden, patches of grass (including lawns) should be left unmowed (or at least mowed less frequently) early and late in the season to provide additional forage for flower visitors.

The results of this work on highly visited flower families do not serve as an exhaustive guide to which specific plants should be included in a garden. Rather they act as a reference for land managers, head gardeners and institutions such as The National Trust and English Heritage, who may wish to consider whether the green spaces in their charge are serving biodiversity in the most environmentally profitable way.

Connectance

The connectance values revealed different results depending on the scenario used (see Methods above). Under Scenario 1 (whereby only those plants recorded as interacting with flower-visitors were considered), the median connectance value for Kirby was found to be significantly higher than that of the other properties (Figure 4.11). Under Scenario 2 (where all plants in the sampled area were included, regardless of whether they were visited) no differences in median connectance values were observed (Figure 4.11).

Although the shift from significance in Scenario 1 to non-significance in Scenario 2 is most likely a function of network size - connectance is known to decrease as network size increases (Jordano, 1987, Santamaria and Rodriguez-Girones, 2007, Blüthgen *et al.*, 2008 and Figure 4.12), it raises questions about which scenario is most informative.

To my knowledge, authors reporting connectance values have only performed calculations according to Scenario 1, e.g. Jordano (1987) and Memmott and Waser (2002). This may be because sampling involving pollinators and plants is routinely focussed on a specific insect or plant species, with little or no consideration given to non-target plant elements in the surrounding area (e.g. Potts *et al.*, 2004). The exclusion of plants that are available (but not visited) when calculating

connectance could be seen to undermine the very meaning of the metric: 'Connectance is the number of pair-wise interactions expressed as a fraction of the *total number of interactions possible'* (Winemiller, 1989, p.960). Although in practice it is not possible to census everything at a site (Magurran and McGill, 2011), a regime that fully samples certain patches to include all plants available is desirable (Thompson *et al.*, 2004). By considering plants that are visited versus those that are available (including sub-categories of whether these are alien or native), a better understanding of community interactions can be gained. In the case of gardens, this can help increase our knowledge about how these areas interact with the wider landscape (Smith, 2006a).

As the major limitation of connectivity is its sensitivity to sampling effort, and therefore matrix size (Blüthgen *et al.*, 2008, Banasek-Richter *et al.*, 2009) direct comparison of absolute connectance values with those of other studies as in Tarrant (2010) was not deemed appropriate.

Generality, vulnerability and linkage density

The mean number of plants that flower-visiting insects interacted with was higher than the mean number of insect species that visited each plant (generality 4.5 ± 3.6 versus vulnerability 3.6 ± 1.0, data not presented). Alarcón (2010) found this situation was reversed for networks in meadows within pine forests in the USA (mean generality value = 2.39, mean vulnerability = 8.33). Large generality values indicate that flower-visitors connect with a diverse range of plants (Alarcón, 2010). The difference in generality and vulnerability values between the current study and that of Alarcón (2010) may reflect the underlying habitat type and therefore floral availability. In large rural gardens many flowering plants are present, and generalists such as hoverflies may visit a wide selection of these. In the Alarcón study the number of pollinator species was typically three to four times greater than the number of plant species, a factor that could limit generality values. In the current study some sessions occasionally had higher numbers of pollinators than plants, as per Alarcón's study sites, but no consistent pattern emerged. A mean linkage density value of 4.1 ± 2.0 partners per plant or animal species was recorded across all properties and sessions in the current study.

The suggestion above that large numbers of ubiquitous generalists such as the hoverfly *Episyrphus balteatus* (the marmalade hoverfly) may significantly alter patterns of generality can be considered in the context of the current study. Generalisation did not differ significantly between properties (Figure 4.13), however when considering values on a seasonal basis, Session 3 (which coincides

with the peak occurrence of *E. balteatus*) had significantly higher generalisation values than the other three sessions (Figure 4.14 and Table 4.8). Across sessions two, three and four the marmalade hoverfly interacted with 194 different plant elements (data not presented) making it a 'super-generalist' (Kaiser-Bunbury *et al.*, 2009). This classification has also been applied to the honey bee in a network context; for example Ebeling *et al.* (2008) found honey bees accounted for almost 50% of visits to flowers in a German grassland setting. The super-generalist label for honey bees is not always appropriate however. Lazaro and Totland (2010) found that, despite accounting for half of all visitors, honey bees behaved as specialists, particularly favouring *Taraxacum officinale*. In the current study, honey bees represented only 8.1% of visitors (Chapter 3). They were not such extreme generalists as *E. balteatus*, but neither were they specialists as they interacted with 102 plant elements (data not presented).

The increased generality observed in Session 3 (Figure 4.14) suggests that during summer, mutualistic webs involving flower-visitors and plant species are more complex. Some authors have interpreted this heightened complexity as a product of the higher attractiveness of an area (Ebeling *et al.*, 2011), whilst others have voiced caution when invoking interpretations about generality, stating it is another metric that is highly sensitive to species richness and sampling effort (Tylianakis *et al.*, 2007, Banasek-Richter *et al.*, 2009). A correlation between generalisation values and the size of the respective matrix for the complete 2010 field season found a strong positive association between the two (two-tailed Spearman's rank r = 0.67, n = 68, $P < 0.01$). Suffice to say, although Session 3 show increased complexity, the exact causes cannot easily be explained.

Although the current study incorporated a repeated sampling design across many gardens, it was not without its limitations. A possible weakness is that the quantified links represented only a single year. As flower-visitor dynamics are known to vary between years (Herrera, 1988, Fründ *et al.*, 2010), and not all visits result in a pollination event (Kwak *et al.*, 1996), extending the study to include multiple seasons and/or pollen transport networks would be advantageous (Alarcón *et al.*, 2008, Alarcón, 2010).

Nestedness

One of the aims of this chapter was to establish whether networks of flower-visiting insects and plants in gardens exhibited a nested structure, thus mirroring those in natural settings. Although the prediction was that there would be some temporal differences (Dupont *et al.*, 2009), no presumption could be made that *any* of the

networks would be significantly nested. The WNODF results (Ulrich, 2012) suggest that networks in large rural gardens do indeed exhibit nestedness. With just over 50% of sessions emerging as significant, and all properties having at least one of their four sampling sessions categorised as such, it is reasonable to state that mutualistic links in garden ecosystems, in common with those in grasslands, pine forest meadows and coffee agroforests (Tylianakis *et al.*, 2007, Alarcón, 2010, Gibson *et al.*, 2011), generate non-random, specialist asymmetry (Figure 4.1b).

Ulrich reports on the 'substantial controversy' in the literature relating to the plethora of methods proposed to define, quantify and test patterns of nestedness (Ulrich *et al.*, 2009). Whilst weighted metrics seem the most logical applications to use (and were therefore selected for this work), other researchers, such as Vazquez *et al.* (2007), have suggested that abundance may be responsible for generating asymmetry.

In addition to analyzing the data for this study in WNODF, two other nestedness packages were used (data not presented): the incidence-based NODF package (the non-weighted version of NODF, Ulrich, 2012) and the abundance-based WINE (Weighted-Interaction Nestedness Estimator) package (Galeano *et al.*, 2009), performed in R (R Development Core Team). The former suggested that 72% of the 68 networks were nested (c.f. 51% using WNODF, Table 4.9). The second package (WINE) also inflated the number of significantly nested networks (pers. obs. and Almeida-Neto and Ulrich, 2011), but posed a more significant problem for comparison purposes as matrix size meant reliable results could not be provided for almost 20% of networks examined. In contrast to this, Gibson *et al.* (2011) recorded that weighted and unweighted metrics both returned similar numbers of nested networks (although the datasets examined contained more pollinators than plants and the mean matrix size was just under half that of the current study, 809 ± 601 versus 1,555 ± 1207).

From a temporal perspective, Sessions 2 and 4 both had a higher proportion of significantly nested networks than either Sessions 1 or 3 (Figure 4.15), although a chi-square test of association did not find these to be significantly higher. This suggests that whilst novel ecosystems such as large rural gardens mirror natural environments in terms of exhibiting nested patterns, they do not show a pattern of temporal variation.

The controversy in the literature highlighted by Ulrich *et al.* (2009) also extends to the interpretation of nested patterns and cuts across both natural and novel

ecosystems, raising two questions. Firstly, if, according to James *et al.* (2012), greater nestedness does not imply community persistence, then what do habitats containing networks with many core generalists actually signify? Secondly, if the notion that networks are cohesive and provide pathways for rare species to exist (as well as offering responses in the face of perturbations) is now held in contention (Bascompte *et al.*, 2003; Blüthgen *et al.*, 2008), then what are their real value? The answers to these questions represent further work that goes beyond the scope of this thesis.

Conclusions

The findings of this chapter can be summarised as follows:

- A high diversity of plants exists in the gardens of large English country houses. More than a fifth of the world's plant families appeared in the 17 gardens examined.

- A strong link exists between flower resources and the diversity of insects that visit them. Flower-visitor species number and abundance both increased as flower diversity increased.

- Despite a wide variety of plants being available, only a subset was visited. In early spring a greater proportion of the flowers available were visited than at any other time.

- Approximately 68% of plants in large rural gardens are 'aliens'. A figure of 70% has been recorded in urban gardens from Mexico City to Scotland (Smith *et al.*, 2006a, Loram *et al.*, 2008b). This is the first inventory taken for rural gardens and it returns a remarkably similar level of non-native resources.

- Flower-visiting insects in novel ecosystems such as rural gardens demonstrate no preference for native plants over aliens.

- Few ubiquitous plant families showed high visitation rates in more than one sampling session. Asteraceae and Lamiaceae were the exception to this. In general, ubiquitous, frequently visited early spring flowers were blue to lilac in colour and tubular in shape. As the season progressed more open flowers were preferred.

- Dandelions emerged as important components of the diets of many different insect guilds. 41 species were recorded visiting them. There is the potential for estate managers to leave more of this resource available, particularly early and late in the season.

- Connectance values, calculated according to plants visited and those available, offer two separate measures of the realised links between flower visitors and plants. Under Scenario 1 (plants visited), the garden at Kirby had a significantly higher mean connectance value than others.

- High connectance values are associated with small matrix size. Kirby networks are characterised by low numbers of insects and plants. This generates small interaction matrices and therefore potentially high connectance values.

- Insects interacted with more species of plant than plants did with insects. High generality values signify greater complexity in a network. The high generality observed in sampling session 3 may be a product of the high number of plants and insects recorded.

- Half of all the networks examined were found to be significantly nested. Assessing the implications for this result is problematic as the topic is a major source of controversy.

In summary, large rural gardens offer an array of nectar and pollen to flower-visiting insects. The results of this study suggest that the predominance of alien plant species is no barrier to extensive use by flower visitors. Plant species richness emerges as being positively correlated with insect richness and abundance, and it is tempting to invoke a causal link between the two. The reality is that many other factors that affect both variables may be at play. These include garden management and its effect on the availability of nesting materials, as well as landscape-scale effects (Steffan-Dewenter and Schiele, 2008, Fründ *et al.*, 2010). The latter will be explored further in the next chapter.

Chapter 5

Spatial and seasonal factors affecting the diversity of flower-visitors

Chapter overview

In this chapter flower-visitor diversity is explored in the context of landscape-scale and within-garden factors, with both spatial and temporal aspects considered. The response of individual insect groups is examined, as well as differences within a single group based on nest-site preferences.

Introduction

Ecosystem service provision can be altered by both local and landscape-scale factors (Haenke *et al.*, 2009). Agricultural intensification is one of several anthropogenic changes that can have profound effects on biodiversity and in particular on pollinating insects (Carré *et al.*, 2009, Carvell *et al.*, 2011). Changes resulting from agricultural intensification include increased production on new or existing areas of land, and the decline and fragmentation of semi-natural habitats (Klein *et al.*, 2007, Kremen *et al.*, 2007 and Henle *et al.*, 2008). Taken in isolation or combination these factors have the potential to disrupt the ecosystem service of pollination by affecting flower-visitor presence and abundance, with implications for both wild plants and crops (Klein *et al.*, 2007).

Understanding how different components in the landscape drive the richness and diversity of beneficial flower-visiting insects has received considerable interest in the past (Steffan-Dewenter *et al.*, 2002, Goulson *et al.*, 2010). Remote sensing techniques, the use of digital maps, and the development of multivariate analysis software have supported this enquiry (Söderström *et al.*, 2001, Lepš and Šmilauer, 2003, Schaffers *et al.*, 2008).

Insect interactions with the wider landscape

Flower-visiting insects are known to perceive and respond to landscape structure in different ways according to their dispersal abilities and foraging range (Steffan-Dewenter *et al.*, 2002). Foraging distance is linked to body size, meaning that bumblebees typically fly further than solitary bees (Greenleaf *et al.*, 2007). Different responses to landscape context also arise because of variation in life history traits. As a result, central place foragers such as bumblebees and solitary bees (which gather food and take it back to a central place, the nest) behave differently to butterflies and hoverflies, which visit flowers to feed, but search out specific (often different) plants or locations for egg laying (Hegland and Boeke, 2006).

In the United Kingdom, 70% of the total land area available is used for agriculture (Defra, 2011). In recognizing that intensively farmed areas can potentially be hostile environments for pollinators, agri-environment schemes (which include financial rewards for farmers who plant flower-rich strips) have been introduced in Europe and North America (Fuentes-Montemayor *et al.*, 2011). As a consequence, a strong research focus has developed to assess the value of these schemes for beneficial insects (Haenke *et al.*, 2009, Carvell *et al.*, 2011, Fuentes-Montemayor *et al.*, 2011). Emerging from such studies is the view that generalized interpretations about pollinator responses to landscape-scale factors are rarely appropriate as different groups and guilds respond in different ways (Jauker *et al.*, 2009). In addition, it has been suggested that such interpretations can lead to 'erroneous recommendations to landscape planning and conservation' Jauker *et al.* (2009, p.553). Instead, insect responses to landscape variables should be assessed using individual groups and by incorporating several spatial scales (Jauker *et al.*, 2009).

Despite the obvious benefits of considering a range of insect groups usually only one or two are the focus for research. For example, Schweiger *et al.* (2007) and Haenke *et al.* (2009) considered only hoverflies, Fuentes-Montemayor *et al.* (2011) recorded farmland moths, and Steffan-Dewenter *et al.* (2002) and Carré *et al.* (2009) analyzed bumblebees, solitary and honey bees. Exceptions to this include Söderström *et al.* (2001), Hegland and Boeke (2006) and Schaffers *et al.* (2008), all of which considered multiple (but different) groups.

Even when a range of taxa are considered, changes in temporal responses to wider landscape factors are rarely considered, with many studies collecting data over only a few months. For example Haenke *et al.* (2009) and Jauker *et al.* (2009) gathered data in only June and July, but see Hatfield and LeBuhn (2007), who considered the seasonal aspect of bumblebee occurrence. To my knowledge no published accounts exist of flower-visitor responses to landscape-scale factors involving multiple groups over multiple spatial scales which also take a temporal perspective. **On this basis it is predicted that the insect groups observed in large rural gardens will respond to landscape variables in different ways across the season.**

Gardens within the wider landscape

Gardens are known to support a diverse range of insects (Owen, 2010). As discussed in Chapter 3, much knowledge is derived from work assessing urban and suburban gardens, with virtually nothing known about their rural counterparts.

Gardens often support a higher density of bumblebee nests than neighbouring semi-natural environments (Osborne *et al.*, 2008b). Additionally, they emerge as the land-use class exerting the greatest effect on the success of *Bombus lapidarius* and *B. pascuorum* nests (Goulson *et al.*, 2010). Notwithstanding the potential benefits rural gardens may bring by supporting pollinators through provision of forage and nesting resources, work to assess whether these insects might spill-over into neighbouring agricultural areas is rare. The research of Samnegard *et al.* (2011) to assess the effect of distance from rural gardens on the abundance of wild bees and the pollination success of a single plant *Campanula persicifolia* is a notable exception to this.

The choice of spatial scale

Selecting the appropriate landscape-scale depends on the insect group of interest. As indicated above, this can relate to both insect body-size and life history traits. Hadley and Betts (2012, p.535) note that 'landscape spatial scale must be justified in biological terms and should be relevant to daily foraging movements and large spatial-scale population dynamics'.

With the exception of honey bees, the foraging range of bumblebees is better described than most other groups, although repeat studies exist for only a few species (Osborne *et al.*, 2008a). Assessments of bumblebee flying distance capacity have been made using several methods including homing experiments, pollen analysis, mark-release-recapture techniques and harmonic radar (Osborne *et al.*, 1999). Bumblebees generally cover between several hundred metres to several kilometres in search of food (Morandin and Winston, 2006, Westphal *et al.*, 2006). Solitary bees, on the other hand, may only forage within a few hundred metres (Morandin and Winston, 2006, Haenke *et al.*, 2009, Jauker *et al.*, 2009). **It is predicted that bumblebees and solitary bees will respond to landscape-scale variables at different spatial scales. In particular, it is expected that proportions of landscape components within larger circles around the centre of sampling sites will offer a better explanation for observed bumblebee richness and abundance than smaller circles.**

Many moths disperse over only short distances (Fuentes-Montemayor *et al.*, 2011). Although some butterfly species are known to migrate many kilometres, little is known about how most species respond within smaller landscape scales (Chinery, 1989). Fuentes-Montemayor *et al.* (2011) noted that both micro and macro moths showed strong responses to landscape variables at a 250m scale from a centroid, whilst Öckinger *et al.* (2009) focussed on the importance of habitat quality

regardless of scale for both nectaring and ovipositing behaviour. **It is predicted that butterflies and day-flying moths will respond to landscape-scale variables in less predictable ways than bees as they are not central place foragers, and that finer spatial scales may be more important than larger scales.**

In parallel with butterflies and day-flying moths, hoverflies also utilise the landscape in a different way to bees. Their response may be further complicated by the wide variety of larval feeding preferences that exist (Rotheray and Gilbert, 2011 and Chapter 3 of this work). Additionally, hoverflies exhibit a diverse range of body sizes, are often highly mobile, and have excellent vision (Haenke *et al.*, 2009). Added to this is the presence of migrant species in summer, such as *Episyrphus balteatus* and *Scaeva pyrastri*, which can occur in great numbers (Sutherland *et al.*, 1999, Dipterists Forum, 2012). Haenke *et al.* (2009) note that hoverflies concentrate on the most rewarding resources available in the landscape, particularly as the proportion of arable land increases, and that these effects are more noticeable at spatial scales of 0.5 – 1km rather than at 2km or 4km. **It is therefore predicted that the response of hoverflies to plant resources in gardens will be stronger than individual land-use categories in the wider landscape. If a landscape-scale effect is present, this is likely to be revealed within smaller circles.**

The competing forces of landscape-scale and within-garden factors

In Chapter 4 the species richness and abundance of flower-visitors was noted to be significantly correlated with the richness of plants available (Figures 4.2 and 4.3). A key finding emerging from Chapter 4 is that whilst plant richness offers a partial explanation for the richness and abundance of the insects observed, other landscape-scale factors are also likely to be involved. **It is predicted that landscape-scale factors will be more important for large-bodied central place foragers such as bumblebees, whilst local plant assemblages make take priority for hoverflies and butterflies.**

For insect groups with short foraging ranges (such as solitary bees), local landscape factors relating to nest-site suitability may play an important role alongside plant species richness and nearby landscape characteristics. Partitioning an insect group according to nesting characteristics may reveal more than by analyzing the group as a whole (Krauss *et al.*, 2003). **It is predicted that ground-nesting and cavity-nesting solitary bees will respond differently to environmental factors.**

Analyzing complex datasets

Various statistical techniques are available for assessing the response of insect species to multiple environmental factors. These include multiple regression, general linear models and generalised linear and mixed effects models (Shaw, 2003). These methods are popular when species richness or abundance data are bulked across samples, giving a single dependent variable to test against multiple causative factors e.g. Hatfield and Lebuhn (2007), Jauker *et al.* (2009) and Carvell *et al.* (2011). If, however, the analysis benefits from multiple dependent variables being included, then ordination using direct gradient analysis such as redundancy analysis (RDA) or canonical correspondence analysis (CCA) can help combine numerous species with many environmental variables (Jongman *et al.*, 1995, Lepš and Šmilauer, 2003). These multivariate methods benefit from the lack of assumptions made about the distribution of the species abundance values, as well as giving good results when only patchy data are available (Jongman *et al.*, 1995, Leps and Smilauer, 2003). In addition, tests for significance (Monte Carlo permutations) can be calculated together with strong visual representations obtained when ordination diagrams are produced (Ter Braak and Šmilauer, 2002).

Aims

The aim of this chapter is to consider how spatial and temporal variation in local and landscape-scale factors affect flower-visitors in the gardens of seventeen large English country houses. Specifically the chapter seeks to answer the following questions:

1. Do insect groups respond to landscape variables at different spatial scales?

2. Are seasonal patterns associated with responses to landscape variables discernible?

3. Are some flower-visitor groups more responsive to landscape variables than others, regardless of scale?

4. Which is the more important driver for flower-visitor presence in gardens: landscape composition or plant richness?

5. Do life history traits, such as nest site preferences, provide insights into which local-scale factors have the greatest influence on the composition of solitary bee communities in walled gardens?

Methods

Study sites and timing of sampling

The gardens of 17 properties in four counties in lowland Central England were used for the study. In 2010 all 17 were sampled four times, with a subset of nine walled gardens sampled three times in 2011. Sampling took place between April and September in both years. Full details of the sites and methods for assessing flower-visitors and plant richness and abundance are given in Chapter 2 (2010 and 2011 field seasons).

Landscape-scale variables

2010 data (17 properties)

Landscape-scale variables were assessed using digital Ordnance Survey mastermaps (EDINA, 2012) overlain with the 2007 Countryside Survey Landcover vector map (NERC, 2011) in ArcGIS software (ESRI, 2011). The centre of each of the seventeen houses was identified and concentric circles of 750m, 1,500m and 3,000m radius drawn around each house point. The areas within each of the three circles categorised as 'arable and horticulture' (AH), 'broadleaved woodland' (BLW), 'built up areas and gardens' (BUG), 'fresh water' (FW), 'improved grassland' (IG) and 'low-productivity grassland' (LPG) were calculated. An example of a single site overlaid with circles of different radii and individual land cover parcels is given in Figure 5.1. The values in the category 'built up areas and gardens' were adjusted down in each case by removing the area of garden sampled. The purpose of this was to reveal whether the presence of other gardens nearby had an effect on the insect diversity observed at the properties sampled. For each spatial scale the percentage contribution of each of the six categories was calculated. Percentages were arcsine transformed before use in analyses (Sokal and Rohlf, 1981).

Figure 5.1 Use of digital maps to assess land cover at different spatial scales using ArcGIS software (ESRI, 2011). **A**: For illustration, two circles of radii 750m (pink) and 1,500m (blue) are shown around the centre of Canons Ashby House (red point). **B**: The same two circles are overlaid with the Countryside Survey Landcover map (NERC, 2011), with each land parcel attributed to a land use category. Scale bar = 750m.

2011 data (9 walled gardens)

Landscape-scale factors were quantified by creating two concentric polygons at 500m and 750m from the perimeter of the wall at each garden, using the same digital maps and software used for the 2010 data. Within each of the two polygons the total land categorised as 'arable and horticulture', 'broadleaved woodland' and 'improved grassland' was summed and calculated as a percentage. Percentages were arcsine transformed as above.

Within-garden variables

2010 data

Plant richness (assessed as the number of plant genera available in each garden at each of four sampling sessions) was used as the within-garden variable for the 2010 flower visitor data (see Chapter 4, Table 4.1).

2011 data

Within-garden data for the 2011 flower-visitor dataset comprised plant richness (assessed as the log-transformed number of plant genera available in each walled garden at each of three sampling sessions) as well as blossom cover (log-transformed values of the area of flower resources available in m^2 – see Chapter 2, 2011 field season). In addition, the percentage of beds and borders within each

walled garden was calculated by using OS Mastermaps (EDINA, 2012) overlain with Bing Aerial maps in ArcGIS software (ESRI, 2011). Also calculated was the combined area of the south and east facing walls within each garden. This was done by measuring out wall lengths using a hand-held GPS device (Garmin Etrex 10) and calculating heights with a clinometer (Silva ClinoMaster).

Data analysis (2010 data)

The relative contribution of landscape-scale and local-scale variables to flower-visitor species richness was assessed using the multivariate analysis software Canoco Version 4.52 (Ter Braak and Smilauer, 2011). For the 2010 data, flower visitors were assessed in each of the four sampling sessions according to four groups: bumblebees (BB), butterflies and day-flying moths (BDM), hoverflies (HF) and solitary bees (SB). The sampling sessions were treated separately to incorporate differences in plant species richness across the season.

Exploratory analysis

To establish which method of direct gradient analysis to use (linear or unimodal), gradient lengths were assessed using detrended correspondence analysis (DCA) on log-transformed ($n + 1$) dependent data (Lepš and Šmilauer, 2003). As the gradient lengths were all short (considerably less than 4.0 SD recommended for unimodal techniques), the linear RDA method was the most appropriate (Ter Braak and Smilauer, 2002).

Exploratory RDAs were performed on each insect group for each session at each of the three spatial scales ($n = 48$). For each RDA the environmental variables assessed were the six landscape categories (listed above), together with the number of plant genera available. The response (dependent) variables were the log-transformed ($n + 1$) number of individuals recorded for each insect species at each property. Automatic forward selection was used to identify environmental variables making the greatest contribution. To test the significance of these variables the software was set to run 499 Monte Carlo permutation tests. These tests shuffle the environmental variables and attribute them at random to any of the dependent variables. The null hypothesis is that observed variation in the dependent variable is independent of the underlying environmental variables. The null hypothesis is rejected for environmental variables returning statistically significant results ($P \leq 0.05$).

Redundancy analysis at specific spatial scales

For each insect group and sampling session ($n = 16$) the spatial scale with the highest amount of variability explained by the first two axes, i.e. the cumulative

percentage explained by the first two eigenvalues, was selected as per Kleijn and Langevelde (2006). These sessions were further examined by performing repeat RDAs (this time without forward selection, with the results plotted as ordination diagrams using CanoDraw (Ter Braak and Šmilauer, 2011). Due to space limitation only ordination diagrams for significant RDA models are presented.

Variance partitioning

To explore the possible overlap between the six landscape categories used in the 2010 data analysis (grouped together and denoted as X_1 in Figure 5.2) and the within-garden variable 'number of session-specific plant genera available' (X_2 in Figure 5.2), the variance partitioning procedure described by Borcard *et al.* (1992) was used. This method returns the individual effect and overlap of environmental variables split into two natural subsets. The percentage contribution of a subset (e.g. **A** in Figure 5.2) is assessed by calculating the difference between the marginal effect of X_1 and that of its conditional effect when the second subset X_2 is accounted for. This is achieved by re-running the redundancy analysis and noting the sum of the eigenvalues of all canonical axes for X_1 measured when X_2 is considered as a covariable. The procedure is reversed to obtain the percentage contribution represented by **B**. The overlap (**C** in Figure 5.2) is obtained by subtracting the sum of **A** and **B** from the amount of variability obtained from an ordination when both X_1 and X_2 are combined (without the use of covariables). The variance partitioning is completed by placing the results in the context of the unexplained (residual) variance (**D**) (Lepš and Šmilauer, 2003).
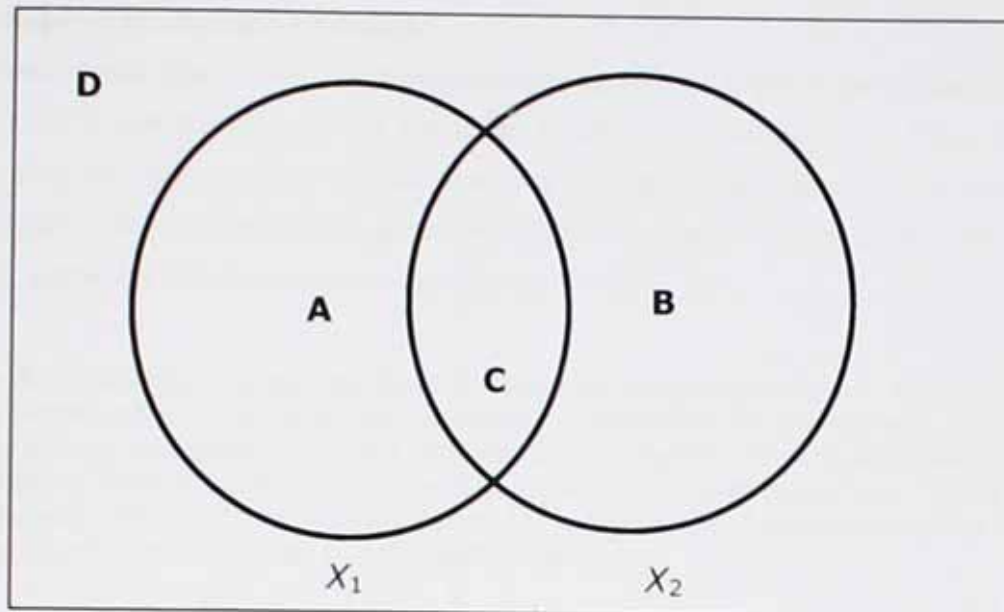
Figure 5.2 Venn diagram illustrating the partitioning of variance in the flower-visitor group data according to the contribution of two subsets of environmental variables (X_1 = landscape-scale variables and X_2 = within-garden plant genera in the session of interest) using the methods of Borcard *et al.* (1992). **A** represents the variance explained by X_1 using X_2 as a covariable, with **B** showing the reciprocal position. **C** is shared variance. **D** represents unexplained (residual) variance. After Lepš and Šmilauer (2003).

Data analysis (2011 data)

Response of an insect group according to differences in nesting biology

To assess whether separation of a group of insects based on their nesting biology delivers insights into local-scale effects, solitary bees recorded within the nine walled gardens in 2011 were used. Due to the low number of solitary bees recorded in the third sampling session only sessions one and two were used. Bees in each session were classified according to whether they were either ground or cavity nesting (BWARS, 2012). The response of each nesting group (log-transformed $n + 1$ data) to three landscape-scale and four within-garden factors was assessed using stepwise forward multiple regression. Bed and border area percentages were arcsine transformed before use in analyses. Standard checks on the results were made according to Field (2009).

Results

Overview of landscape variables

The three landscape-scale categories accounting for the highest percentage of land use for 2010 and the same three variables for 2011 are quantified in Table 5.1. Depending on year and spatial scale the two highest categories were for arable and horticulture (AH) and improved grassland (IG). The mean values for the within-garden variables for the two years are given in Table 5.2.

Table 5.1 Landscape-scale variables for the two sampling seasons (2010 and 2011) showing the three land-use categories accounting for the highest percentage of area within concentric polygons around the properties. AH = arable and horticulture, BLW = broadleaved woodland, IG = improved grassland. [1] Area based on a defined radius from the main house (17 properties); [2] area based on a defined distance from the outer wall of nine walled gardens.

2010

Radius of area[1]	AH (%)			BLW (%)			IG (%)		
	mean	SD	range	mean	SD	range	mean	SD	range
750m	40.2	14.0	15.6–63.6	9.4	7.6	1.0-23.0	45.5	11.3	26.2-67.7
1500m	55.7	13.9	24.8-81.1	6.7	4.1	1.0-13.6	30.5	9.6	13.5-43.3
3000m	57.9	9.0	41.8-76.7	5.3	4.0	1.9-17.1	28.7	7.1	17.4-43.0

2011

Radius of area[2]	AH (%)			BLW (%)			IG (%)		
	mean	SD	range	mean	SD	range	mean	SD	range
500m	31.4	17.3	8.7-56.4	13.8	10.2	3.3-30.5	50.3	15.1	30.9-81.7
750m	43.0	18.0	15.2-69.1	10.2	6.9	2.4-20.2	42.0	13.0	22.1-63.8

Table 5.2 Within-garden variables for the two field seasons (2010 and 2011) showing the mean number of plant genera for Sessions 1 – 4 (2010 field season) and mean number of plant genera and mean blossom density for Sessions 1 and 2 (2011 field season). The mean area of beds and borders and the mean combined area of the south and east facing walls are also given for the 2011 field season.

2010

Number of plant genera		Session 1	Session 2	Session 3	Session 4
	mean	25.9	57.1	57.1	46.4
	SD	9.0	19.0	23.2	20.0
	range	10.0-42.0	14.0-91.0	12.0-88.0	14.0-84.0

2011

Number of plant genera		Session 1	Session 2	Session 3	Session 4
	mean	13.8	35.4	-	-
	SD	8.2	22.1	-	-
	range	8.0-34.0	10.0-83.0	-	-
Blossom cover (m^2)					
	mean	13.9	49.6	-	-
	SD	15.1	57.9	-	-
	range	0.8-34.4	1.2-175-2	-	-
Beds and borders (% of walled garden)		All sessions			
	mean	18.0	-	-	-
	SD	22.8	-	-	-
	range	0.2-75.1	-	-	-
Combined area of the south and east facing walls (m^2)		All sessions			
	mean	350.0	-	-	-
	SD	148.8	-	-	-
	range	115.2-570.0	-	-	-

Exploratory redundancy analysis

The results of the redundancy analysis for each group per session according to each of three spatial scales for the 2010 data are given in Table 5.3. The shaded cells represent the highest variation explained by the first two axes and are therefore the spatial scale that is deemed to have the most influence on the diversity of flower-visitors observed.

Table 5.3 Results of redundancy analysis for each insect group across four sampling sessions (2010 data) at three spatial scales. BB = bumblebees, BDM = butterflies and day-flying moths, HF = hoverflies and SB = solitary bees, AH = arable and horticulture, BLW = broadleaved woodland, BUG = built up areas and gardens, IG = improved grassland, LPG = low productivity grassland, PltGen = plant genera. ns = no significant environmental variables. Shaded cells = highest explained variation hence scale used for further exploration.

Insect group (session)	750m		1500m		3000m	
	Variation explained	Significant envir. factors (individual contribution to variation), F values and sig.	Variation explained	Significant envir. factors (individual contribution to variation), F values and sig.	Variation explained	Significant envir. factors (individual contribution to variation), F values and sig.
BB (1)	38.1	BLW (0.17) 3.05, $P = 0.01$	44.8	BUG (0.19) 3.53, $P < 0.01$ LPG (0.11) 2.20, $P < 0.05$	40.8	LPG (0.17) 3.03, $P = 0.02$ BLW (0.16) 3.31, $P < 0.01$
BB (2)	30.1	ns	29.6	ns	44.4	BLW (0.18) 3.26, $P < 0.01$ IG (0.16) 3.32, $P = 0.03$
BB (3)	26.8	ns	28.7	ns	41.4	BLW (0.21) 3.90, $P < 0.02$
BB (4)	54.0	PltGen (0.37) 8.70, $P < 0.01$	58.2	PltGen (0.37) 8.70, $P < 0.01$ BUG (0.12) 3.37, $P < 0.02$	50.1	PltGen (0.37) 8.70, $P < 0.01$
BDM (1)	27.5	AH (0.13) 2.23, $P < 0.05$	27.6	ns	26.0	ns
BDM (2)	18.8	ns	23.4	ns	25.4	BLW (0.13) 2.32, $P = 0.02$
BDM (3)	36.8	AH (0.15) 2.68, $P < 0.01$	33.6	IG (0.17) 3.00, $P < 0.01$	32.6	AH (0.17) 3.14, $P < 0.01$
BDM (4)	31.3	ns	31.4	IG (0.15) 2.61, $P < 0.03$	31.3	ns

147

Table 5.3 continued

Insect group (session)	750m		1500m		3000m	
	Variation explained	Significant envir. factors (individual contribution to variation), F values and sig.	Variation explained	Significant envir. factors (individual contribution to variation), F values and sig.	Variation explained	Significant envir. factors (individual contribution to variation), F values and sig.
HF (1)	23.6	ns	26.9	BUG (0.11) 1.91, $P < 0.05$	30.6	BUG (0.12) 2.04, $P < 0.03$
HF (2)	23.7	ns	25.5	ns	25.2	ns
HF (3)	45.5	IG (0.17) 3.08, $P < 0.04$ BUG (0.13) 2.77, $P < 0.03$	35.5	AH (0.16) 2.79, $P < 0.05$	27.4	ns
HF (4)	35.7	PltGen (0.16) 2.87, $P < 0.02$	31.4	PltGen (0.16) 2.87, $P < 0.02$	30.1	PltGen (0.16) 2.87, $P < 0.02$
SB (1)	23.8	ns	27.9	BLW (0.14) 2.48, $P = 0.02$	32.4	BLW (0.13) 2.15, $P < 0.04$
SB (2)	27.2	ns	25.2	ns	25.0	ns
SB (3)	28.9	ns	26.1	ns	25.4	ns
SB (4)	30.5	ns	28.3	ns	26.3	ns

Redundancy analysis at specific spatial scales

Using the results in Table 5.3, secondary RDAs were performed on the landscape scale showing the most explained variance. Full details of the significance of the first and subsequent axes, together with correlations between environmental variables and axes 1 and 2 are given in Table 5.4. Ordination diagrams for the five significant models (bumblebees - Sessions 1, 2 and 4 and Session 3 for both butterflies and day-flying moths and hoverflies) are presented in Figures 5.3, 5.4, 5.5, 5.6 and 5.7.

Figure 5.3 Ordination diagram created after redundancy analysis using the 2010 Session 1 bumblebee data at a 1,500m spatial scale. Red arrows indicate environmental variables, blue indicate individual species. Species names are composed of *Bom* (*Bombus*) plus three or four letters from the species, e.g. *Bom_lap* = *Bombus lapidarius*. Full species names are listed in Appendix VI.

Figure 5.3 shows that the first ordination axis is positively correlated with an increasing area of land categorised as 'built up areas and gardens' (BUG) and 'broadleaved woodland' (BLW) and negatively correlated with an increasing area of 'low productivity grassland (LPG), whilst the second is positively correlated with an increasing area of 'arable and horticultural' (AH) land and 'fresh water' (FW). The

first axis explains 30% of the variation in the bumblebees observed ($F = 3.83$, $P = $ <0.01). The sum of all canonical axes (including those not shown) explains 57% of variation ($F = 1.68$, $P = 0.03$). Bumblebee abundance in early spring is positively correlated with an increased number of plant genera available in the areas sampled as well as responding positively to the landscape variable 'arable and horticulture'. As the latter increases, some species of bumblebee show an increased presence in gardens.
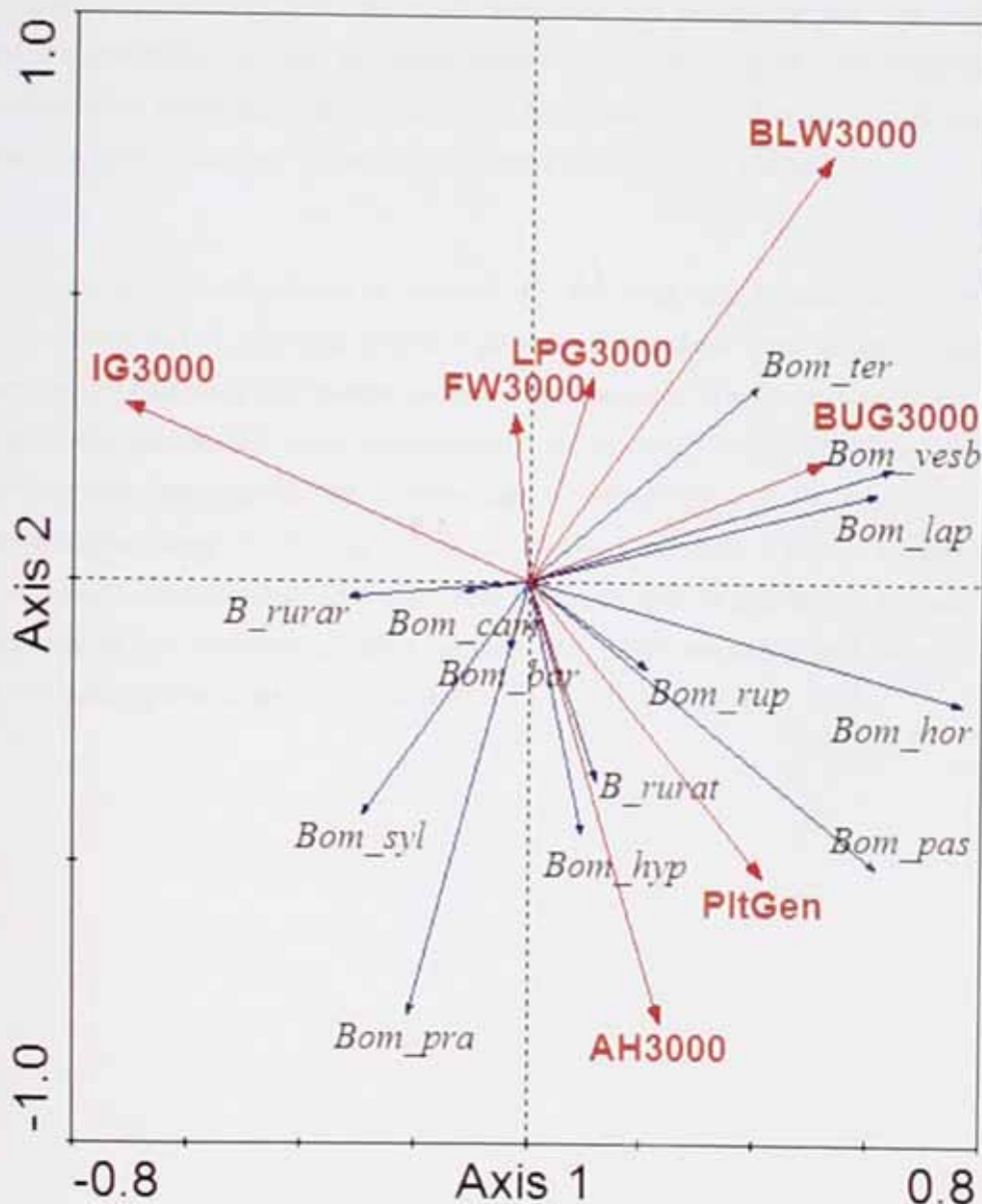
Figure 5.4 Ordination diagram created after redundancy analysis using the 2010 Session 2 bumblebee data at a 3,000m spatial scale. Red arrows indicate environmental variables, blue indicate individual species. Species names are composed of *Bom* (*Bombus*) plus three or four letters from the species, e.g. *Bom_lap* = *Bombus lapidarius*. Full species names are listed in Appendix VI.

In the ordination diagram describing the response of bumblebees in Session 2 (Figure 5.4) the first axis is positively correlated with an increasing area of land categorised as 'broadleaved woodland (BLW) and negatively correlated with 'improved grassland' (IG), whilst the second is also positively correlated with an increasing area of BLW and negatively correlated with 'arable and horticulture' (AH). The first axis explains 27% of the variation in the bumblebees observed ($F = 3.26$, $P = 0.05$). The sum of all canonical axes (including those not shown) explains 59% of variation ($F = 1.82$, $P = 0.02$). Bumblebee abundance in early summer is positively correlated with increased broadleaved woodland and the number of plant genera available, as well as responding negatively to both improved and low productivity grassland. As 'arable and horticulture' land use increases, some species of bumblebee show an increased presence in gardens.

In Figure 5.5 (bumblebees in Session 4), the first axis is positively correlated with an increase in the number of plant genera available in the sampled area, whilst the second is positively correlated with an increase in 'arable and horticulture' (AH) and negatively correlated with 'broadleaved woodland' (BLW). The first axis explains 48% of the variation in the bumblebees observed ($F = 8.26$, $P = 0.03$). The sum of all canonical axes (including those not shown) explains 71% of variation ($F = 3.07$, $P = 0.008$). Bumblebee abundance in late summer is positively correlated with an increase in the number of plant genera (Plt_gen) available and responds negatively to increasing amounts of AH and BLW.
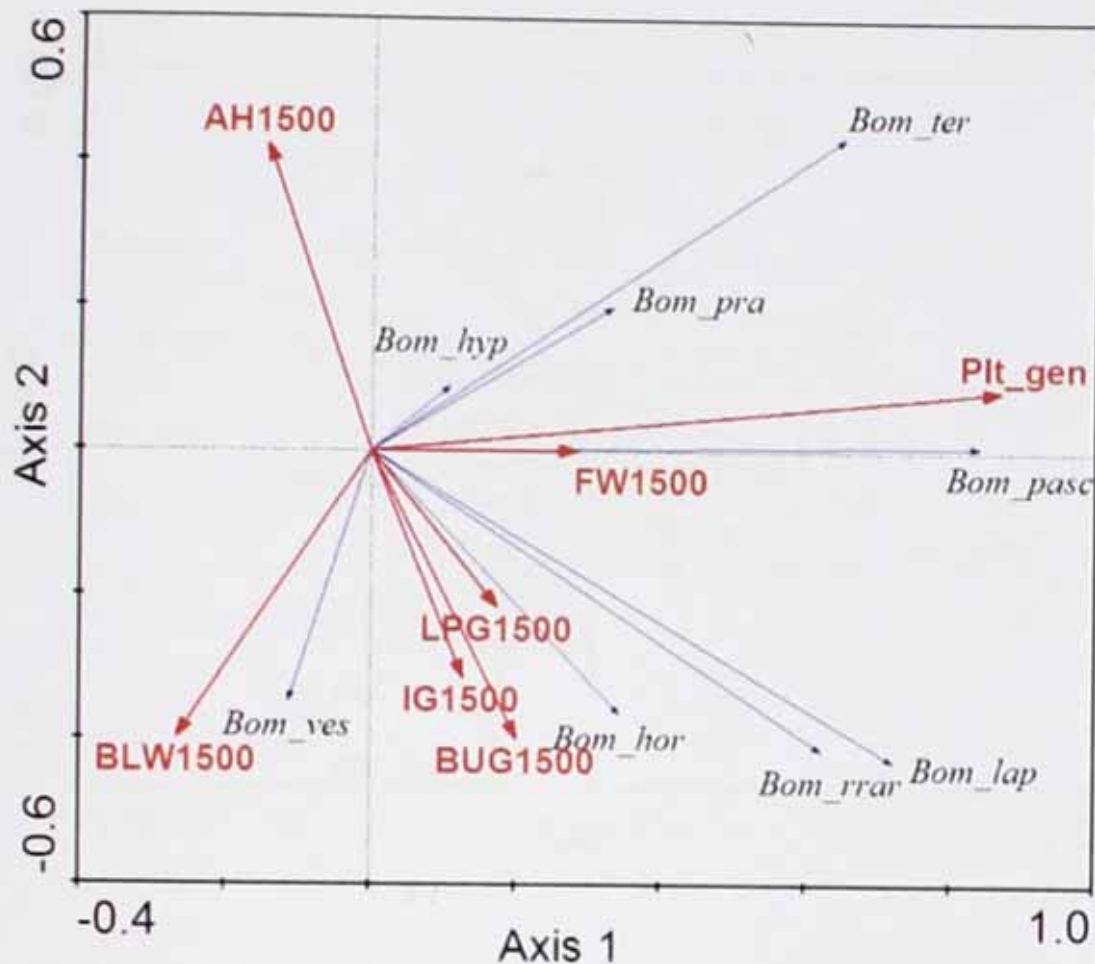
Figure 5.5 Ordination diagram created after redundancy analysis using the 2010 Session 4 bumblebee data at a 1,500m spatial scale. Red arrows indicate environmental variables, blue indicate individual species. Species names are composed of *Bom* (*Bombus*) plus three or four letters of the species, e.g. *Bom_lap* = *Bombus lapidarius*. Full species names are listed in Appendix VI.

For butterflies and day-flying moths in Session 3 (Figure 5.6), the first axis is positively correlated with an increase in the landscape variable 'improved grassland' (IG) and negatively correlated with land categorised as 'arable and horticulture' (AH), whilst the second is positively correlated with an increasing area of 'fresh water' (FW) and negatively correlated with 'broadleaved woodland' (BLW). The first axis explains 23% of the variation in the butterflies and day-flying moths observed ($F = 2.69$, $P = 0.01$). The sum of all canonical axes (including those not shown) explains 55% of variation ($F = 1.59$, $P = 0.01$). Butterfly and day-flying moth abundance in summer is positively correlated with an increase in grassland (improved and low productivity) and increasing amounts of broadleaved woodland. Some species are negatively affected by, or invariant to, an increase in the area of land described as arable and horticulture.
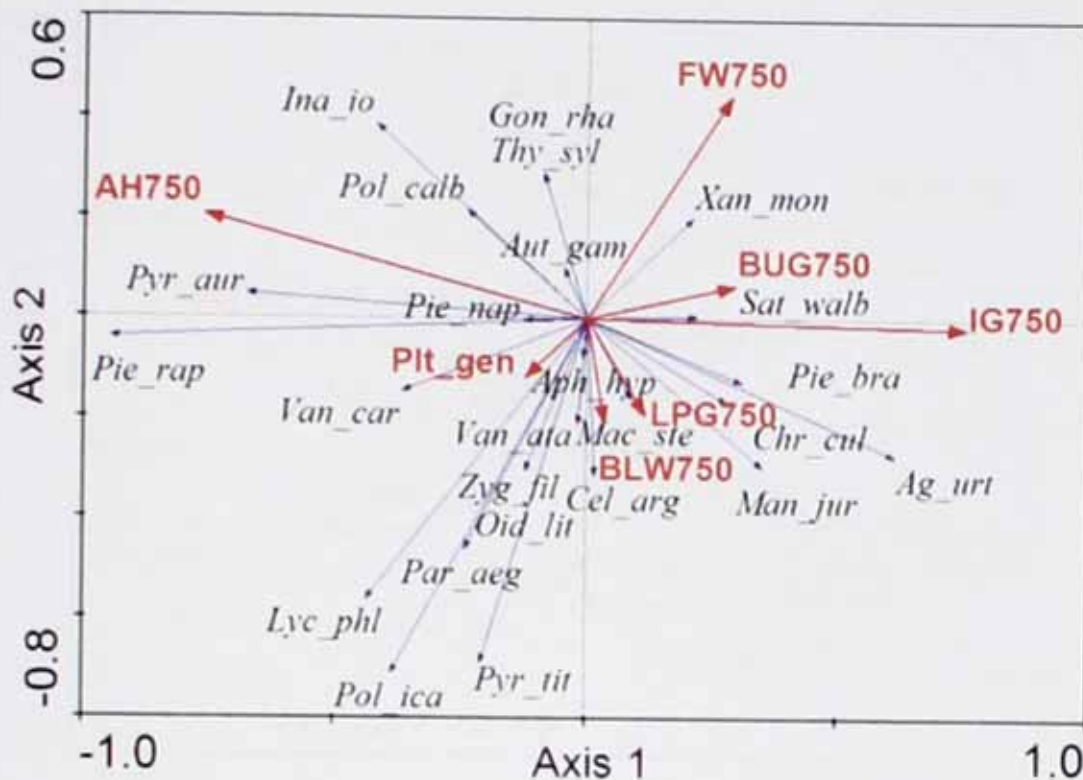
Figure 5.6 Ordination diagram created after redundancy analysis using the 2010 Session 3 butterfly and day-flying moth data at a 750m spatial scale. Red arrows indicate environmental variables, blue indicate individual species. Species names are composed of the first three letters of the genus followed by the first three or four of the species, e.g. *Pie_rap* = *Pieris rapae*. Full species names are listed in Appendix VI.

Figure 5.7 shows the response of hoverflies in Session 3 to landscape variables. The first axis is positively correlated with an increase in the landscape variable 'improved grassland' (IG) and negatively correlated with the land category 'arable and horticulture' (AH), whilst the second is positively correlated with an increasing area of IG and negatively correlated with the number of plant genera in the area sampled (Plt_gen). The first axis explains 39% of the variation in the hoverflies observed ($F = 5.72$, $P = 0.03$). The sum of all canonical axes (including those not shown) explains 58% of variation ($F = 1.75$, $P = 0.05$). The presence and abundance of some hoverfly species in summer is positively correlated with an increase in land categorised as arable and horticulture as well as the number of plant genera in the sampled area. An increase in the amount of improved grassland and nearby built areas and gardens negatively affects the presence of certain species.
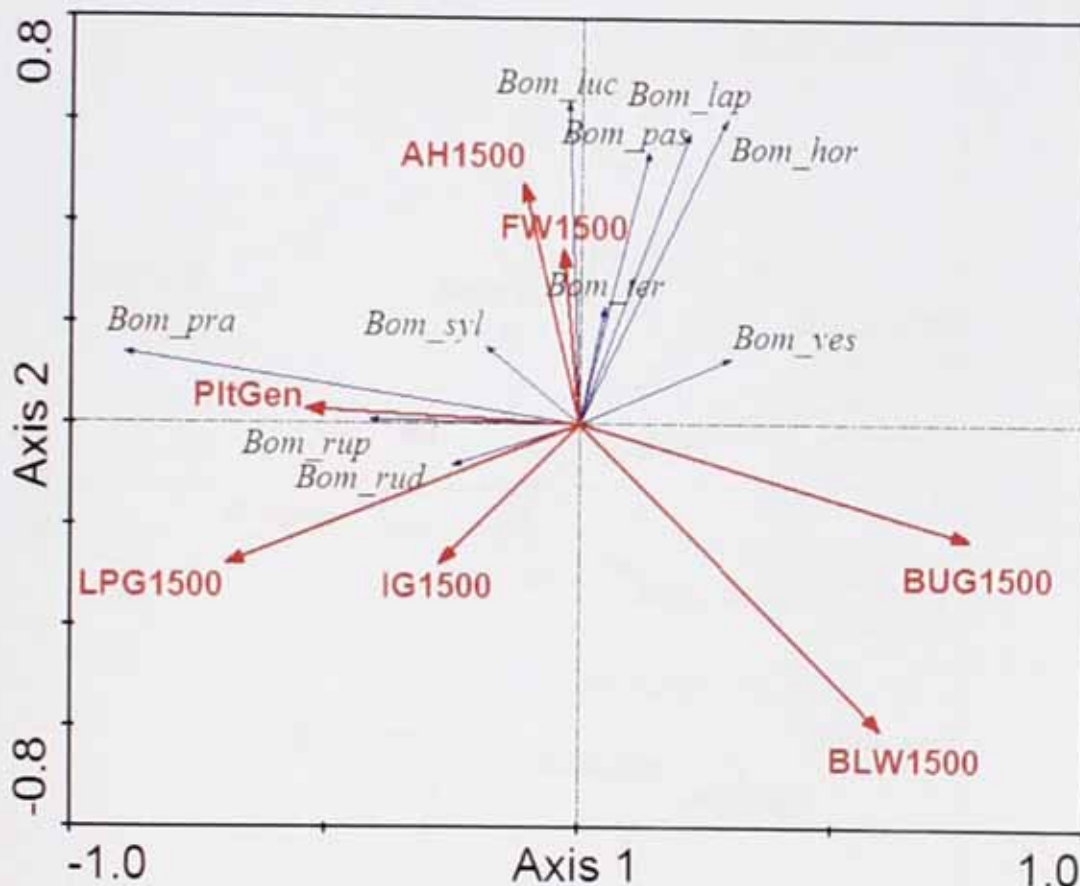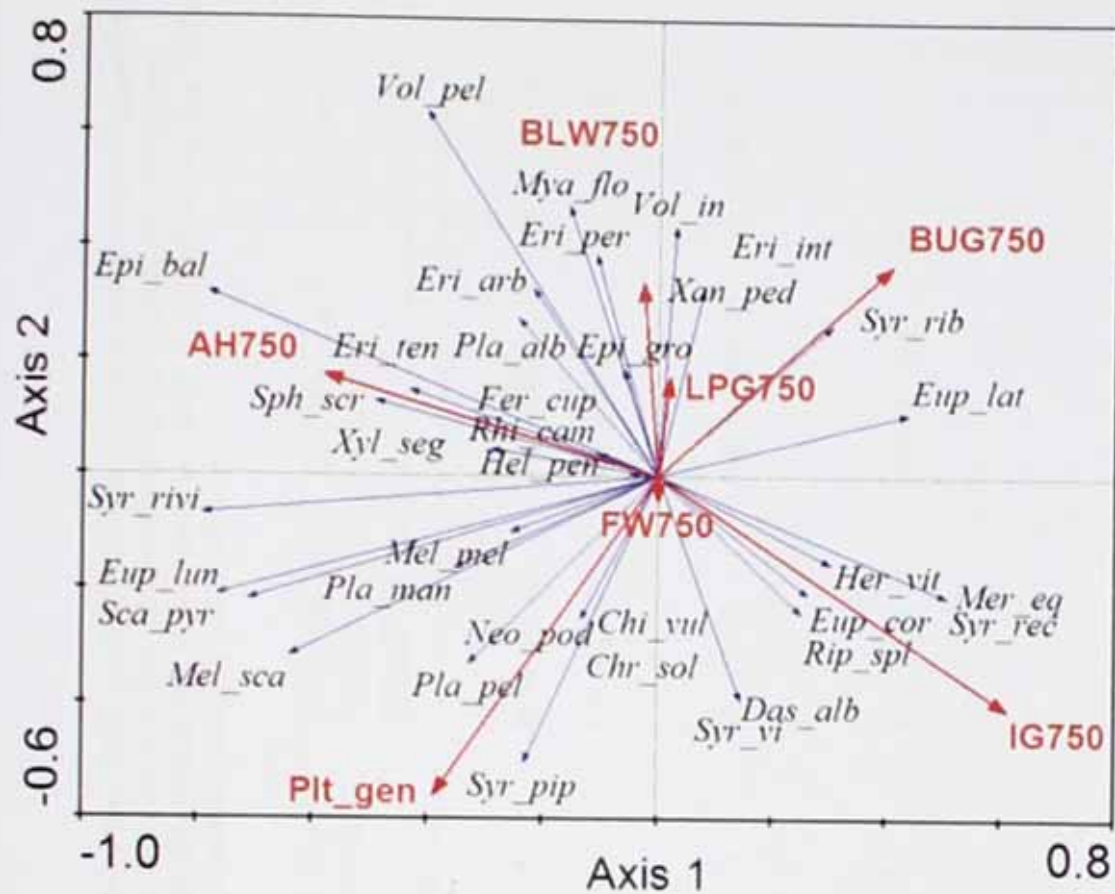
Figure 5.7 Ordination after redundancy analysis using the 2010 Session 3 hoverfly data at a 750m spatial scale. Red arrows indicate environmental variables, blue indicate individual species. Species names are composed of the first three letters of the genus followed by the first three or four of the species, e.g. *Mya_flo* = *Myathropa florea*. Full species names are listed in Appendix VI.

Table 5.4 Results of RDAs for each insect group and session using the landscape scale derived from the exploratory analysis (Table 5.3). Models where the first and/or all canonical axes are significant are given in bold ($P \leq 0.05$). Where significance occurs, the landscape variables exhibiting the highest correlations with the first two axes are also presented. BB = bumblebees, BDM = butterfly and day-flying moths, HF = hoverflies and SB = solitary bees. For descriptions of environmental variables see methods.

Insect group (session)	First canonical axis			All canonical axes			Axis 1 highest correlation	Axis 1 second highest correlation	Axis 2 highest correlation	Axis 2 second highest correlation
	Eigenvalue	F	P	Trace	F	P				
BB (1)	**0.30**	**3.83**	**0.01**	**0.57**	**1.68**	**0.03**	BUG +0.72	LPG -0.65	BLW -0.47	AH +0.37
BB (2)	**0.27**	**3.26**	**0.05**	**0.59**	**1.82**	**0.02**	IG -0.65	BLW +0.48	AH -0.67	BLW +0.64
BB (3)	0.33	4.42	0.14	0.53	1.42	0.14	-	-	-	-
BB (4)	**0.48**	**8.26**	**0.03**	**0.71**	**3.07**	**0.008**	PltGen +0.77	FW +0.25	AH +0.40	BLW -0.38
BDM (1)	0.20	2.21	0.40	0.40	0.84	0.75	-	-	-	-
BDM (2)	0.17	1.87	0.32	0.40	0.84	0.80	-	-	-	-
BDM (3)	**0.23**	**2.69**	**0.01**	**0.55**	**1.59**	**0.01**	AH -0.72	IG +0.72	FW +0.39	BLW -0.19
BDM (4)	0.24	2.79	0.19	0.45	1.03	0.44	-	-	-	-
HF (1)	0.19	2.08	0.12	0.50	1.28	0.12	-	-	-	-
HF (2)	0.17	1.90	0.11	0.43	0.97	0.58	-	-	-	-
HF (3)	**0.39**	**5.77**	**0.03**	**0.58**	**1.75**	**0.05**	IG +0.54	AH -0.52	PltGen -0.52	IG -0.38
HF (4)	0.22	2.52	0.16	0.53	1.47	0.07	-	-	-	-
SB (1)	0.25	3.01	0.15	0.48	1.18	0.27	-	-	-	-
SB (2)	0.19	2.04	0.41	0.44	0.99	0.51	-	-	-	-
SB (3)	0.18	1.98	0.47	0.50	1.26	0.14	-	-	-	-
SB (4)	0.22	2.46	0.50	0.43	0.98	0.54	-	-	-	-

Variance partitioning

The results of the variance partitioning procedures for each of the significant RDAs (plus Session 3 for bumblebees for comparison) are given in Figure 5.8. The shared variance fraction (C) is negative for all groups in Session 3. Lepš and Šmilauer (2003) state negative values are not unusual and that they simply indicate the joint explanatory effect of the two groups of variables is stronger than the sum of their marginal effects.
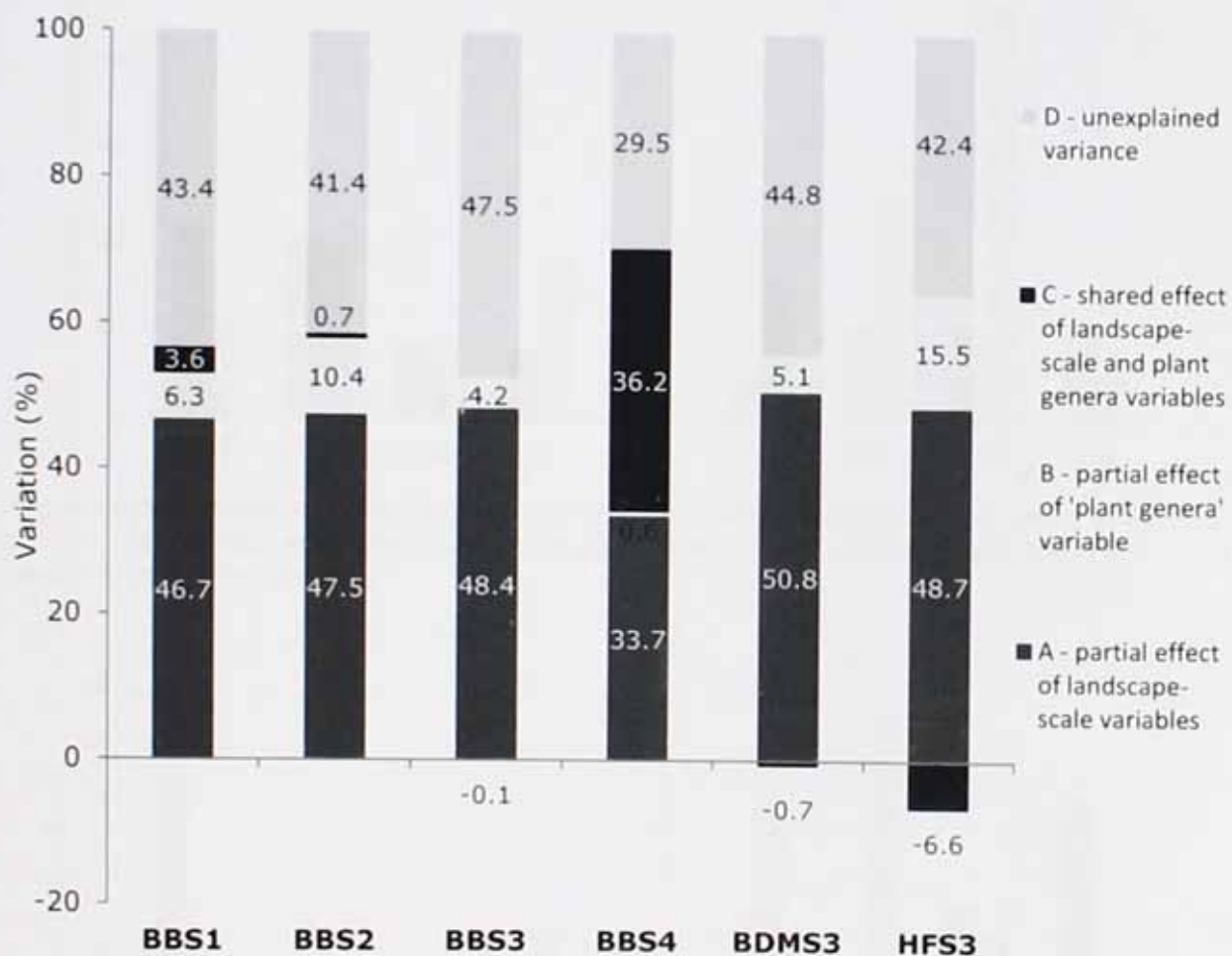
Figure 5.8 Results of variance partitioning (Borcard *et al.*, 1992) for each of the five significant RDAs plus Session 3 for bumblebees.

The response of ground and cavity-nesting solitary bees to environmental factors

The variability in the number of ground and cavity-nesting bees recorded at each property during Sessions 1 and 2 in 2011 is shown in Figures 5.9 and 5.10. A total of 256 individuals from six species were recorded in Session 1, versus 132 individuals from seven species in Session 2.
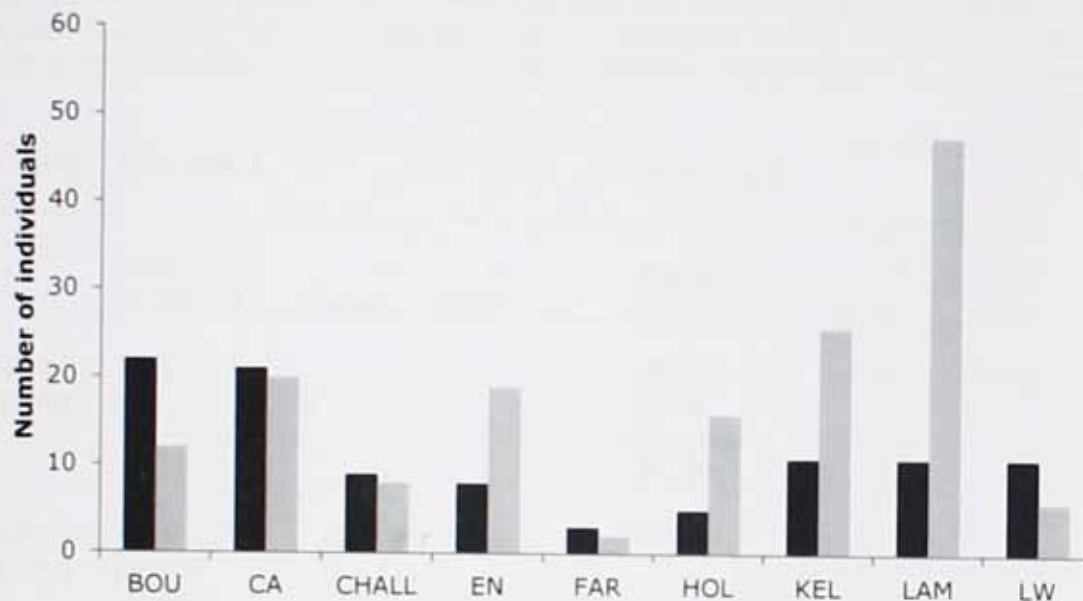
Figure 5.9 Number of solitary bee individuals recorded in Session 1 at each walled garden categorised according to whether they are ground nesting (dark grey) or cavity nesting (light grey).
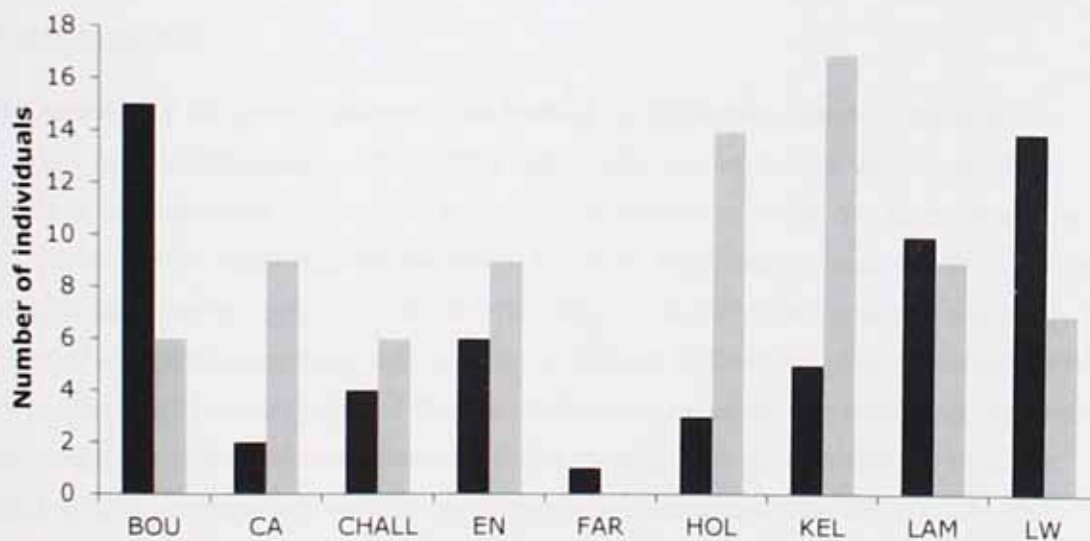
Figure 5.10 Number of solitary bee individuals recorded in Session 2 at each walled garden categorised according to whether they are ground nesting (dark grey) or cavity nesting (light grey).

The results of four multiple regressions showing significant environmental factors linked to the number of solitary bees in each nesting category for each session are given in Table 5.5. In Session 1 the percentage area of beds and borders in a walled garden was a significant variable explaining the abundance of cavity-nesting bees ($P = 0.04$), whilst in Session 2, the number of plant genera available explained the abundance of ground nesters ($P = 0.02$).

Table 5.5 Results of stepwise forward multiple regressions for the log-transformed number of solitary bees in walled gardens for Sessions 1 and 2. Only significant explanatory variables ($P \leq 0.05$) are shown. Degrees of freedom = 1,7 in all cases.

Nesting type	Session 1			Session 2		
	Significant factor (R^2)	F value	P value	Significant factor (R^2)	F value	P value
Ground nesting	N.S.	-	-	Number of plant genera (0.58)	8.81	0.02
Cavity nesting	Area of beds (0.48)	6.49	0.04	N.S.	-	-

Discussion

The response of insect groups according to different landscape scales

As predicted, bumblebees consistently responded to landscape variables within circles of greater radii than other groups. The results in Table 5.3 show that the highest variance explained for Sessions 1 – 4 for bumblebees was in the landscape scales measured at radii of 1,500m and 3,000m. Bumblebees may be either: (a) nesting beyond the gardens and visiting to forage at flowers, or (b) nesting within the gardens and making use of the available resources. Whilst sampling, several nest locations were directly observed in transects, with their presence in other areas of the gardens highlighted by gardeners. Goulson *et al.* (2010) note that bumblebees favour garden settings for nest creation and that nests within gardens are likely to experience higher levels of survival. What is not clear is whether this preference for gardens is a direct response to the perceived suitability of sites for nest creation and foraging, or a measure of the potential inhospitality of the landscape beyond them (Goulson *et al.*, 2010). As the aim of this study was not to

establish the suitability of gardens or the surrounding area for nests, this remains un-assessed in the context of large rural gardens. Hedgerows provide good nesting opportunities for bumblebees (Osborne *et al.*, 2008b); therefore quantifying the presence of these linear features would be one way to establish whether landscapes around some properties are more favourable than others.

In the current study bumblebees were considered as a single group to gain maximum statistical power with respect to assessing the influence of spatial scales. This allowed generalizations to be made about the group (c.f. the weakness highlighted by Jauker *et al.* (2009) when all pollinators are considered together), but ignored any differences between species. Pursuing the species-level approach of Kreyer *et al.* (2004), who noted that different bumblebee species respond to the landscape in different ways, would allow for tighter interpretation at a species level.

Of the four insect groups considered, two (butterflies and day-flying moths, and hoverflies) showed no discernible pattern in their landscape-scale response (Table 5.3). This was not unexpected when the life history of these groups is taken into account, i.e. they are not central place foragers and some migrate over large distances (Jauker *et al.*, 2009).

Solitary bees exhibited the weakest response to landscape-scale factors. Only Session 4 linked to a scale explaining a significant landscape factor (Table 5.3, 3,000m radius, broadleaved woodland, $P < 0.04$). Taking the known flight ranges of sixteen European species of solitary bee into account - up to 600m (Gathmann and Tscharntke, 2002), no obvious explanation is apparent for this result.

Temporal patterns

Clear temporal patterns were not discernible across groups. In part, this was due to only one group (the bumblebees) having three sampling sessions containing significant variables. Depending on the sampling session considered, different variables took on increasing importance; a fact reflected by the composition of the two main ordination axes. In the first sampling session two bumblebee species *Bombus pratorum* and *B. rupestris* responded positively to the number of plant genera available (axis 1, Figure 5.3). However many more species appeared to respond to the landscape variable 'arable and horticulture' (axis 2, Figure 5.3) with more bumblebees from more species observed as the area of this land category increased. This is a surprising result in spring when flower-rich hedgerows in the landscape are suggested to provide abundant resources (Hannon and Sisk, 2009).

The reality however is that most hedgerows are not managed to allow regular and abundant flowering. More than 90% of hedgerows bordering agricultural land in a 1,000m radius around one of the properties (Lois Weedon) were severely cut back using flails during the winter of 2010/2011 (pers. obs.), meaning few flowers were produced. Although this observation relates to only one of the 17 properties, there is no reason to assume that other hedgerows are being managed differently. As a result, bumblebees may be attracted into gardens in spring because of a dearth of flower resources in the wider landscape.

In Session 2 bumblebees appeared to primarily respond to the percentage of broadleaved woodland and improved grassland in the wider landscape (axis 1, Figure 5.4) and the percentage of arable land (axis 2, Figure 5.4 and Table 5.4). Greater numbers of bumblebees from a range of species appeared in gardens as the percentage of broadleaved woodland and arable land increased. To a lesser extent, the variable 'number of plant genera' also influenced the diversity of bumblebees observed in gardens. A plentiful supply of flowering plants may act as a focus for workers visiting from nests beyond the garden (Osborne et al., 1999), or may signify that nest occupants within gardens are making use of resources available.

In Session 4 the strongest influence to emerge was that of the number of plant genera available (axis 1, Figure 5.5, which explains 48% of variation). This result reinforces the importance of forage resources being available throughout the season and extending into late summer, as described in Goulson et al. (2010).

The temporal influence of monocultures such as the mass-flowering crop, oilseed rape (OSR) is not directly obvious from these results. For example, there is no strong response (positive or negative) to arable land in Session 2 which is when this crop is in flower, yet OSR is known to influence bumblebee foraging behaviour (Knight et al., 2009, Goulson et al., 2010). Visual inspection of photographs for the seventeen sites show OSR growing within 1,500m of the gardens in 2009 - the year before sampling took place (GetMapping PLC). However ground truthing to ascertain the type of crops within the category 'arable and horticulture' was beyond the scope of the 2010 and 2011 field seasons. A useful follow-up to this work would be to repeat the assessment, focussing on bumblebees and quantifying the area planted with OSR.

The response of insect groups to landscape-scale variables

Whilst a seasonal pattern was not discernible, some groups appear to be consistently influenced by certain landscape features regardless of spatial scale. An example of this is the response of the group butterflies and day-flying moths and that of hoverflies to the landscape variables 'arable and horticultural land' and 'improved grassland' (Figures 5.6 and 5.7). In both instances, there was a negative association with the amount of improved grassland in the landscape, and more species observed as the amount of arable land increased. This broadly agrees with Öckinger et al. (2009) who found butterfly species richness and abundance was not significantly related to flower abundance per se. Notwithstanding this, some species did respond to the number of plant genera available. This effect was stronger for hoverflies than it was for butterflies and day-flying moths (Figures 5.6 and 5.7), possibly reflecting their documented habit of preferentially selecting flower-rich patches (Haenke et al., 2009). This agrees with the observations of Schweiger et al. (2007), who noted that hoverfly richness was less affected by landscape-scale factors and more greatly influenced by flower patches.

Solitary bees were notably unresponsive to landscape variables (Tables 5.3 and 5.4), probably due to their shorter foraging ranges (Gathmann and Tscharntke, 2002, Greenleaf et al., 2007).

Which better explains flower-visitor presence: plant richness or landscape-scale factors?

All groups with significant results from the redundancy analysis showed higher levels of overall explained variance than unexplained variance (Figure 5.8). The variance explained due to landscape factors alone (excluding bumblebees Session 3 – BBS3, which is included in Figure 5.8 for comparison purposes) ranged between 46.7% (bumblebees Session 1 – BBS1) and 50.8% (butterflies and day-flying moths Session 3 – BDMS3). Plant genera on the other hand explained much lower variance, ranging from 0.6% (bumblebees Session 4 – BBS4) to 15.5% (hoverflies Session 3 – HFS3). The low variance due to plant genera for bumblebees in Session 4 (despite being an important component of the ordination diagram Figure 5.5), is countered by the shared effect of landscape variables and plant genera together (accounting for 36.2% of variance, Figure 5.8). This interacting effect of both within and beyond-garden variables only becomes apparent when this procedure is used, highlighting its value.

The response of ground and cavity-nesting bees to within and beyond walled garden environmental factors

The sampling in early spring of 2011 (Session 1) revealed a higher number of solitary bees (256) than in Session 2 (132), (Figures 5.9 and 5.10). Splitting these bees into two groups according to whether they were ground or cavity nesting allowed an additional assessment to be made of whether proximal environmental factors were significant. The multiple regressions considering the landscape effects at 500m and 750m from the walls of the gardens were non-significant. This result was partially expected as solitary bees are central place foragers and are known to have short foraging ranges (Gathmann and Tscharntke, 2002). As such they are restricted to collecting pollen and nectar reserves needed for their offspring in areas geographically close to their nests (Jauker et al., 2009).

Of the four within-garden factors only two were significant. In Session 1 the percentage of walled gardens used as beds and borders was the significant variable explaining the abundance of cavity-nesting bees ($P = 0.04$, Table 5.5), whilst in Session 2 the number of plant genera was significantly related to the number of ground-nesting bees ($P = 0.02$, Table 5.5).

The link between cavity nesting bees and the area of beds and borders probably relates to the requirement for soil for nest construction by some species. Of all the bees recorded in Session 1, 49% were from a single species, *Osmia bicornis* (data not presented). This species uses soil to create partitions between individual cells (Raw, 1972). The importance of this resource was noted by Westrich (1998) who stated that even in the event that abundant nesting space and forage resources are available, without a supply of soil, female bees cannot successfully reproduce.

By Session 2 (which occurred between 11 June and 4 July 2011) few *O. bicornis* females were on the wing (pers. obs.) and they accounted for only 3% of the bees recorded. As such, the variable 'beds and borders' was no longer significant for cavity-nesting bees. Ground-nesting bees, on the other hand, showed a significant positive relationship with the number of plant genera available. The ground-nesting bees recorded were from three genera (*Andrena*, *Lasioglossum* and *Nomada*) and represented approximately 45% of all the bees observed in Session 2.

In summary, the splitting of a single insect group into two based on their nesting biology appears to offer new insights into responses to local-scale variables where wholesale treatment fails.

Conclusions

The findings of this chapter can be summarised as follows:

- Bumblebees responded to landscape-scale factors within circles of greater radii than all other groups. The typical radius was 1,500 – 3,000m.

- Butterflies and day-flying moths and hoverflies showed no consistent scale-dependent responses to environmental factors. This is not surprising when their life history traits are taken into account.

- Solitary bees were invariant to landscape-scale factors.

- Temporal patterns were weak, due in part to only a few groups and sessions containing significant variables. Assessing the seasonal effect of mass-flowering crops such as oilseed rape on bumblebee presence would be a useful complement to the current findings.

- Bumblebees showed a strong response to the availability of flowering plants late in the season, highlighting the important role gardens play in providing forage over an extended period.

- Butterflies and day-flying moths and hoverflies both responded to the landscape variables 'arable and horticultural land' and 'improved grassland' in similar ways.

- As the percentage of arable land increased in the landscape, more hoverflies were observed in gardens.

- Hoverflies, which are noted for their preference for flower-rich patches, were also influenced by the number of plant genera available.

- For the three groups, bumblebees, butterflies and day-flying moths and hoverflies, landscape-scale factors rather than within-garden factors best explained the number of individuals observed.

- Bumblebees were most strongly influenced by a combination of landscape-scale and within-garden scale factors late in the summer.

- Splitting solitary bees according to their nesting biology revealed that cavity-nesting bees respond to the area of beds and borders in spring, whilst ground-nesting bees respond to the number of plant genera in summer.

The next chapter examines the nesting behaviour and reproductive success of the most ubiquitous solitary bee species observed in walled gardens, *Osmia bicornis*.

Chapter 6

Trap-nest bees in walled gardens

Chapter overview

In this chapter, the potential of walled kitchen gardens to support populations of cavity-nesting bees is explored. Commercial trap-nests are used to establish the range of species present and to permit an in-depth look at the causes of mortality for *Osmia bicornis*, the most ubiquitous species present. By using *k* values, different mortality factors are compared in a consistent way across sites. The primary causes of mortality (developmental failure and parasitism) are considered in the light of their disproportionate effects on female bees.

Introduction

Understanding how landscape resources and natural enemies shape local populations is a fundamental area of ecological enquiry (Kareiva, 1990). For bioindicators such as flower-visiting insects, i.e. species that indicate changes in ecosystem-service functioning or success, this takes on even greater importance (Christensen *et al.*, 1996, Tscharntke *et al.*, 1998).

An important aspect of understanding how species are affected by factors at a variety of scales is to ensure that mortality losses of juveniles are taken into account (Steffan-Dewenter and Leschke, 2003, Carré *et al.*, 2009).

Nest and food requirements of solitary bees

Wild bee reproductive success is dependent on both adequate food resources and suitable nesting sites (Westrich, 1998). Healthy wild bee offspring are the product of an area fulfilling three basic criteria: (a) physical space for nest sites; (b) materials for nest construction and (c) food plants that support both adults and larvae (Westrich, 1998, Figure 6.1).

Resources

Nesting sites	Building materials	Food
below ground	gland secretions	nectar
suitable soil	mud/soil	pollen
rodent nests	leaves	floral oils
above ground	masticated leaves	
cavities	plant hairs	
dead wood or stems	resin	
exposed nests		
empty snail shells		
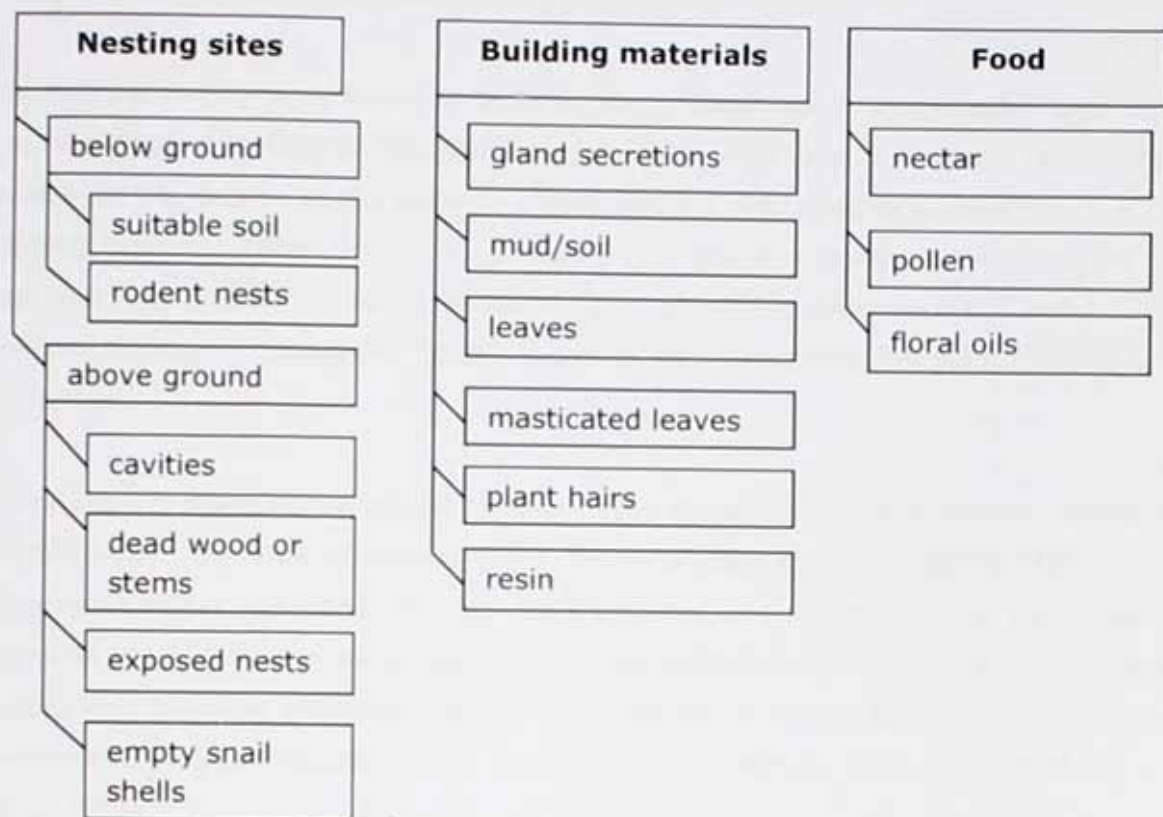
Figure 6.1 Nesting and foraging resources required by bees in temperate locations (after Westrich, 1998).

In temperate climates approximately 70% of bees and wasps are ground-nesters (Westrich, 1998). The initial occupancy and persistence of ground-nesting bees is believed to be more closely linked to the abundance of suitable floral rewards than nest sites *per se*, as suitable nest areas are rarely limited (Holzschuh *et al.*, 2010). Aerial nesters, on the other hand, are more likely to be affected by limited nest materials and sites than food resources (Tscharntke *et al.*, 1998, Potts *et al.*, 2003, Holzschuh *et al.*, 2010).

The availability of suitable nesting areas is an example of a resource-driven, bottom-up effect. In general, nest site availability is density-independent, but can limit population growth in a density-dependent fashion when organisms are spatially aggregated (Gillman, 2009). In contrast to this, natural enemies such as predators and parasites can have a top-down regulatory effect and act in a density-dependent way (Steffan-Dewenter and Schiele, 2008). Efforts to understand the relative importance and contribution of both top-down and bottom-up effects on various taxa have involved a variety of methods including manipulation experiments, time-series

analyses and life-tables (Raw, 1972, Preszler and Price 1988, Hunter *et al.*, 1997, Hunter, 2001). To date, herbivores have been the main focus of this research, but see Steffan-Dewenter and Schiele (2008).

The interest in native aerial-nesters comes as concerns about global honey bee losses escalate (vanEngelsdorp and Meixner, 2010, Breeze *et al.*, 2011). The major causes for the decline of the western honey bee are discussed extensively in vanEngelsdorp and Meixner (2010) and include a range of diseases and parasites e.g. *Nosema* spp. and *Varroa destructor*, 'unresolved disorders' such as Colony Collapse Disorder (Watanabe, 2008), together with direct and indirect poisoning by pesticides.

A study using a simulation model to explore the potential of native bees to facilitate pollination of a commercial crop in North America found these insects had the capacity to buffer reductions in crop yields incurred as a result of honey bee losses (Winfree *et al.*, 2007). How to capitalise on this potential is an area that has started to receive increasing attention, with several species of solitary bee now managed for commercial crop pollination (Bosch, 1994, Bosch and Kemp, 2002, Gruber *et al.*, 2011, Table 6.1).

Table 6.1 Examples of solitary bee species used as pollinators of commercial crops.

Bee species	Crop	Location and effect on pollination if known	Source
Megachile rotundata Fabricius, 1787 (Megachilidae)	alfalfa	USA Tripled seed production in the second half of the 20th century	Pitts-Singer and Cane (2011)
Osmia cornuta Latrielle, 1805 (Megachilidae)	apples	Europe	Bosch (1994), Vicens and Bosch (2000)
Osmia cornifrons Radoszkowski, 1887 (Megachilidae)	apples	Japan	Maeta and Kitamura (1974)
Osmia lignaria Say, 1837 (Megachilidae)	sweet cherry	USA Doubled sweet cherry yield in a 5-year period	Bosch *et al.* (2006)

Trap-nesting bees and artificial nests

Suitable solitary bee species for management comprise those that readily nest in pre-existing cavities and are termed trap-nesting bees (Raw, 1972). In a natural setting these bees utilise dead wood, plant stems, beetle borings and holes in vertical landscape features to construct their nests, but when managed they occupy artificial nests (O'Toole, 2011).

Although a range of artificial nest materials have been used for experimental purposes - including bundles of paper drinking straws, plant stems and drilled wooden blocks (Free and Williams, 1970, Bosch and Kemp, 2002), the majority of studies mimic nest cavities by using internodes of the common reed *Phragmites australis* (Cav.) Trin. ex Steud, (Poaceae). The reeds are tied together and are used to encourage females to establish cells within them. This method is inexpensive and convenient, but has disadvantages. For example female bees, in the absence of standard reed-widths, may create greater numbers of cells containing eggs of a particular sex (Raw, 1972), and parasites may respond differently depending on reed length and size of opening (Krunic *et al.*, 2005).

Alternatives to reed-based trap-nests are available commercially. Although primarily aimed at meeting the needs of individuals wishing to increase biodiversity in their gardens, their design and uniformity makes them ideal for experimental use. The nests comprise plastic hexagonal structures that are open at one end (Figure 6.2A-C) and contain 30 individual cardboard tubes, each lined with a paper cylinder. The outer plastic casing affords protection from inclement weather, whilst the cardboard tubes and paper liners allow easy examination of the contents (Bates *et al.*, 2011a). In addition to their value for experimental work, these nests serve as important educational tools. The bees using them are considered safe near children and pets and can be used to help raise the public's understanding of the importance of native bees as pollinators of crops and wild flowers (O'Toole, 2002, Bates *et al.*, 2011a, Everaars *et al.*, 2011).

There are several advantages associated with using trap nests, regardless of type. They provide abundant nesting resources when a species is used at high densities for a specific pollination purpose (Wilkaniec and Giejdasz, 2003); they act as effective monitoring tools to assess Hymenoptera diversity in fragmented areas (Jenkins and Matthews, 2004) and they can be used experimentally to explore the top-down regulatory effects of parasites and predators (Seidelmann, 2006, Pitts-Singer and Cane, 2011), progeny sex-ratios (Bosch and Vicens, 2005, Seidelmann *et al.*, 2010), and the effects of habitat management on bee species richness (Steffan-Dewenter and Leschke, 2003, Holzschuh *et al.*, 2010, Schueepp *et al.*, 2011).
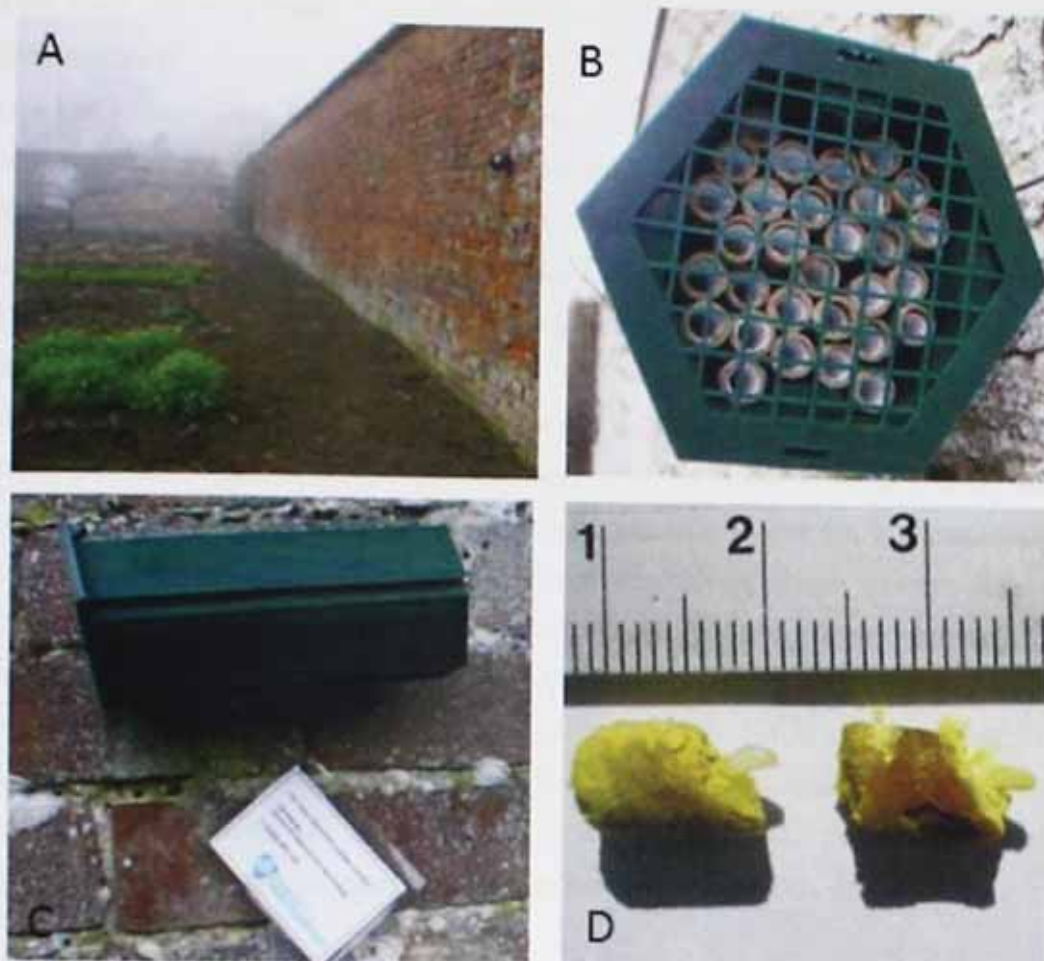
Figure 6.2 Commercial trap-nests for solitary bees: A) Placement in Lamport Hall walled garden in early spring 2011, B) Plastic grill protecting tubes from birds/squirrels, C) Public information label attached to nest, D) Contents of two *O. bicornis* brood cells (pollen and nectar resources plus eggs). Images: Erenler (2011).

Past research has shown that, regardless of the type of artificial nest offered, occupancy by solitary bees is common, even in the centre of urban areas (Wilkaniec and Giejdasz, 2003, Gaston *et al.*, 2005). Although bundles of reeds help augment numbers of potential pollinators, they are less useful to assess parasitism levels and the ratio of female to male offspring. Instead, a more standardised approach is necessary. By controlling for differences in tube lengths and widths (through the use of pre-prepared tubes rather than reed stems), other variables that may explain levels of occupancy, parasitism and reproductive success may be more accurately explored. These variables include, but are not limited to, the abundance of pre-existing cavities in the area, floral species richness and landscape composition (Steffan-Dewenter and Schiele, 2008, Holzschuh *et al.*, 2010).

The red mason bee

Life history

The red mason bee, *Osmia bicornis*, syn. *O. rufa*, is a solitary, univoltine, trap-nesting species with a Palaearctic distribution. It is common in England and Wales and regularly occurs in rural and urban gardens (Edwards, 1998). This ubiquitous bee is polylectic, visiting a variety of plants for both pollen and nectar (Edwards, 1998). Males commence their flight period in mid to late March in England (females appear approximately one week later), and continue through to early July. Males are 6 - 11mm in length; females are larger at 10 – 16mm (Edwards, 1998). The flight period for this species coincides with the flowering time of a wide range of commercially grown mass-flowering rosaceous fruit in the UK such as apples, pears and strawberries, as well as spring and early summer native flowers (Edwards, 1998, Roberts and Dean, 2012). The red mason bee's ability to warm up at a faster rate than expected for its body size enables it to visit flowers in high numbers at a time when other pollinators such as bumblebees (*Bombus* spp.) are yet to build their colonies to full-strength (Stone and Willmer, 1989, O'Toole, 2002). Despite these qualities, *O. bicornis* has not yet been used as a managed pollinator in the United Kingdom by commercial growers and farmers (Dean, pers. comm.).

A red mason bee nest consists of a linear set of brood cells. Each cell is provisioned with a quantity of pollen and nectar, with a single egg laid atop (Figure 6.2D and Figure 6.3A). Individual cells are separated by soil partitions and eventually sealed with a textured mud capping, often beyond a final empty gap or vestibulum (Seidelmann, 1999) (Figure 6.3B, C).

In common with other Hymenoptera, sex-determination is through haplodiploidy. This occurs by means of facultative fertilization of the egg at the point of laying, using sperm stored in the spermatheca (Gerber and Klostermeyer, 1970). Daughters occur when fertilization takes place (diploidy) with sons the product of unfertilised eggs (haploidy) (Bosch and Vicens, 2005). Females decide the sex of the egg they will lay at the onset of cell construction by using a mud partition-like structure known as Fabre's threshold (Raw, 1972). This delimits the size of the cell and the extent of provisions that will be stored in it. Male *O. bicornis* are smaller than females and are allocated less food reserves. This is similar to many other megachilid bees, e.g. male *Megachile rotundata* receive 17% less provisions than females (Pitts-Singer and Cane, 2011).

Female red mason bees collect dry pollen in their abdominal scopae (pollen carrying hairs, Figure 6.3A) for transport back to the nest. This is in contrast to bumblebees and honey bees which orally wet their pollen, transporting it in corbiculae (pollen baskets) on their hind tibiae (O'Toole, 2002). The transport of a dry pollen-mass means more loose pollen may be available for pollination when the bee visits successive flower heads, and the absence of oral moistening means stigma-deposited pollen is unlikely to experience inhibited germination from enzymes transferred to it during the wetting process, (O'Toole, pers. comm.). Based on this (and the ubiquity of the species) it seems reasonable to suggest that the red mason bee is likely to be making an important, but as yet unquantified, contribution to the pollination of commercially grown fruit and native plants early in the season.

Figure 6.3 Red mason bee cell provisioning and cell parasitism: A) female with pollen in abdominal scopae entering nest tube, B) female bringing in mud to create anterior wall of vestibulum, C) female sealing a tube (note *Cacoxenus indagator* top left on cardboard outer), D) exoskeleton remains of a red mason bee - all soft tissues consumed by *Monodontomerus obscurus* larvae whilst within the cocoon, E) *C. indagator* larvae and frass within a single cell (*O. bicornis* cell provisions and possibly egg/larva consumed). Images: Erenler (2011).

Several authors have recorded the red mason bee as the most abundant cavity-nesting species, making it ideal for experimental purposes (Table 6.2). Another advantage of *O. bicornis* is that its taxonomy, biology and associated parasites and predators are well documented. These include the drosophilid fly *Cacoxenus indagator* Loew (Diptera: Drosophilidae) which is host-specific and is known to affect *O. bicornis* cells in great numbers, and *Monodontomerus obscurus* Westwood (Hymenoptera: Torymidae), a chalcid wasp whose larvae feed on pre-emerged adult bees (Raw 1972, Krunic *et al.*, 2005), (Figure 6.3C, D and E). Combined mortality losses at the larval stage due to developmental failure and the presence of the specialist *C. indagator* can occur in more than a third of all *O. bicornis* brood cells (Steffan-Dewenter and Schiele, 2008, Jauker *et al.*, 2012a).

Table 6.2 Studies highlighting the dominant use of trap-nests by the red mason bee.

Location of study	Total number of bee brood cells	Percentage of total bee brood cells created by *O. bicornis*	Source
Orchard meadows in Germany	17 278	84%	Steffan-Dewenter and Leschke (2003)
Conventional and organic wheat fields in Germany	8644	96%	Holzschuh *et al.* (2010)
Farmland sites in Switzerland	1003	71%	Schueepp *et al.* (2011)

In common with other *Osmia* species, female red mason bee progeny are preferentially located at the innermost part of each nest (Bosch and Kemp, 2002). As a consequence, mortality losses occurring in anything other than a random fashion throughout the nest have the potential to disproportionally affect the survival of each sex. In the event that females are more adversely affected, this may have important implications for flower visitation and pollination. This arises for two reasons; first, females are the sole nest provisioners and therefore visit more flowers

than males and second, reduced female numbers could eventually lead to a smaller contribution to overall population size (Bosch and Kemp, 2002).

Previous research using *O. bicornis* has focussed on methods for augmenting population numbers (Krunic and Stanisavljevic, 2006, Gruber *et al.*, 2011), as well as attempting to understand the drivers for the sex ratios observed (Bosch and Vicens, 2005, Seidelmann, 2006, Seidelmann *et al.*, 2010). The former emphasises the need for supplying sufficient bees for commercial pollination purposes, whilst the latter tests ideas about adaptive strategies used by females to alleviate the effects of open-cell parasitism.

Although parasitism losses in relation to brood cell position within the nest have been reported (Strohm, 2011), losses due to developmental failure do not appear to have been assessed. To my knowledge no studies have explored broad causes of mortality in relation to both cell position and gender. In gaining an understanding of the mortality differences experienced by males and females, the timing and control methods needed to mitigate against these losses can be developed.

The red mason bee in gardens

The red mason bee is known to frequent both rural and urban gardens, and freely utilises existing holes in walls and mortar (pers. obs., Figure 6.4) as well as occupying artificial nests placed in sunny locations (Gaston *et al.*, 2005). During 2010, the red mason bee was recorded at fifteen of the seventeen sampling sites (Chapter 2 – 2010 field season).

Figure 6.4 Existing cavities in the mortar between bricks in the walled garden at Lamport Hall. These holes are used by *O. bicornis* and other cavity nesting bees. Image: Erenler (2012).

Analysing bee life-cycles using stage-dependent life tables

Stage-dependent life tables document the key mortality events during the life of an insect. Events are expressed in their natural order without reference to calendar time (Varley *et al.*, 1975, Hunter, 2001).The term 'mortality' is used in the broadest sense, encapsulating losses regardless of whether death occurs, e.g. when males are discounted from a population or lost through dispersal (Yamamura, 1999). Calculating mortality rates at each stage allows populations to be compared across space or time. Each stage is ascribed a *k* value (the 'killing power'), with all stages considered independent. The *k* value is calculated as the negative logarithm of survival, with individual *k* values summed to give a total mortality value, expressed as *K* (Yamamura, 1999). An important difference between the commonly used mortality percentages and *k* survival values is that the latter are additive (Varley *et al.*, 1975, Yamamura, 1999).

As the red mason bee completes its life-cycle in a single year, is without overlapping generations and has distinct developmental and predation stages (Table 6.3), it lends itself well to this type of analysis.

Table 6.3 Descriptions of mortality and loss factors for *O. bicornis* using the stages described in Raw (1972).

Stage	Description	Mortality/loss factor	k value
1	constructed cells	developmental failure (cell inadequately provisioned, sub-optimal egg laid, egg dies before hatching). Result = no live larvae	$k1$
2	provisioned cells	parasitism by *Cacoxenus indagator* causing death of pre-pupae	$k2$
3	provisioned cells	parasitism by vector other than *C. indagator* causing death of pre-pupae	$k3$
4	cocoons	parasitism by *Monodontomerus obscurus* causing death of pupae/adult	$k4$
5	cocoons containing male and female adults	males discounted as females are main contributors to the number of offspring in the next generation	$k5$
6	cocoons containing female adults	death during the overwintering, quiescent phase	$k6$
	Overall 'mortality' from egg to reproductive female		K (sum of all k values)

Despite the potential commercial importance of understanding the point(s) at which losses occur in the developmental phase of *O. bicornis*, life tables with k values do not appear to have been used (but see Sekita and Yamada, 1993).

Walled kitchen gardens

Historic use

Walled 'kitchen' or 'productive' gardens have been an integral part of the English country-house estate for centuries. Up until the 1930s these 'rooms', bounded by walls, hedges or simple fences, provided the household with its fruit and vegetable needs throughout the year. The walls provided a microclimate conducive for vegetable growing whilst keeping out unwelcome animal and human visitors (Wilson, 2003, Musgrave, 2009, Campbell, 2010).

Up until the end of the seventeenth century most walled gardens were square, with their internal space divided into four distinct sections or 'quarters' (Campbell, 2005). The design mimicked ancient classical gardens and the partitions (comprised of pathways) afforded country-house owners the possibility of taking visitors and family on strolls through the highly managed garden environment (Campbell, 2010).

With a greater appreciation of the heat retention properties of certain building materials, the design of rectangular gardens (built with brick walls) became popular (Campbell, 2005). These allowed fruit to ripen early on espalier-grown trees trained against the longest walls (Campbell, 2005, 2010).

The size of kitchen gardens often ranged between one acre to 20 or 30 acres according to taste and resources, with a one acre walled garden able to supply sufficient produce for 12 people (Campbell, 2010).

The fashions of the day usually dictated what was grown. The experimental practices involved in raising exotic fruit and vegetable specimens led to new innovations within walled gardens. This saw the introduction of heated glass houses, often with the aid of hotbeds (Musgrave, 2009). In addition to growing exotics and traditional vegetables, aromatic plants and flowers were cultivated. The popularity of preparing herbal remedies meant these plants were needed for homemade tinctures, salves and tonics; a practice that continued until the late 18th century. The flowers of these aromatic shrubs, many of which originated from the Mediterranean, offered pleasing olfactory and visual distractions from the often less pleasant muck heaps that were needed to fuel the hotbeds (Musgrave, 2009, Campbell, 2010).

As well as their medicinal and aesthetic properties, aromatic plants would have attracted pollinating insects. It is known that the Romans grew thyme, rosemary and marjoram for the bees in their gardens, but it is believed this was to ensure fragrant honey was produced rather than actively encourage bees to visit and pollinate nearby crops (Campbell, 2005).

Honey bees have actively been kept in walled gardens for centuries (Campbell, 2005). Early hives took the form of straw skeps, with some garden walls designed specifically to incorporate recesses (or bee boles) for colonies (Campbell, 2005). As in Roman times, the focus was purely on obtaining products from bees, e.g. honey and beeswax (Ebert, 2011). Some early writers on the subject of apiculture were keen to emphasize other advantages of bees, citing how bee behaviour (hard work and a clearly demarked organisational structure) was a positive role-model for human society (Warder, 1720). Others, meanwhile, extolled the virtues of beekeeping as a cottage activity offering financial gain to the rural poor as well as a stimulating intellectual hobby for the rich (Keys, 1780).

The earliest understanding of the structure of social bee colonies came with Charles Butler's *The Feminine Monarchie* in 1609 (Butler, 1609), but it was not until the late eighteenth century that observations about the inhumane methods of obtaining honey, which required the majority of bees to be immobilised and killed with smoke and brimstone, led to hive design moving away from skeps to formal bee hives. The latter were both functional and decorative and were placed in walled gardens for the amusement of owners and house guests (Campbell, 2005). The role of bees as pollinators was only appreciated in the 18th century; with the naturalist Joseph Kölreuter establishing that the purpose of nectar was to reward insects (Proctor *et al.*, 1996).

Today, few walled gardens contain hives. The gardens themselves are often shadows of their former selves, with a minority in ruins and some with only a fraction of the original area cultivated for fruit and vegetables (Campbell, 2010). The shift away from high productivity came with the increased availability of cheap foodstuffs from around the world and escalating labour costs for maintaining kitchen gardens (Campbell, 2010). Tennis courts and swimming pools are frequently found in walled gardens in place of land that would previously have given a continuous supply of fresh vegetables. Examples from the present study include Courteenhall, Easton Neston and Lois Weedon House. Another feature of today's walled gardens is the extensive area laid to turf. Often closely mown, lawns offer few flower resources for insects.

Despite the change in use of walled gardens, the walls themselves remain as potential nest sites for cavity-nesting bees. The situation is helped, in part, by the many holes remaining from the habit of driving metal pins into mortar to anchor wires needed to support wall-grown fruit trees (Campbell, 2010).

Aims

The aims of this chapter are to quantify nest site occupancy, cell parasitism and reproductive success in nine walled gardens, with a strong focus on the most ubiquitous species, *Osmia bicornis*. Specifically, the work seeks to answer the following questions:

1. Does tube usage by a) a range of trap-nesting bees and b) the red mason bee differ across the nine properties?

2. Is there a relationship between the abundance of *O. bicornis* cells created and those of other bee species, and is *O. bicornis* abundance correlated with the number of pre-existing cavities in the walls?

3. Do the k values relating to developmental and parasitism losses ($k1$-4) differ between properties?

4. Is there a relationship between the number of cells parasitized by *Cacoxenus indagator* and the number of cells present?

5. Do rates of developmental and parasitism loss vary according to brood cell location in the nest and, if so, do these losses affect equal numbers of males and females?

6. Is the sex ratio of *O. bicornis* observed in the current study consistent with other locations and other trap-nest species?

7. Is there a difference in mortality rates for overwintering male and female bees within and between properties?

Methods

Sampling

Nine walled gardens were used for the study (Chapter 2 - 2011 field season, Table 6.4). Commercial trap-nests were placed at study sites in spring 2011, with the experimental work completed in the spring of 2012.

The trap-nests (Vivara brand) were purchased from CJ Wildbird Food, Upton Magna, Shrewsbury, England. Nests consisted of a green plastic casing containing thirty cardboard tubes together with a protective grill (Figure 6.2B). Each tube contained a paper liner measuring 150mm in length and 0.7mm in diameter that could be withdrawn using a plastic stopper at one end. Three nests were affixed to south or east facing walls in each garden between 15th and 24th March 2011. The nests were attached to mortar between bricks or stone at a height of 1.6m - 1.8m in areas free of vegetation, and separated by a minimum horizontal distance of 5m.

Table 6.4 Details of the nine walled gardens used in the trap-nest study.

Location						Location of nest aspect of wall/height placed (m)		
Property	Abbreviation	Present on 1890 OS map Y/N	Walled garden area (m²)	Wall type	Mean no of holes or cavities per m² ± SD	Nest 1	Nest 2	Nest 3
Boughton House	BOU	Y	7843	Stone	13.83 ± 6.85	S 1.8m	S 1.8m	S 1.8m
Canons Ashby	CA	Y	1605	Stone	29.50 ± 13.10	SW 1.7m	SW 1.7m	SW 1.7m
Courteenhall	CHALL	Y	7009	Brick	3.67 ± 1.97	S 1.6m	S 1.6m	S 1.6m
Easton Neston	EN	Y	9142	Brick	11.17 ± 7.23	SSW 1.6m	SSW 1.6m	ESE 1.6m
Farnborough Hall	FAR	Y	8723	Brick	23.33 ± 12.16	E 1.8m	E 1.8m	E 1.8m
Holdenby House	HOL	Y	4359	Stone	7.67 ± 3.44	SSW 1.8m	SSW 1.8m	SSW 1.8m
Kelmarsh Hall	KEL	Y	7298	Brick	13.33 ± 11.88	S 1.8m	S 1.6m	S 1.8m
Lamport Hall	LAM	Y	8204	Brick	42.33 ± 11.55	SSE 1.6m	SSE 1.6m	SSE 1.6m
Lois Weedon	LW	N	3227	Brick	0.67 ± 1.03	S 1.6m	S 1.6m	S 1.6m

Between the 24th August and 15th September 2011 the cardboard tubes were removed, leaving just the nest casings in place. Each tube was marked with a unique property, nest and tube number and stored in dry conditions (temperature range 12 – 16°C, relative humidity 40 – 45%) until it was opened.

Examination of the nest contents

To ensure the fly larvae of the specialist cleptoparasite *Cacoxenus indagator* were found *in situ* (they are known to migrate towards nest entrances – Strohm, 2011), the tubes were examined within three months of collection (between 11th and 23rd of November 2011).

Paper liners were removed from their tubes and opened by making a small incision at the end opposite the stopper. The paper was then unravelled in a spiral fashion (Bates *et al.*, 2011a). The contents were recorded according to the categories described in Figure 6.5. In addition, a random subset of ten nests had their cell contents recorded according to their exact location within each tube. The innermost cell in each tube was designated as cell one.

Where a cell contained a cocoon, this was examined by slicing open the nipple-like structure at one end. The sex of the occupant was determined by noting the presence or absence of female clypeal horns on the head (Raw, 1972). In opening the cocoons, instances where larvae of the solitary parasitic wasp *Monodontomerus obscurus* had consumed the non-chitinous parts of the adult bee within were revealed (Figure 6.3D).

For the subset of ten nests, the sex of a failed individual (resulting from developmental failure or parasitism, Figure 6.5 categories D, E and F) was inferred from the sex of occupants in adjacent cells. This was possible as cells are aggregated according to sex in this species (Seidelmann *et al.*, 2010). As a precautionary measure, any failed cell with a female as one neighbour and a male as another was excluded from analyses as the occupant's sex could not reliably be inferred.

Overwintering storage and survival

After examination the cocoons were bulked according to nest and placed in plastic disposable food containers between two layers of paper kitchen-towel. The containers were pierced to prevent the build-up of CO_2 and placed in cold storage at 4°C (Sekita and Yamada, 1993, Bates *et al.*, 2011a). Between 21st and 23rd March 2012 the overwintered cocoons were returned to their nests. In late May 2012 the gardens were re-visited to establish the number of bees of each sex within each nest that had failed to emerge.
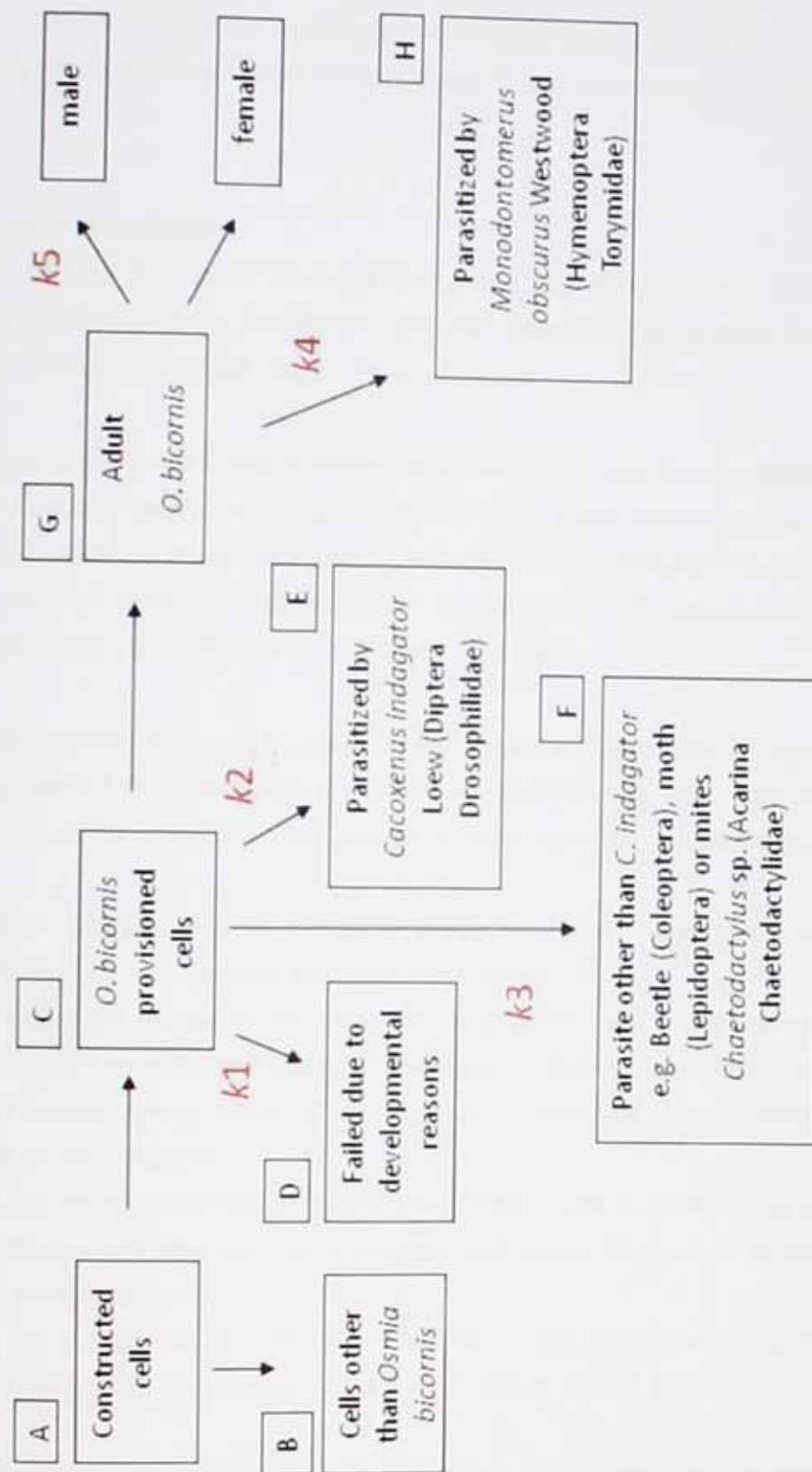
Figure 6.5 Flow diagram showing the fate of trap-nest cells according to 8 categories, together with *k* values derived from the life-table stages in Table 6.3.

Pre-existing wall cavities

The mean density of pre-existing cavities in the mortar was calculated by randomly assigning six 50cm x 50cm quadrats to the south-facing wall in each garden, counting the number of holes present in each, and generating a mean hole-density value.

Statistical analyses

In order to take account of one nest containing twenty-nine rather than thirty tubes (Canons Ashby, Nest 3), the fraction of tubes colonised rather than the absolute number of tubes colonised was used for analysis.

Life tables were created and k values calculated following the protocols of Varley *et al.* (1975) and Yamamura (1999), Appendix VIII. The k values for Lois Weedon (LW) were not calculated as cell numbers were low or non-existent in two of the three nests, meaning reliable values could not be obtained. Differences between properties were examined using Kruskal-Wallis tests on k values $1 - 4$.

Linear regression was used to examine the total number of deaths due to developmental failure in relation to brood cell position in a tube, and also for total deaths due to the presence of *C. indagator* against brood cell position.

To establish whether female or male progeny were more likely to be affected by the mortality factors a three-step approach was taken:

Step 1: Using the subset of ten nests and only those cells where the sex of the occupant could reliably be inferred, the actual number of females and males recorded at each brood cell position was used to calculate the relative proportion of each sex at each position.

Step 2: The relative proportions were multiplied by the number dying at each position to estimate the number of females and males dying from each mortality event at each location.

Step 3: The fraction of each sex at each location was calculated using the estimated number dying (step 2) divided by the total number across all cells

The difference in estimated numbers of females and males dying at each location (step 2) was analysed with a G-test for independence using the methods described in Sokal and Rohlf (1981). As the observed values for the four outer cells (cells 7, 8, 9 and 10) were 1 or less for females, these were bulked with the nearest cell, (cell 6).

A two-sample Kolmogorov-Smirnov test was used to examine differences in the distribution of male and female overwintering losses. This test allows the comparison of two sets of distribution data from a population (Dytham, 2011).

Results

Use of nests and tubes by solitary bees

All twenty-seven artificial nests were occupied by solitary bees. Of the 809 available tubes across all sites, 490 (61%) were used by a range of bees. Usage was defined as either a) initiation of a cell(s) within a tube, b) provisioning of cells, whether completed or not, or c) outer end of tube sealed, regardless of whether it was later found to contain cells. Only one property, Lamport (LAM), had all thirty tubes in each of its three nests fully used (Figure 6.6).
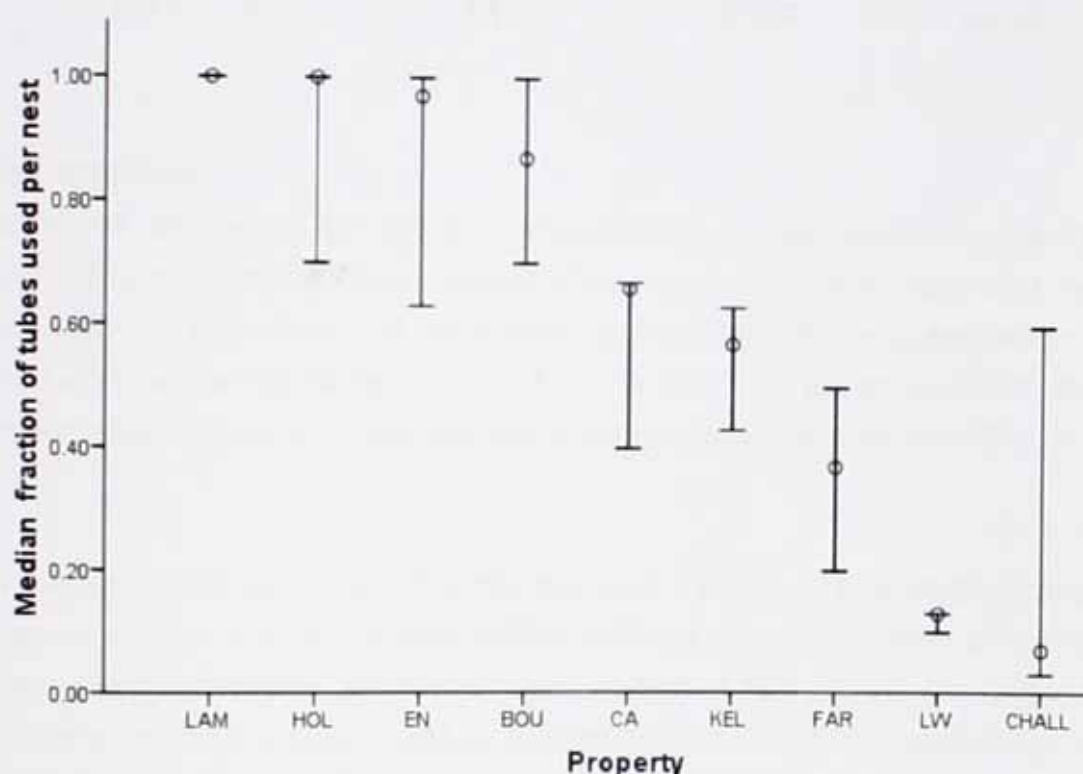
Figure 6.6 Median fraction of tubes used at each property, ranked highest to lowest, with range as error bars.

As the tube-usage data violated Levene's test for homogeneity of variance, both as a fraction and when arcsine transformed ($P = 0.01$), the non-parametric Kruskal-Wallis test was used. Tube usage (by all species) differed significantly between the nine gardens, $H(8) = 22.12$, $P = 0.005$. This result was followed up with *post hoc* tests as described by Siegel and Castellan (1988), (Appendix IX, Table 6.5).

Table 6.5 Results of *post hoc* tests on mean ranks of fraction of tubes used after a Kruskal-Wallis test using the procedure described in Siegel and Castellan (1988). Differences in mean ranks ≥ 10.53 are significant ($P ≤ 0.05$) and shown in bold.

	BOU	CA	CHALL	EN	FAR	HOL	KEL	LAM	LW
BOU	-	-	-	-	-	-	-	-	-
CA	7.17	-	-	-	-	-	-	-	-
CHALL	**15.17**	8.00	-	-	-	-	-	-	-
EN	0.47	6.70	**14.70**	-	-	-	-	-	-
FAR	**12.5**	5.33	2.67	**11.50**	-	-	-	-	-
HOL	1.66	8.83	**16.83**	2.66	**14.16**	-	-	-	-
KEL	9.0	1.83	6.17	**18.00**	3.50	**10.66**	-	-	-
LAM	3.83	**11.00**	**19.00**	4.83	**16.33**	2.17	**12.30**	-	-
LW	**16.17**	9.00	1.00	**15.17**	3.67	**17.83**	7.17	**20.00**	-

Cell creation

Of the 490 used tubes, 467 (95.3%) contained fully provisioned cells. A total of 2,657 cells representing all bee species (Category A, Figure 6.5, Table 6.6), were recorded from across the nine properties. Lamport Hall had the highest mean number of cells across all three nests (174.7 ± 19.4 SD), but the nest with the highest overall number of cells was at Easton Neston - 214 cells (nest EN3, Table 6.6).

Of the 2,657 cells recorded 2,521 (94.9%) were those of *O. bicornis* (Category C, Figure 6.5, Table 6.6). A one-way ANOVA revealed the mean number of cells for this species was significantly different between properties $F_{8,18} = 5.90$, $P = 0.001$. *Post hoc* tests (REGWQ) showed that Lois Weedon, Courteenhall and Farnborough had significantly fewer cells than Holdenby and Lamport (Figure 6.7).

Table 6.6 Use and contents of nests and tubes per property. *Canons Ashby trap-nest 3 contained only 29 tubes. Categories A–C described in Figure 6.5.

Location and trap-nest number	No of tubes used	Fraction used	Total cells in nest (A)	Cells other than O. bicornis (B)	O. bicornis cells (C)	Failed O. bicornis cells (D)	Cells occupied by C. indagator (O. bicornis larvae dead) (E)	Cells occupied by C. indagator and O. bicornis	Cells failed due to other parasite at larval stage (F)	O. bicornis cocoons (G)	cocoons parasitized by M. obscurus (H)	O. bicornis females	O. bicornis males
BOU 1	26	0.87	101	0	101	40	6	1	0	55	0	11	44
BOU 2	30	1.00	168	0	168	40	27	4	0	101	0	17	84
BOU 3	21	0.70	103	21	82	25	16	6	0	41	0	7	34
CA 1	12	0.40	56	0	56	15	5	3	1	35	1	15	19
CA 2	20	0.67	103	0	103	20	24	7	5	54	3	11	40
CA 3*	19	0.66	83	0	83	15	16	2	1	51	6	16	29
CH 1	18	0.60	86	4	82	13	11	2	0	58	1	8	49
CH 2	2	0.07	9	6	3	1	0	0	0	2	0	1	1
CH 3	1	0.03	6	0	6	1	0	0	0	5	1	1	3
EN 1	29	0.97	124	0	124	40	5	5	0	79	0	19	60
EN 2	19	0.63	61	0	61	21	0	0	0	40	0	19	21
EN 3	30	1.00	214	0	214	53	0	2	1	160	0	68	92
FAR 1	11	0.37	81	35	46	7	0	2	0	39	0	22	17
FAR 2	15	0.50	83	2	81	17	1	0	0	63	6	21	36
FAR 3	6	0.20	15	5	10	2	0	0	0	8	0	4	4
HOL 1	30	1.00	195	2	193	55	6	4	0	132	7	19	106
HOL 2	21	0.70	118	0	118	23	7	1	0	88	11	14	63
HOL 3	30	1.00	162	0	162	48	14	1	0	100	4	23	73
KEL 1	17	0.57	108	5	103	17	10	2	0	76	1	26	49
KEL 2	19	0.63	118	4	114	39	14	2	0	61	1	13	47
KEL 3	13	0.43	79	27	52	4	2	1	0	46	0	9	37
LAM 1	30	1.00	162	0	162	46	0	2	0	116	2	60	54
LAM 2	30	1.00	165	0	165	46	3	2	0	116	4	34	78
LAM 3	30	1.00	197	0	197	41	5	0	1	150	2	44	104
LW 1	3	0.10	14	6	8	7	0	0	1	-	-	-	-
LW 2	4	0.13	19	19	0	0	0	0	-	-	-	-	-
LW 3	4	0.13	27	0	27	3	0	0	-	24	0	10	14
TOTAL	490		2,657	136	2,521	639	172	49	10	1,700	50	492	1,158
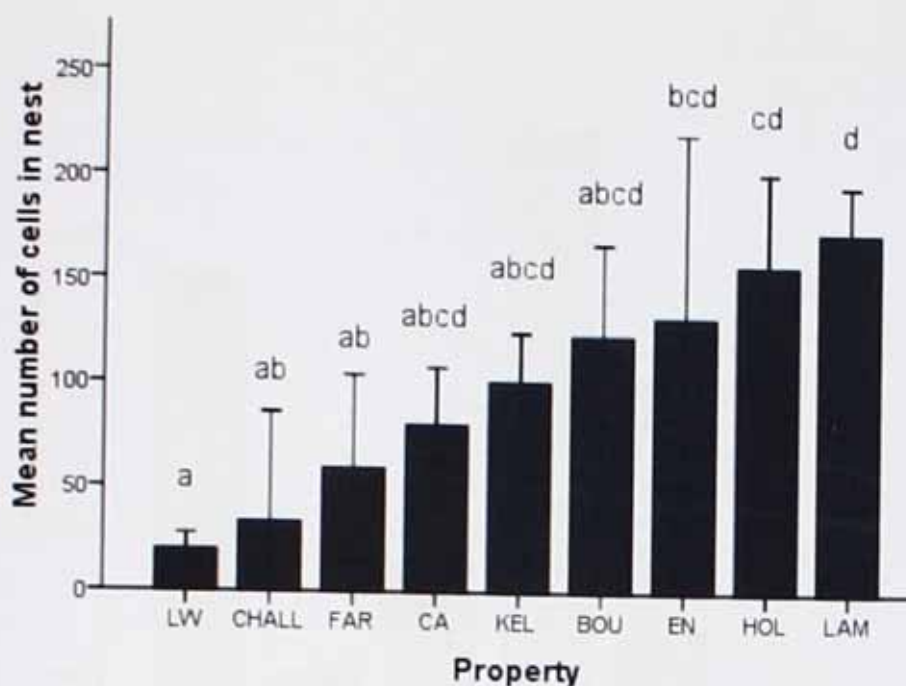
Figure 6.7 Mean number of *O. bicornis* cells per nest for each property (arithmetic mean ± SE). Identical letters show homogeneous groups (REGWQ *post hoc* tests).

Red mason bee cells and cells of other trap-nesting bee species

The absolute number of *O. bicornis* cells and those of other species (Appendix X) is given in Figure 6.8. Three walled gardens (Canons Ashby, Easton Neston and Lamport) only had *O. bicornis* cells present. For the six gardens with both *O. bicornis* and other species present there was no relationship between the number of cells of other species and those of *O. bicornis*, Pearson's $r = 0.42$, P (two-tailed) > 0.05.
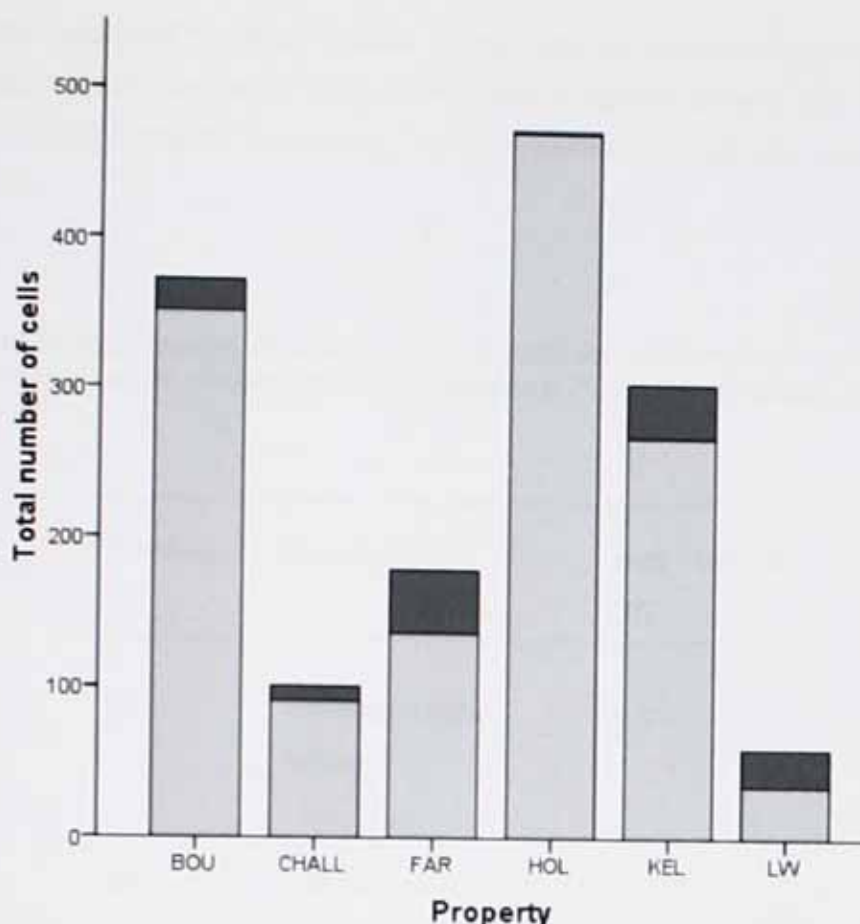
Figure 6.8 Total number of *O. bicornis* (light grey) and cells of other species (Appendix X), (dark grey) at properties where they co-occurred.

Pre-existing wall cavities and the creation of cells

No significant relationship was found between the mean number of holes in a 0.25m^2 area of south-facing wall and the number of *O. bicornis* cells (Spearman's *r*, one-tailed, 0.26, d.f. = 26, *P* = 0.12).

Failure and parasitism of *O. bicornis* cells

From the original 2,521 *O. bicornis* cells, only 1,700 (67.4%) individuals reached the quiescent adult stage, hereafter called cocoons, (category G Figure 6.5, Table 6.6). The loss of the remaining 821 cells was accounted for by: developmental failure (639), the presence of *Cacoxenus indagator* (172), and the presence of other parasites and cleptoparasites (10) – categories D, E and F (Table 6.6). Larvae of *C. indagator* were present in 101 of the 468 tubes used by the red mason bee (21.6%) and occurred in 221 (8.8%) *O. bicornis* cells. In general, the presence of *C. indagator* usually resulted in the death of the bee larva (≈78% mortality, Table 6.6).

The results of the four Kruskal-Wallis tests to consider the differences in $k1 - k4$ life-table values revealed that developmental failure of cells ($k1$) was not significantly different between properties, but that parasitism ($k2$) did vary significantly, (Table 6.7).

Table 6.7 Results of Kruskal-Wallis tests for differences in *O. bicornis* k values between eight properties (LW excluded). $P \leq 0.05$, degrees of freedom = 7 for each test.

k value	Description	Test statistic (H)	P value
$k1$	developmental failure	8.16	0.34
$k2$	cell parasitism by *Cacoxenus indagator*	15.72	< 0.01
$k3$	cell parasitism by others	17.08	< 0.01
$k4$	cocoon parasitism by *Monodontomerus obscurus*	14.23	< 0.02

The significant result for $k2$ (parasitism by *C. indagator*) was followed up with *post hoc* tests as described by Siegel and Castellan (1988), (Appendix IX, Table 6.8).

Table 6.8 Results of *post hoc* tests on mean ranks of $k2$ after a Kruskal-Wallis test using the procedure described in Siegel and Castellan (1988). Differences in mean ranks ≥ 9.38 are significant ($P \leq 0.05$) and are given in bold.

	BOU	CA	CHALL	EN	FAR	HOL	KEL	LAM
BOU	-	-	-	-	-	-	-	-
CA	1.33	-	-	-	-	-	-	-
CHALL	**10.67**	**12.00**	-	-	-	-	-	-
EN	**12.67**	**15.00**	2.00	-	-	-	-	-
FAR	**14.34**	**15.67**	4.33	2.33	-	-	-	-
HOL	5.00	6.33	5.67	7.67	9.34	-	-	-
KEL	4.00	5.33	6.67	8.67	**10.34**	1.00	-	-
LAM	**12.00**	**13.33**	2.67	0.67	2.34	7.67	8.00	-

To consider the density-dependent nature of *C. indagator* parasitism, the $k2$ values were regressed over the number of *O. bicornis* cells created. There was a significant non-linear relationship between the two variables ($F_{2,23} = 5.22$, $R^2 = 0.31$, $P = 0.01$, Figure 6.9).

k2

Number of *O. bicornis* cells created
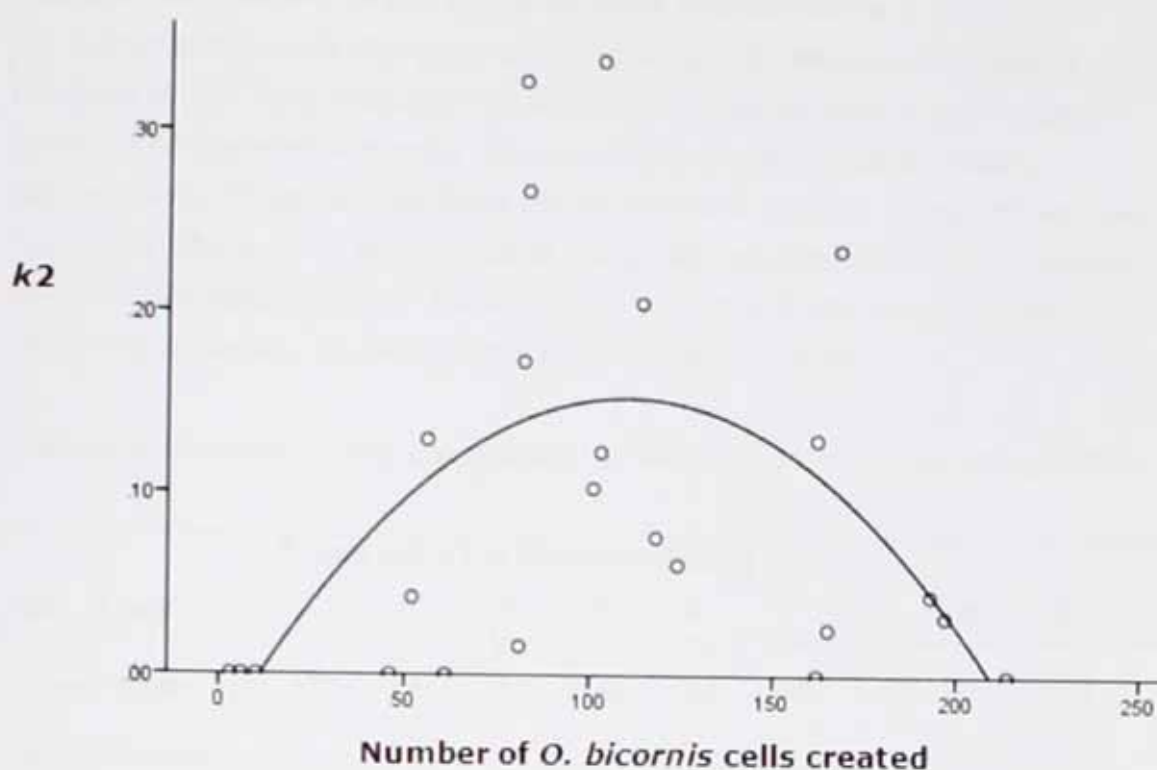
Figure 6.9 *k*2 values regressed over the starting number of *O. bicornis* cells.

The significant test result seen for *k*3 (parasitism by species other than *C. indagator*) was not pursued as only 10 out of a possible 1710 cells were found to be affected.

Fourteen nests at six of the eight properties were affected by *M. obscurus* (*k*4 in analysis). *Post hoc* tests (Siegel and Castellan, 1988) showed significant differences between six pairs of properties (Table 6.9).

Table 6.9 Results of *post hoc* tests on mean ranks of *k*4 after a Kruskal-Wallis test using the procedure described in Siegel and Castellan (1988). Differences in mean ranks ≥ 9.38 are significant ($P \leq 0.05$) and are given in bold.

	BOU	CA	CHALL	EN	FAR	HOL	KEL	LAM
BOU	-	-	-	-	-	-	-	-
CA	**13.83**	-	-	-	-	-	-	-
CHALL	9.00	4.83	-	-	-	-	-	-
EN	0.00	**13.83**	9.00	-	-	-	-	-
FAR	5.17	8.66	3.83	5.17	-	-	-	-
HOL	**14.50**	0.67	5.50	**14.50**	9.33	-	-	-
KEL	4.33	**9.50**	4.67	4.33	0.84	**10.17**	-	-
LAM	9.17	4.66	0.17	9.17	4.00	5.33	4.84	-

Position of failed and parasitized cells within tubes

The subset of ten nests examined to record brood cell category and position consisted of 248 used tubes and 1,404 cells. The total number of cells at each position and the relative number for each of the categories (spun cocoon, developmental failure and mortality due to the presence of C. *indagator*) are given in Table 6.10. The level of developmental failure did not differ significantly between the subset of ten nests (one-way ANOVA, $F_{3,6} = 1.91$, $P > 0.05$), nor did mortality as a result of C. *indagator* (Kruskal-Wallis $H(3) = 6.34$, $P > 0.05$).

Table 6.10 Number of cells per category at each brood cell position ($n = 1,404$).

	Brood cell (1 = innermost cell)									
Fate of cell	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Cocoon spun	130	123	119	109	108	98	99	75	44	17
Developmental failure	105	82	55	50	33	30	17	8	5	1
Failure due to C. *indagator*	13	13	10	12	13	11	7	11	4	2
Total cells	248	218	184	171	154	139	123	94	53	20

The proportion of cells failing due to developmental reasons showed a significant relationship with position in the tube ($F_{1,8} = 279$, $R^2 = 0.97$, $P < 0.001$), with a higher proportion affected at the innermost part (Figure 6.10A). Cells failing due to the presence of C. *indagator* showed the opposite effect ($F_{1,8} = 7.73$, $R^2 = 0.49$, $P = 0.024$ - Figure 6.10B). When combined, higher mortality rates occurred at the inner rather than the outermost part of each tube ($F_{1,8} = 191.6$, $R^2 = 0.96$, $P < 0.001$, Figure 6.10C).
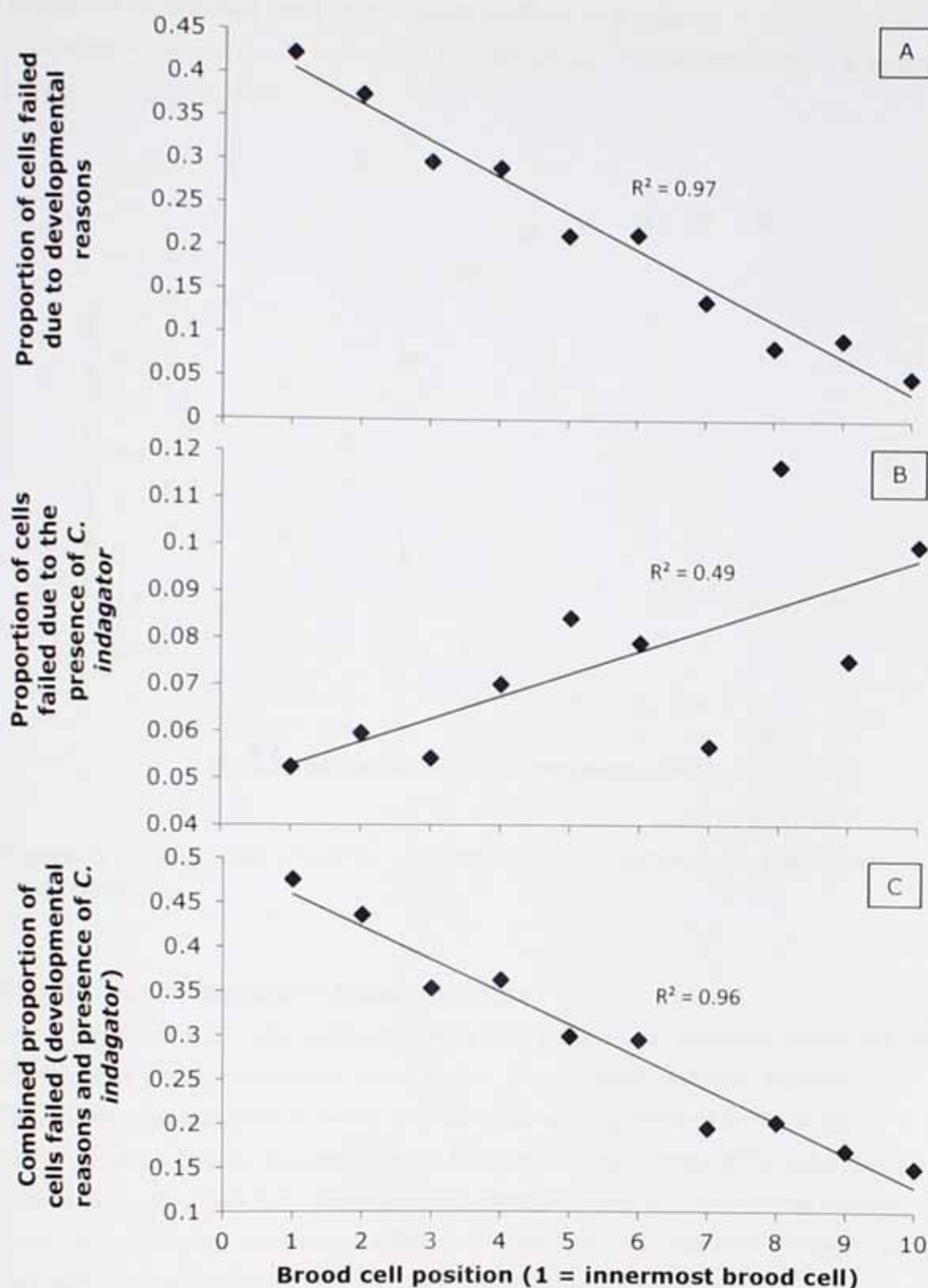
Figure 6.10 Proportion of failed cells at each brood cell position (1 = innermost cell) due to: A) mortality at the developmental stage, B) the presence of *C. indagator* and C) combined mortality factors. Total number of cells across all positions = 1,404.

Position of female and male cells within the tubes

The relative proportion of males and females at each brood cell position is given in Figure 6.11 ($n = 1,080$).
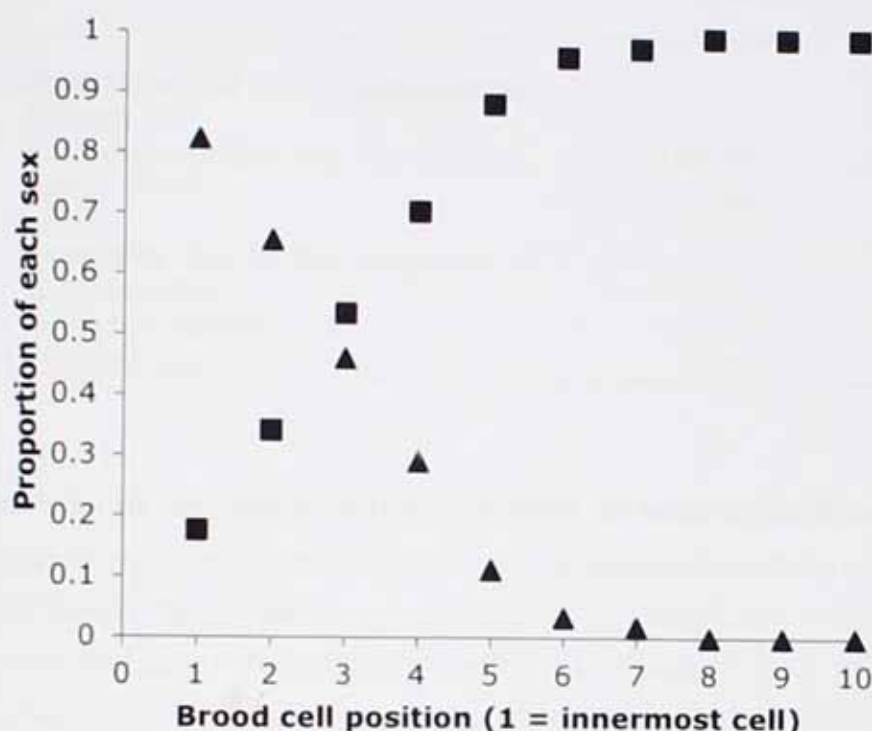
Figure 6.11 Proportion of males (squares) and females (triangles) at each brood cell position.

Proportion of male and female deaths

Using the female to male ratios, the predicted sex-specific mortality rates and the fraction lost per sex were calculated for the two mortality factors (Table 6.11). Despite similar numbers of males and females being predicted to die from developmental failure, the sex-specific fractions reveal a large difference between female and male losses. In the case of *C. indagator*, almost double the number of males are estimated to die compared to females. On this occasion however, identical sex-specific fractions were lost to this mortality cause (Table 6.11).

Table 6.11 Predicted number of males and females (and fraction) lost to two causes based on 1,080 individuals of known sex (Figure 6.11).

	Females	Males
Total in cells	342	738
Mortality due to developmental failure		
Predicted number lost	185.48	200.52
Fraction lost	0.54	0.27
Mortality due to the presence of _C. indagator_		
Predicted number lost	29.35	66.65
Fraction lost	0.09	0.09

Proportion of female and male deaths at each brood cell position

The proportion of males and females lost to developmental failure was significantly different across the cell positions examined (G = 159.03, d.f. = 5, P < 0.001), as were those lost as a result of the presence of _C. indagator_ (G = 46.73, d.f. = 5, P < 0.001, Figure 6.12A-B). A greater proportion of females in brood cell positions one and two was lost to the two combined mortality factors. In these two inner positions 160 female cells out of 342 (47%) died (Figure 6.12C).
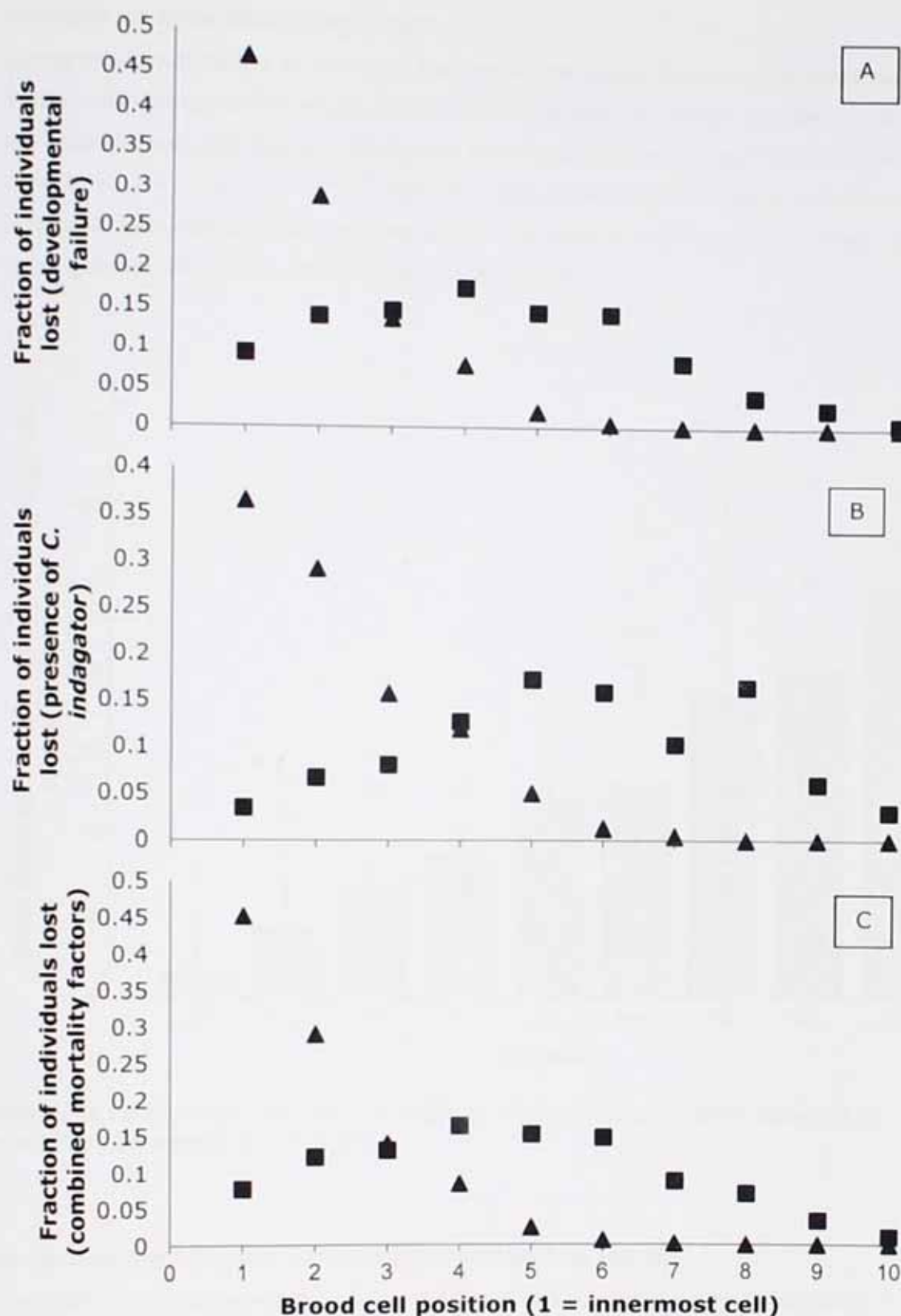
Figure 6.12 Fraction of female (triangles) and male (squares) individuals lost at each brood cell position (1 = innermost cell) as a result of: A) developmental failure B) the presence of *C. indagator* and C) the two mortality factors combined.

Number of overwintering adults

During the examination to establish the sex of each bee, fifty cocoons were found to contain *Monodontomerus obscurus* larvae. The remaining 1,650 cocoons (containing live adults) were significantly differently distributed across the gardens (one-way ANOVA, $F_{8,18} = 5.19$, $P = 0.002$). *Post hoc* tests (REGWQ) revealed a significant difference between cocoon numbers at Lois Weedon, Courteenhall, Farnborough and Canons Ashby and those at Lamport (Figure 6.13).
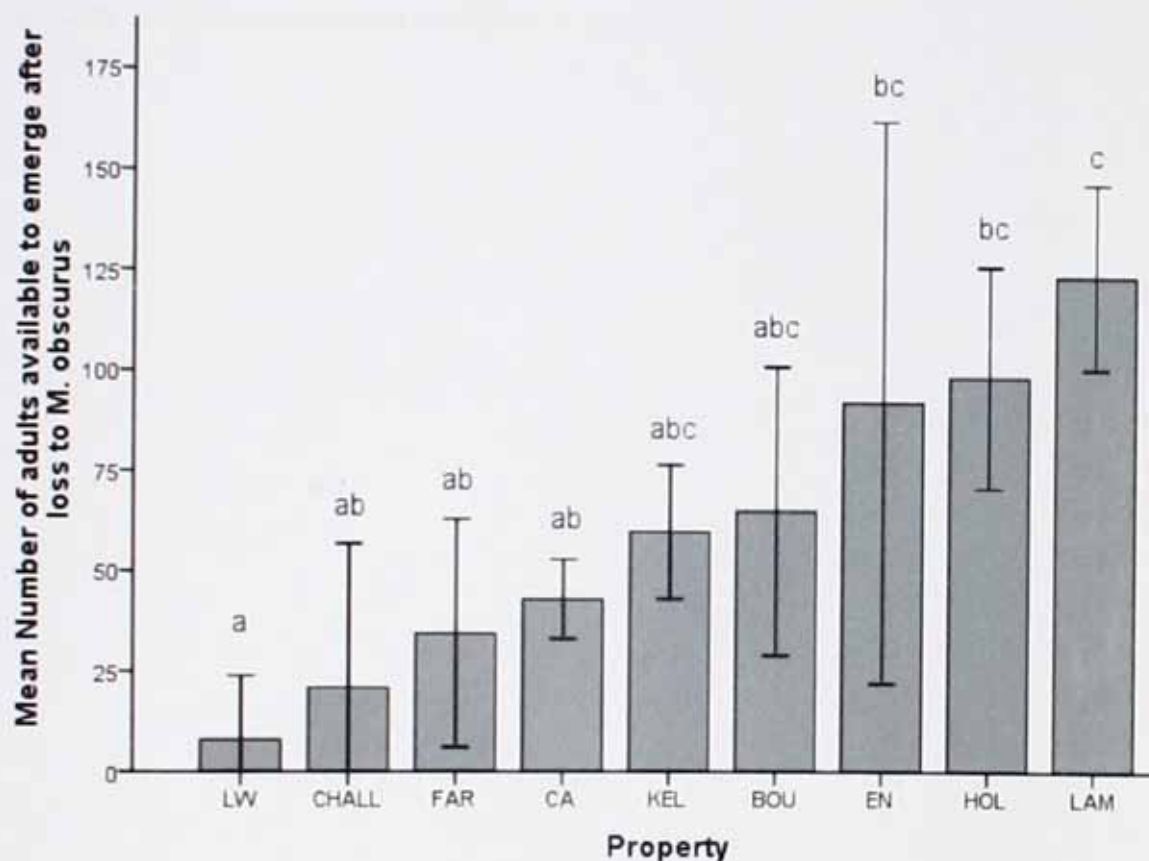
Figure 6.13 Difference in mean number of adult *O. bicornis* after losses to *M. obscurus* (Arithmetic mean ± SE).

O. bicornis male and female overwintering losses

The mortality rates between male and female overwintering bees (measured as the proportion of deaths per number of live bees in cocoons pre-winter) differed significantly, with a greater proportion of males failing to emerge (two-sample Kolmogorov-Smirnov $D_{24} = 1.59$, $P = 0.02$).

*k*6 life-table values – female overwintering mortality

Analysis of the *k*6 values, representing losses due to female mortality during the overwintering phase, revealed that there was no significant difference in female mortality between properties (Kruskal-Wallis H (7) = 11.88, $P > 0.05$).

Summary of *k* value losses

The losses experienced at each stage of the life-cycle for the red mason bee, from developmental failure at the start of the process (*k*1) to losses due to female mortality (*k*6), are presented in Figure 6.14.

Female

Adult

Provisioned cell

k1
0.35
(0.08 – 2.08)

k2
0.09
(0 – 0.34)

k3
0.005
(0 – 0.09)

k4
0.03
(0 – 0.22)

k5
1.19
(0 – 1.96)

k6
0.03
(0 – 0.17)

k values and descriptions
k1 – developmental failure
k2 – parasitism by C. indagator
k3 – parasitism by vector other than C. indagator
k4 – parasitism by M. obscurus
k5 – males discounted
k6 – overwintering deaths (females)
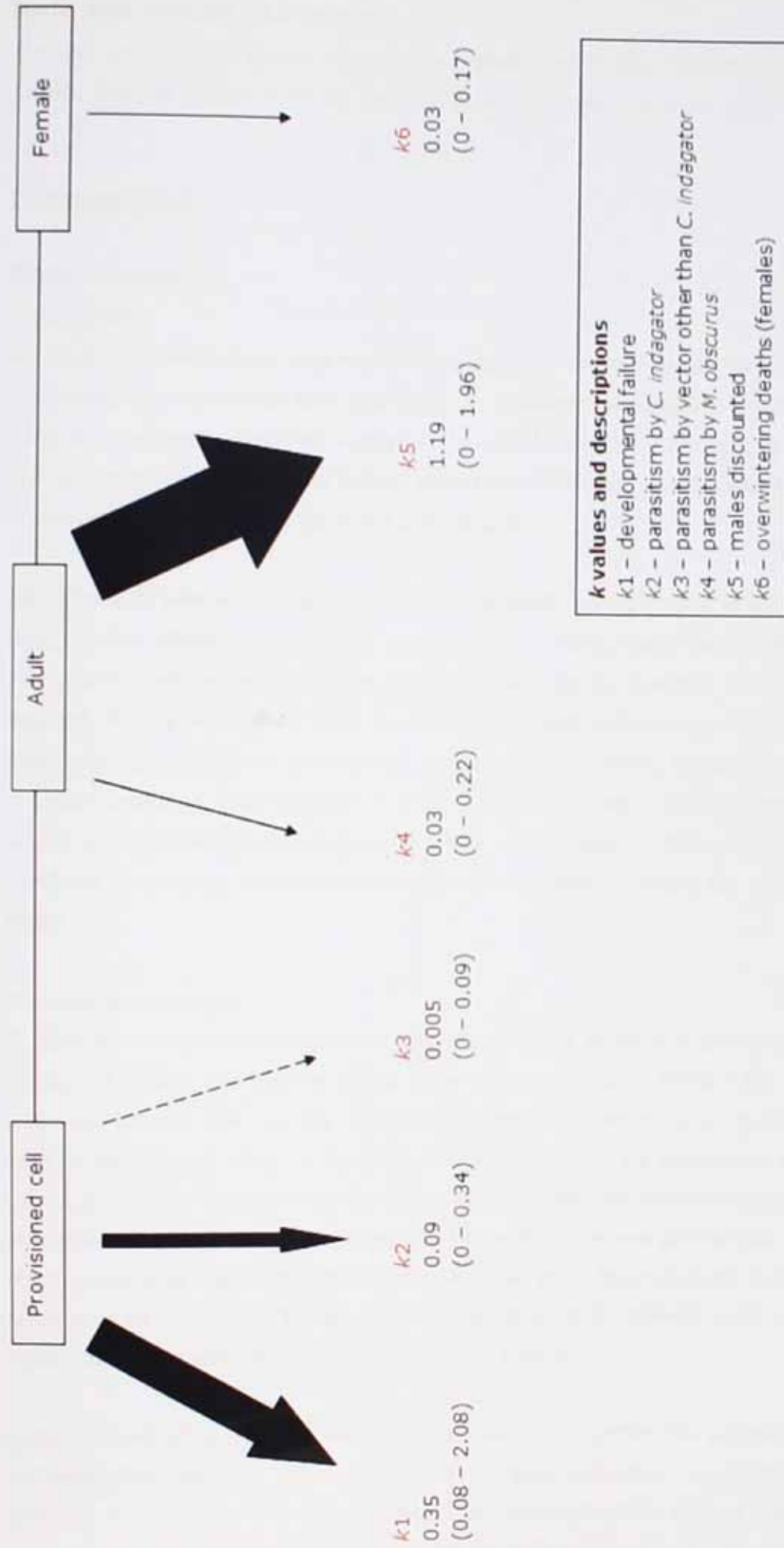
Figure 6.14 Summary of losses experienced at each life stage based on k values 1 – 6 as described in Figure 6.5. Thickness of arrows corresponds to mean loss at each stage. Values are mean k values with range in brackets.

Male and female sex ratios

The sex ratio for the subset of nests examined was 2.16:1 (males to females), $n = 1,080$. The pre-winter ratio for cocoons from all nests was 2.35:1 ($n = 1,650$).

Discussion

Nest occupancy

All species

All 27 of the commercial trap-nests were used by solitary bees (Table 6.6). This high occupancy rate contrasts with the study by Everaars et al. (2011), who found only 46% of *Phragmites* nests were used in an urban location. Although all nests in the current study contained used tubes, tube usage differed significantly between properties ($P = 0.005$), (Figure 6.6, Table 6.5).

The choice of where to locate nests and the preferred light regime appears to be a major factor affecting occupancy. Gaston et al. (2005) found nests placed in full sun were more likely to be used than those in shade. In the present study only south and east-facing walls were used for nest placement, taking care to avoid overhanging vegetation. In contrast, Everaars et al. (2011) placed nests in a range of light conditions, recording the lowest occupancy rates in nests attached to trees in shade, and the highest occupancy on walls in full sunlight. The current study confirms that sunny, unencumbered walls make ideal locations for artificial trap-nests.

The red mason bee

O. bicornis is a ubiquitous species, and was present in all nine gardens in 2010. In 2011, red mason bee cells occurred in 26 of the 27 nests (Table 6.6). As with other trap-nest studies this was the dominant species. It accounted for 95% of the created cells in the present study, a figure similar to that found by Holzschuh et al. (2010), (Table 6.2). Although other solitary bee species used the trap-nests provided, their abundance was low and there was little congruence across properties. No relationship was observed between the number of *O. bicornis* cells and those of other species ($P > 0.05$, Figure 6.8). The number of *O. bicornis* cells differed significantly between properties ($P = 0.001$, Figure 6.7).

High numbers of *O. bicornis* may be found nesting together for a number of reasons. Wilkaniec and Giejdasz (2003) noted that females aggregate if suitable cavities are present, however the method by which bees locate suitable sites is not fully understood. Mandibular gland secretions are believed to act as pheromone

aggregation cues, despite the solitary nesting habits of this species (Bosch and Kemp, 2004). A problem of nesting in close proximity to other females is that increased parasitism and predation may occur; a cost which must be balanced with that of searching for a more isolated nesting habitat (Rosenheim, 1990). Bischoff (2003) suggested that for one ground-nesting species (*Andrena vaga* Panzer, 1799) the high costs associated with searching for nest sites in early spring, when provision-collecting days are limited by weather constraints, act as a strong selective force for gregarious nesting behaviour. As red mason bees face similar weather-imposed 'down-time', it is possible that newly emerged females behave like *A. vaga*, i.e. they preferentially establish nests close to where they originally developed (philopatry).

The current study did not seek to establish the source of foundress populations, but the lack of any obvious relationship between the density of wall cavities and the number of cells created does not lend support to the idea that philopatry causes gregarious nesting.

Developmental failure and losses to parasitism

Developmental failure

Developmental failure accounted for the greatest loss of *O. bicornis* cells at the pre-pupal stage (Table 6.6, Figure 6.14). In the current study the mean developmental failure rate across all nests was 26.3% ± 14.8, $n = 26$. This was higher than the 12.1% failure rate recorded by Bosch and Vicens (2005) for *O. cornuta*, and 16.2% for *O. bicornis* by Gruber *et al.* (2011), but similar to that reported by Danks (1971), who found an average developmental failure rate of 23.6% for seventeen stem-nesting species. Of significance for the current study was the absence of any statistical difference in developmental mortality between the eight sites analyzed and also between the subset of properties examined ($P > 0.05$, Table 6.7). This suggests a consistent background failure rate may be occurring. This observation would benefit from further testing using additional gardens and/or greater nest density at some properties.

Mortality from developmental failure disproportionately affected cells located towards the innermost part of the tubes (Figure 6.10A). Although parasitism has been recorded according to cell position (Strohm, 2011), to my knowledge this is the first study to report on developmental failure according to cell position. The causes for cell failure at this stage include: fungal pathogens, inadequate cell provisioning and sub-optimal eggs (Danks, 1971, Steffan-Dewenter and Schiele, 2008). Methods to mitigate losses have been explored for other solitary bee species include avoiding

the re-use of nest tubes and observing good hygiene to reduce the spread of pathogens at the nest preparation stage (Sekita and Yamada, 1993, Bosch and Kemp, 2002). As new nests and tubes were purchased for the present study, hygiene is unlikely to have been an issue. The observed high rate of developmental failure demonstrates one of several important challenges that need to be overcome if this species is to be considered a candidate for managed-pollinator use.

Losses to *Cacoxenus indagator*

After developmental mortality, loss to the specialist fly *C. indagator* was the second highest cause of death (Table 6.6, Figure 6.14). Levels of parasitism ($k2$ values) were significantly different between properties ($P < 0.01$, Table 6.7). *Post hoc* tests showed that Boughton House and Canons Ashby had significantly higher levels of parasitism than the other seven properties (Table 6.8). A common factor linking these two gardens and a third, Holdenby, is that the walls in these gardens are constructed from stone (Table 6.4). Further work exploring whether wall materials influence rates of parasitism is needed.

Many studies have found *C. indagator* to be the main nest associate of the red mason bee, and it is often cited as the primary cause of larval mortality (Krunic *et al.*, 2005, and Strohm, 2011). These flies are frequently observed at the entrance of nest tubes waiting for female bees to depart, thereby allowing them access to the pollen and nectar reserves gathered by the host. When a female leaves to collect more larval food the fly enters and lays her own eggs on the pollen/nectar mass (pers. obs.). In the current study the presence of fly larvae did not always result in the death of the developing bee (22.2% of affected cells contained both fly larvae and cocoons containing live bees), but in the majority of cases mortality ensued. This result is similar to that found by Raw (1972) who noted that some bees were able to develop normally alongside *C. indagator*.

Management techniques to prevent the build-up of large populations of these flies when *Osmia* spp. are used as managed pollinators include the removal of infected bee cells by hand during the winter months, and successive-year removal of flies by aspirators during their flight period (Krunic *et al.*, 2005, Gruber *et al.*, 2011).

In contrast to the position of cells affected by developmental failure, mortality from *C. indagator* was more likely to occur towards the outermost part of the nesting tubes (Figure 6.10B). This pattern of increasing parasitism towards nest entrances has also been noted by Seidelmann (2006). Strohm (2011) found no relationship between brood cell position and parasitism rate, although the sample size was low (total cells = 189).

Parasitism and the density of *O. bicornis*

An unexpected result from the current work was that *C. indagator*-induced mortality (measured as $k2$ values) was significantly related (in a non-linear way) to the density of *O. bicornis* cells, with reduced mortality observed at both low and high cell densities (Figure 6.9).

The absence of a relationship between the hole-density of walls and both the mean number of cells created and those parasitized ($P > 0.05$, $n = 8$), suggests *C. indagator* may be able to locate nests independently of the presence of bees from previous years. A possible explanation is that at low bee densities, host nests might be patchily distributed, whilst at high densities, fly numbers may lag behind those of nesting females; a commonly observed feature of predator-prey systems (Maynard Smith, 1977). An alternative for the observed inverse density-dependence (where bee abundance is high) has been proposed by Steffan-Dewenter and Schiele (2008). These authors suggest that in areas where nests are frequented by many *O. bicornis* females, increased activity may serve to disturb patrolling flies, thereby reducing the incidence of parasitism. Observations of *O. cornuta* by Krunic *et al.* (2005) corroborate this. The authors note that female bees proactively dispel flies and 'dive frequently' on *C. indagator* females.

Differential mortality losses for males and females

Evidence from the current study shows a strong shift from predominantly female cells in the innermost positions (brood cell position one; 82% females, 18% males), to a more equitable distribution at position three (46% females, 54% males), followed by increased male cell dominance towards the outer part of the tube (Figure 6.11). The observed differences in the numbers of females and males at specific locations within tubes, combined with differential mortality factors, make females particularly vulnerable to the two mortality factors examined (Figure 6.10C, Figure 6.11). Although the estimated number of females and males perishing as a result of developmental failure did not differ greatly (185 versus 201), the fraction of females dying was notably high (0.54, Table 6.11, Figure 6.12A). This results from the strong male bias associated with this genus (Bosch and Vicens, 2005).

The position of *O. bicornis* females at the rear of the nest and males towards the front has been attributed to protandry (Raw, 1972), but is also considered a response to an increased risk of parasitism towards the outer part of nests (Seidelmann, 2006). According to the hypothesis of Seidelmann (2006), open-cell parasitism is believed to act as a selection pressure, causing females to preferentially switch from provisioning cells for females, to creating cells for males.

As males are smaller than females they require less food, resulting in fewer foraging trips of shorter duration by the mother bee. Reduced time away from the nest therefore reduces the incidence of parasitism (Bosch and Vicens, 2005, Seidelmann, 2006, Seidelmann et al., 2010). In contrast to this view, others have argued that a reduction in floral quantity and quality as the season progresses leads to reduced provisioning and therefore an increase in male offspring (Torchio and Tepedino, 1980). In some of the gardens sampled for the present study, both the number of genera and floral area available increased as the season progressed (data not presented), suggesting that limited floral resources are unlikely to have caused a switch to a higher number of male offspring. Whilst offering no evidence of causality, these results lend support to the hypothesis of Seidelmann (2006).

Male : female sex ratio

The diameter of nest materials influences the sex ratio of Osmia spp., with higher female to male ratios reported when wider reed stems are available (Krombein, 1967, Raw, 1972, Bosch and Kemp, 2002, Seidelmann et al., 2010). Tube length also affects sex ratios, with shorter lengths giving a more even ratio (Gruber et al., 2011). Together, these findings highlight the importance of using nest materials of standard widths and lengths. Despite this, to my knowledge no studies have adopted the use of commercial trap-nests to explore male to female sex ratios and parasitism. The use of standardised tubes with paper inners in the current study allows confidence to be placed in the sex ratios observed. This ratio is reasonably high (2.16 : 1), but still within the limits of other published accounts (Table 6.12).

Table 6.12 Observed male to female sex ratios for *O. bicornis* and *O. cornuta* from the current study and other published work. Studies are listed according to species and then in order of decreasing male to female ratios. Values for the current study are for the subset of ten nests examined.

Species	M : F sex ratio	*n*	Year(s)	Source
O. bicornis	1.35 - 2.68 : 1	range 200 -1,200	1996-99	Krunic and Stanisavljevic (2006)
O. bicornis	**2.16 : 1**	**1,080**	**2011-12**	**This study (subset of 10 nests)**
O. bicornis	1.59 : 1	411	1997-99	Seidelmann *et al.* (2010)
O. bicornis	1.11 : 1	236	1967/68	Raw (1972)
O. bicornis	0.91 – 1.53 : 1	range 2,850 – 22,633	2007-9	Gruber *et al.* (2011)
O. cornuta	1.46 – 3.22 : 1	range 400 - 2,500	1994-99	Krunic and Stanisavljevic (2006)
O. cornuta	1.78 : 1	998	1995	Vicens and Bosch (2000)

Overwintering losses

Overwintering losses have not previously been reported for this species, and the return of cocoons to their natal sites is rarely reported. To my knowledge, this is the first time that cocoons have been returned to sites to establish if male and female overwintering survival rates are similar. Results show that a significantly greater proportion of males than females failed to emerge after being returned to their nests ($P < 0.02$). Female overwintering mortality ($k6$ in life-table analysis, Table 6.3) did not differ between properties ($P > 0.05$).

Linking male : female sex ratios and the causes of larval mortality

In accordance with Fisher's theory of sex allocation, parental investment should be equally distributed between male and female offspring (Fisher, 1930). Where an organism is sexually dimorphic in terms of size - such as *O. bicornis*, where females

are approximately 1.6 times heavier than males, (Raw, 1972), the cost to female fitness of producing daughters is higher, and therefore a lower number of this sex should be produced. An addendum to this is Trivers and Willard's hypothesis that varying maternal condition results in deviations from a 50:50 investment in the two sexes (Trivers and Willard, 1973). Seidelmann (2006) demonstrated that for *O. bicornis*, body size is a good measure of maternal condition and that smaller females overcome the disadvantage of reduced ability to forage economically (measured as mass of reserves collected and time taken to acquire them), by shifting the sex ratio of their offspring towards smaller male progeny.

Combining these theories with Seidelmann's hypothesis that open-cell parasitism leads to increased numbers of males (Seidelmann, 2006) suggests that multi-faceted and sometimes competing forces operate to alter progeny sex ratios. This is evidenced in the current study in three ways: (i) nests typically had more male than female progeny, (Table 6.6), (ii) females experienced higher overall mortality than males due to the combined factors of developmental failure and parasitism (Figure 6.12C), and (iii) higher proportions of males were lost during the overwintering phase.

Teasing out whether position within the nest (and therefore incidence of parasitism and developmental failure), maternal condition (which determines the level of food reserves collected and therefore the sex and size of offspring) or the top-down effect of parasitism (*C. indagator* shaping maternal investment as per Seidelmann, 2006), work together or differentially to drive observed sex ratios is an area requiring further study.

Conclusions

The findings of this chapter can be summarised as follows:

- The standardised nature of commercial trap-nests makes them ideal for exploring the differential effects of mortality on male and female progeny of cavity-nesting bees.

- Commercial trap-nests placed in walled kitchen gardens were readily used by bees. *Osmia bicornis* was the most frequent occupant of these nests.

- No relationship exists between pre-existing hole density in wall mortar and the number of *O. bicornis* cells created and parasitized.

- The calculation of *k* values is a useful way of allowing *O. bicornis* mortality factors to be compared across sites.

- The greatest loss of *O. bicornis* progeny was observed at the developmental stage. This mortality factor disproportionately affected cells at the rear of the nest.

- The specialist parasite *Cacoxenus indagator* was the second highest cause of larval mortality. This mortality factor disproportionately affected cells towards the front of the nest.

- Due to the strong male bias associated with this species, fewer female cells were created than male cells.

- Female cells were preferentially located at the rear of nests, making them particularly vulnerable to losses arising from developmental failure. More than half of all female cells were predicted to fail.

- As females are the main flower visitors, high losses have implications for the development of this species as a managed pollinator.

- *C. indagator* mortality was found to be related in a non-linear way to *O. bicornis* cell density. Density independence was observed when both low and high bee-cell densities occurred. High densities of bees may deter *C. indagator* from entering nests, thereby reducing parasitism.

- A significantly greater number of males did not emerge after the overwintering period than females.

In summary, walled gardens have the potential to support populations of cavity-nesting bees. The dominance of *O. bicornis*, which is known to visit a wide range of flowers in spring and early summer, has been recorded at these locations for the first time. The importance of this species (and other solitary bees) as a backup for commercial pollination in the face of honey bee declines is increasingly acknowledged (Bosch and Kemp, 2002). By using commercial trap nests this work has shown (for the first time) the differential effects of mortality on male and female bees. If *O. bicornis* is to be used as a managed pollinator, suitable methods to control for these effects will be needed.

The next chapter summarizes the findings of the study, offers a critique of the methods and highlights areas for further investigation.

Chapter 7

Conclusions

Chapter overview

In this chapter, the key findings of the study are re-visited and a critique of the methods is given. Areas for further work are suggested in the context of the study's findings.

Key findings of the study

The results from this work offer new insights into the role that large rural gardens play in supporting insects regarded as potential pollinators.

The key findings are presented in two parts. Firstly the diversity of insects in gardens is discussed in relation to local and landscape-scale factors, and secondly the knowledge gained from the experimental use of commercial trap nests is considered.

The value of gardens

Insect diversity and community structure

English country houses have long been appreciated for their cultural heritage, but until now there has been limited focus on their natural-heritage value. This is the first study of its kind to provide base-line data on the species richness and abundance of a suite of flower visitors across the season in a significant sample of country-house gardens.

The results show that rural-garden habitats support a wide range of flower-visiting insects. In the 2010 field season almost 10,000 flower visitors, from 174 species, were recorded in 17 gardens (Appendix VI, Chapter 3), whilst in 2011, almost 2,500 individuals were recorded from 136 species in nine walled gardens (Appendix VI, abundance data not presented). Overall, 189 flower-visiting insect species were identified across the 17 gardens over a two-year period (Appendix VI).

The study found that, despite gardens containing different habitat components, the diversity they supported was highly similar, comparing favourably to vice-county data (Chapter 3). For example, 14 of the potential 17 species of bumblebee known from the region were found in the surveyed gardens.

By considering flower-visiting insects on a group basis it was possible to make comparisons across the whole community. Hoverfly species richness differed

significantly between properties; a result not seen for bumblebees, solitary bees or butterflies and day-flying moths (Table 3.3).

As a result of incorporating information on the flowers that insects visit, this study has revealed, for the first time, how floral resources in novel ecosystems are used by insects.

Flower diversity

High flower diversity emerged as a common theme across the properties surveyed, with more than a fifth of the world's plant families recorded from just 17 sites. Despite this high richness, only a subset of these plants were visited by insects. A higher proportion of flowering plants were visited in spring than at any other time, suggesting that gardens help to support populations of insects when floral resources in the landscape may be patchy or inadequate.

A strong positive link between the floral resources present and the diversity of insects observed was noted. Both the number and abundance of flower visitors increased as flowering plant resources increased.

The study also revealed, for the first time, the composition of floral resources in rural gardens in terms of their native or alien status. Approximately 68% were alien, a remarkably similar percentage to that found in urban gardens in the UK and Mexico (Smith *et al.*, 2006a, Loram *et al.*, 2008b).

Another novel finding was that the insects recorded showed no preference for native over alien plants, and that certain families (exhibiting different colours and morphology) were preferred in different seasons. These findings suggest that, regardless of the domination of gardens by alien plant species, the presence of these non-native floral resources does not act as a barrier for insects visiting flowers for food.

Although the complexity of plant-flower interactions were considered in terms of a number of metrics, including connectivity and nestedness, the study found that inherent weaknesses with these meant meaningful interpretation of the results was limited.

Despite floral resources partially explaining the diversity of insects observed, they were only one factor driving insect presence at a site. Landscape-scale factors were also important.

Wider landscape-scale effects

The study revealed that across the four insect groups, different landscape scales and factors played a role in explaining species richness to a greater or lesser extent. Bumblebees were affected by landscape factors within larger areas than other groups, and solitary bees were invariant to landscape-scale factors; instead being more influenced by within-garden effects. The response of bumblebees to plant richness late in the season (a local-scale effect) provides further evidence that the availability of resources in gardens across the whole season is an important attribute within agriculture-dominated landscapes.

The study also revealed that splitting a group of insects according to their nesting biology could reveal previously unappreciated responses to local-scale effects. Ground-nesting solitary bees showed a positive response to floral diversity whilst cavity-nesting bees responded to the area of beds and borders available. These results highlight the value of not only identifying insects to species level, but also incorporating an understanding of their life-history traits into interpretations about their presence.

Trap-nest bees

This study has shown for the first time that the deployment of commercial trap-nests can reveal new and important insights into the mortality factors affecting males and females of a single solitary bee species, *Osmia bicornis*. As honey bees are known to be suffering global declines (vanEngelsdorp and Meixner, 2010) these results take on increasing significance as the potential for new commercially-managed pollinators is explored.

The study found that the greatest mortality loss for *O. bicornis* was at the juvenile developmental stage and that this disproportionately affected cells at the rear of nests. Parasitism by a specialist fly, *Cacoxenus indagator*, was the second highest cause for mortality; this time affecting cells at the front of the nest. Due to the strong male bias associated with the species, and the preferential occurrence of females at the rear of nests, this resulted in females being disproportionately affected by these combined mortality causes. As a result, more than half of all female cells were deemed unlikely to produce healthy bees, with potential

consequences for future pollination effectiveness. Although offering no solutions for this, the study has drawn attention to the fact that the issue of losses needs to be addressed if this species is to be developed as a managed pollinator.

Summary

The main aim of this project, as described in Chapter 1, was to explore the structure and composition of plant-pollinator assemblages in English country-house gardens. The work addressed four broad research questions and found that these novel ecosystems supported a diverse array of flower-visiting insects, with some groups such as bumblebees particularly well represented. Flower resources and their use were categorized, revealing the dominance of alien plants with no obvious preference for natives by the insects present. Bumblebees were affected by landscape factors at large spatial scales throughout the season, whilst solitary bees were influenced by within-garden factors. The use of commercial trap-nests offered new insights into the differing effects of mortality on male and female offspring of the red mason bee. Overall, English country-house gardens emerged as previously unappreciated novel ecosystems that can be classed as important sites for flower-visiting insects.

Critique of methods

The methods employed at the planning, data gathering and analysis stages are reviewed here in turn.

Project planning

As described in Chapter 2, a Ph.D. project is necessarily limited by both time and resources. This project is no exception. The decision to focus on a single geographic area delivered advantages through the amelioration of potential differences in the distribution of species, as well as allowing more time to be spent sampling at properties.

Despite a range of country houses being selected, a possible criticism of an early planning decision was that sufficient replicates of similar types of property were not made. Kirby Hall is a good example. Described in the past as having 'Ye finest garden in England' (Burton, 1994), it was one of only two English Heritage properties within the seventeen sites chosen. Additionally, Kirby Hall was the only site not to possess a fully inhabitable house. Results from the study consistently found this garden to be an outlier in terms of both insect and plant species richness. The absence of similar sites to Kirby Hall makes it difficult to draw conclusions about why this garden was so species poor. Was it simply because the

gardens did not support a wide range of flowering plants, or were management practices (consistently tightly mown lawns and strimmed grass banks) the underlying cause? The percentage of land categorized as 'arable and horticulture' within a 750m radius of Kirby Hall was relatively low compared to many others (data not presented), but it had a moderately high percentage of improved grassland in the same area. Could the effect of these landscape-scale characteristics have interacted with the floristically-poor gardens to reduce the number of flower visitors observed at Kirby Hall? Without the availability of similar sites for comparison, it is difficult to gauge the true cause.

Another possible issue is the lack of direct comparison between the gardens sampled and areas beyond the property boundaries. This was partly solved by comparing the results obtained with other studies (albeit not on a like-for-like basis) as well as to vice-county data (Chapter 3). This is considered further in the section 'areas for further work' below.

Data gathering

The methods used at the data gathering stage allowed standardised sampling to take place. The observation and netting of individuals by a single person (the author) reduced recorder variation but the introduction of recorder bias cannot be ruled out (UKBMS, 2010a).

Despite some anticipated visits to gardens being cancelled and rescheduled for later dates (some of which occurred during the following sampling session), this did not appear to impact on the robustness of the methods used (Figure 4.6).

A possible drawback of the method chosen to assess flower-visitors in the 2010 field season was the restriction of observations to only those where an insect was in contact with flower reproductive structures. This decision served to limit direct comparisons with other studies where a full inventory of all insects was made (e.g. Edwards, 2003). In spite of this, it also yielded benefits by providing hitherto unpublished data on the interactions between flower visitors and the many alien plants found in rural gardens.

Data analysis

The use of standard techniques for analyzing data and the employment of null models where appropriate (e.g. for WNODF and redundancy analysis in CANOCO) allowed the robust testing of research questions and confidence to be placed in the results obtained. Limitations arising from the nestedness procedures manifested

themselves in the form of data interpretation issues rather than the analyses themselves.

Areas for further work

The suggested areas for further work are discussed at scales ranging from individual gardens to the wider-landscape, and incorporate interactions between English country-house gardens and the visiting public.

Within-garden management

In addition to the floral resources available within gardens, the management of these habitats is likely to influence the diversity of insects found there. The suggestion by Galluzzi et al. (2010) that gardens are 'resilient ecosystems' that are shaped by the close interactions between humans and nature, has not been explicitly tested and would benefit from an assessment of the impacts of different management approaches. Whilst a laissez-faire approach to gardening is known to be beneficial for biodiversity (Head, 2012), this is rarely adopted at country-houses. Instead, the management of flower-rich areas close to the house is usually deemed a vital component of the overall appearance of a property.

To assess the effects of different management styles, the tilling and mowing regimes adopted in individual gardens could be considered. The hoeing of soil on flower beds and borders allows areas to be kept free of weeds, whilst at the same time creating habitat for solitary bees that prefer vegetation-free areas for nest sites (Roubik, 1992). The requirement for most gardens to be maintained to a high visual standard (i.e. completely weed free), in combination with numerous volunteer gardeners at some sites means, however, that some beds receive continual soil disturbance, thereby reducing nesting opportunities and success. Identifying whether continual hoeing and weeding limits the occurrence of ground-nesting species is an area that could be investigated.

Similarly, mowing regimes (in particular the methods and frequency of mowing) could be assessed. Enquiries at many of the sites where sampling took place revealed external mowing contracts were in place. As a result, lawns were being mowed on a weekly basis regardless of their growth state, resulting in flower patches (such as red and white clover and dandelions) that were favoured by insects being continually removed. Added to this was the mechanical destruction of bees whilst they nectared on flowers present in lawns. This occurred due to the use of fast-moving ride-on lawn mowers which gave insufficient time for bees to fly off

and escape the mowers' blades. Bumblebees were observed to be the most frequent victims of this practice (Figure 7.1).

Figure 7.1 Selection of bumblebees killed as a result of ride-on mowers. These individuals were collected along a 10m stretch of newly mown grass at one of the study sites and were still alive at the time the image was taken. Image: Erenler, (2010).

Comparisons with other sites

The decision about whether to use pesticides and herbicides at a property clearly rests with the head gardener or estate manager. The extent to which these chemicals are used, and the conditions and seasons in which they are applied may affect the health of flower-visiting insects (Whitehorn *et al.*, 2012). In the current study a mismatch between the responses recorded from head gardeners in a questionnaire about the use of spray-applied pesticides and herbicides and their *actual* application by gardeners was observed on a number of occasions. Pairing

properties where sprays are known to be used with gardens that reject the application of chemicals may reveal differences in insect species richness and/or abundance. The pairing of sites with reference sites is an established method of assessing the biodiversity value of a habitat (Tarrant *et al.*, 2012).

Wider landscape effects

The results presented in Chapter 5 of this thesis reveal that landscape-scale processes have the potential to affect flower-visitor richness and abundance but that this may vary according to the group of interest (Table 5.4 and Jauker *et al.*, 2009). The United Kingdom, and particularly Central England, is currently seeing an expansion of the area planted with oilseed rape (OSR) – up 9.8% in 2011 from the previous year (Defra, 2011). Assessing the effect of this mass-flowering crop on insect pollinators both within and beyond garden boundaries is a subject demanding further attention. Whilst a range of pollinators is known to visit OSR and enhance yields (Bommarco *et al.*, 2012, Jauker *et al.*, 2012b), it has also been shown to distort plant-pollinator interactions (Diekotter *et al.*, 2010). Building on the results of Chapter 5, and specifically addressing questions about seasonality, the temporary (or otherwise) movement of beneficial insects beyond gardens into the wider landscape to forage on OSR could be examined.

Assessing the influence of country-house gardens on the public

As the number of people living in urban environments continues to rise, people's own gardens and those they choose to visit take on increasing importance for human wellbeing (Davies *et al.*, 2009). The extent to which country-house gardens influence attitudes to biodiversity, garden design and plant purchasing decisions remains unknown. What is not in question, however, is that visiting culturally important sites remains a popular activity. As noted in Chapter 1, the National Trust alone had more than 19 million paid visits to their sites in 2011 (The National Trust, 2012b). A qualitative assessment of how these sites influence the general public may reveal both the positive and negative aspects of highly managed and maintained garden areas.

Whilst an increasing awareness of the importance of biodiversity is broadly acknowledged by owners and managers of country-house gardens, this does not always translate into a realistic appreciation of the true diversity of some groups. Native bees are a good example of this. Improving the awareness of the habitat requirements of a range of solitary and social bees in addition to the needs of honey bees requires knowledge to be shared about this important group of pollinators.

Concluding remarks

The decline and potential extinction of charismatic species make headlines, whilst cumulative losses of biodiversity rightfully raise concern (WWF, 2012, Natural England, 2010). Less appreciated, and less easy to observe however, is the erosion of ecological interactions (Kearns and Inouye, 1997). As the unprecedented threat to the ecosystem service of pollination continues, English country-house gardens emerge as important novel ecosystems capable of supporting biodiversity and ecological webs.

Humankind did not weave the web of life -

We are but one thread within it.

Whatever we do to the web we do to ourselves.

All things are bound together.

All things connect.

Adapted from an original version created in 1972 by Ted Perry for the film *Home* (Berkes, 1999).

References

Ahrné, K., Bengtsson, J. and Elmqvist, T. (2009) Bumblebees (*Bombus* spp) along a gradient of increasing urbanization. *Plos One*. **4** (5) E5574.

Alarcón, R. (2010) Congruence between visitation and pollen-transport networks in a California plant-pollinator community. *Oikos*. **119** (1), 35-44.

Alarcón, R., Waser, N. M. and Ollerton, J. (2008) Year-to-year variation in the topology of a plant-pollinator interaction network. *Oikos*. **117** (12), 1796-1807.

Allen-Wardell, G., Bernhardt, P., Bitner, R., Burquez, A., Buchmann, S., Cane, J., Cox, P. A., Dalton, V., Feinsinger, P., Ingram, M., Inouye, D., Jones, C. E., Kennedy, K., Kevan, P., Koopowitz, H., Medellin, R., Medellin-Morales, S., Nabhan, G. P., Pavlik, B., Tepedino, V., Torchio, P. and Walker, S. (1998) The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conservation Biology*. **12** (1), 8-17.

Allesina, S. (2012) Ecology: The more the merrier. *Nature*. **487** (7406), 175-176.

Almeida-Neto, M. and Ulrich, W. (2011) A straightforward computational approach for measuring nestedness using quantitative matrices. *Environmental Modelling & Software*. **26** (2), 173-178.

Althorp Estate *Althorp Hospitality - Wedding venue* [online]. Available from: http://www.althorp.com/hospitality/wedding.php [Accessed 21 September, 2012].

APG III (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society*. **161** (2), 105-121.

Aslet, C. (1982) *The Last Country Houses*. London, England: Yale University Press.

Atmar, W. and Patterson, B. D. (1993) The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia*. **96** (3), 373-382.

Ball, S. G., Morris, R. K. A., Rotheray, G. E. and Watt, K. R. (2011) *Atlas of the Hoverflies of Great Britain (Diptera, Syrphidae)*. Wallingford, England: Biological Records Centre.

Baltanas, A. (1992) On the use of some methods for the estimation of species richness. *Oikos*. **65** (3), 484-492.

Banasek-Richter, C., Bersier, L., Cattin, M., Baltensperger, R., Gabriel, J., Merz, Y., Ulanowicz, R. E., Tavares, A. F., Williams, D. D., De Ruiter, P. C., Winemiller, K. O. and Naisbit, R. E. (2009) Complexity in quantitative food webs. *Ecology*. **90** (6), 1470-1477.

Bartomeus, I., Ascher, J. S., Wagner, D., Danforth, B. N., Colla, S., Kornbluth, S. and Winfree, R. (2011) Climate-associated phenological advances in bee pollinators and bee-pollinated plants. *Proceedings of the National Academy of Sciences of the United States of America*. **108** (51), 20645-20649.

Bascompte, J., Jordano, P., Melian, C. J. and Olesen, J. M. (2003) The nested assembly of plant-animal mutualistic networks. *Proceedings of the National Academy of Sciences of the United States of America*. **100** (16), 9383-9387.

Bates, A., Sadler, J. and Dean, R. (2011a) *Photographic guide to pre-adult tube-nesting aculeates and their parasites.* Unpublished material.

Bates, A. J., Sadler, J. P., Fairbrass, A. J., Falk, S. J., Hale, J. D. and Matthews, T. J. (2011b) Changing bee and hoverfly pollinator assemblages along an urban-rural gradient. *Plos One.* **6** (8), e23459.

BBC *BBC Weather - next 24 hours* [online]. Available from: http://news.bbc.co.uk/weather/forecast [Accessed 18 April, 2010].

BBCT (Bumblebee Conservation Trust). *BBCT Home page* [online]. Available from: http://bumblebeeconservation.org/ [Accessed 24 September, 2012].

Beccaloni, G. W. and Gaston, K. J. (1995) Predicting the species richness of Neotropical forest butterflies - Ithomiinae (Lepidoptera, Nymphalidae) as indicators. *Biological Conservation.* **71** (1), 77-86.

Beckett, M. *England's Lost Country Houses* [online]. Available from: www.lh.matthewbeckett.com [Accessed 12 September, 2012].

Beekman, M. and Ratnieks, F. L. W. (2000) Long-range foraging by the honey-bee, *Apis mellifera* L. *Functional Ecology.* **14** (4), 490-496.

Benedek, Z., Jordan, F. and Baldi, A. (2007) Topological keystone species complexes in ecological interaction networks. *Community Ecology.* **8** (1), 1-7.

Bergh, J. C. and Short, B. D. (2008) Ecological and life-history notes on syrphid predators of woolly apple aphid in Virginia, with emphasis on *Heringia calcarata*. *Biocontrol.* **53** (5), 773-786.

Berkes, F. (1999) *Sacred Ecology.* 2nd Edition. New York, USA: Taylor and Francis.

Bersier, L. F., Banasek-Richter, C. and Cattin, M. F. (2002) Quantitative descriptors of food-web matrices. *Ecology.* **83** (9), 2394-2407.

Bezerra, E. L. S., Machado, I. C. and Mello, M. A. R. (2009) Pollination networks of oil-flowers: a tiny world within the smallest of all worlds. *Journal of Animal Ecology.* **78** (5), 1096-1101.

Biesmeijer, J. C., Roberts, S. P. M., Reemer, M., Ohlemueller, R., Edwards, M., Peeters, T., Schaffers, A. P., Potts, S. G., Kleukers, R., Thomas, C. D., Settele, J. and Kunin, W. E. (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science.* **313** (5785), 351-354.

Binney, M. *Victoria and Albert Museum. 1974 Exhibition 'The Destruction of the Country House'* [online]. Available from: http://www.vam.ac.uk/content/articles/s/save-britains-heritage-1975-2005-30-years-of-campaigning/ [Accessed 12 September, 2012].

Bischoff, I. (2003) Population dynamics of the solitary digger bee *Andrena vaga* Panzer (Hymenoptera, Andrenidae) studied using mark-recapture and nest counts. *Population Ecology.* **45** (3), 197-204.

Blamey, M., Fitter, R. and Fitter, A. (2003) *Wild flowers of Britain and Ireland.* London, England: A & C Black Publishers Ltd.

Blüthgen, N., Fründ, J., Vazquez, D. P. and Menzel, F. (2008) What do interaction network metrics tell us about specialization and biological traits? *Ecology.* **89** (12), 3387-3399.

Bommarco, R., Marini, L. and Vaissiere, B. E. (2012) Insect pollination enhances seed yield, quality, and market value in oilseed rape. *Oecologia.* **169** (4), 1025-1032.

Borcard, D., Legendre, P. and Drapeau, P. (1992) Partialling out the spatial component of ecological variation. *Ecology.* **73** (3), 1045-1055.

Bosch, J. (1994) The nesting-behavior of the mason bee *Osmia cornuta* (Latr) with special reference to its pollinating potential (Hymenoptera, Megachilidae). *Apidologie.* **25** (1), 84-93.

Bosch, J. and Kemp, W. P. (2002) Developing and establishing bee species as crop pollinators: the example of *Osmia* spp. (Hymenoptera : Megachilidae) and fruit trees. *Bulletin of Entomological Research.* **92** (1), 3-16.

Bosch, J. and Kemp, W. P. (2004) Effect of pre-wintering and wintering temperature regimes on weight loss, survival, and emergence time in the mason bee *Osmia cornuta* (Hymenoptera : Megachilidae). *Apidologie.* **35** (5), 469-479.

Bosch, J., Kemp, W. P. and Trostle, G. E. (2006) Bee population returns and cherry yields in an orchard pollinated with *Osmia lignaria* (Hymenoptera : Megachilidae). *Journal of Economic Entomology.* **99** (2), 408-413.

Bosch, J. and Vicens, N. (2005) Sex allocation in the solitary bee *Osmia cornuta*: do females behave in agreement with Fisher's theory? *Behavioral Ecology and Sociobiology.* **59** (1), 124-132.

Boughton House *Website for Boughton House, Northamptonshire* [online]. Available from: www.boughtonhouse.org.uk [Accessed 21 September, 2012].

Breeze, T. D., Bailey, A. P., Balcombe, K. G. and Potts, S. G. (2011) Pollination services in the UK, how important are honeybees? *Agriculture Ecosystems & Environment.* **142**, 137-143.

Breeze, T. D., Roberts, S. P. M. and Potts, S. G. (2012) *The Decline of England's Bees.* Reading, England: The University of Reading.

Brickell, C. (ed.) (1999) *RHS New encyclopedia of plants and flowers.* 3rd ed. London, England: Dorling Kindersley.

Brooks, M. and Knight, C. (1982) *A complete guide to British butterflies.* London: Jonathan Cape Ltd.

Burgos, E., Ceva, H., Perazzo, R. P. J., Devoto, M., Medan, D., Zimmermann, M. and Delbue, A. M. (2007) Why nestedness in mutualistic networks? *Journal of Theoretical Biology.* **249** (2), 307-313.

Burkle, L. A. and Alarcón, R. (2011) The future of plant-pollinator diversity: Understanding interaction networks across time, space, and global change. *American Journal of Botany.* **98** (3), 528-538.

Burton, N. (1994) *English Heritage from the air.* 2nd ed. London, England: Sidgwick and Jackson Limited.

Butchart, S. H. M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J. P. W., Almond, R. E. A., Baillie, J. E. M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K. E., Carr, G. M., Chanson, J., Chenery, A. M., Csirke, J., Davidson, N. C., Dentener, F., Foster, M., Galli, A., Galloway, J. N., Genovesi, P., Gregory, R. D., Hockings, M., Kapos, V., Lamarque, J., Leverington, F., Loh, J., McGeoch, M. A., McRae, L., Minasyan, A., Morcillo, M. H., Oldfield, T. E. E., Pauly, D., Quader, S., Revenga, C., Sauer, J. R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S. N., Symes, A., Tierney, M., Tyrrell, T. D., Vie, J. and Watson, R. (2010) Global biodiversity: Indicators of recent declines. *Science.* **328** (5982), 1164-1168.

Butler, C. (1609) *The Feminine Monarchie or A treatise concerning bees and the due ordering of them.* Oxford, England: Joseph Barnes.

Butterfly Conservation. *BC Home page* [online]. Available from: http://www.butterfly-conservation.org/ [Accessed 25 September, 2012].

BWARS. *Bees, Wasps and Ants Recording Society* [online]. Available from: www.bwars.com [Accessed 1 September, 2012].

Campbell, C. (2005) *A history of kitchen gardening.* London: Frances Lincoln Ltd.

Campbell, C. (2010) *Walled kitchen gardens.* 2nd ed. Oxford: Shire Publications Ltd.

Cane, J.H. and Sipes, S. (2006) Characterizing floral specialization by bees: Analytical methods and a revised lexicon for oligolecty. In: Waser, N. M. and Ollerton, J. (eds.) *Plant-pollinator interactions: From specialization to generalization.* Chicago, USA: The University of Chicago Press. pp. 99-122.

Cane, J. H., Minckley, R. L. and Kervin, L. J. (2000) Sampling bees (Hymenoptera : Apiformes) for pollinator community studies: Pitfalls of pan-trapping. *Journal of the Kansas Entomological Society.* **73** (4), 225-231.

Cannon, A., Chamberlain, D., Toms, M., Hatchwell, B. and Gaston, K. (2005) Trends in the use of private gardens by wild birds in Great Britain 1995-2002. *Journal of Applied Ecology.* **42** (4), 659-671.

Carré, G., Roche, P., Chifflet, R., Morison, N., Bommarco, R., Harrison-Cripps, J., Krewenka, K., Potts, S. G., Roberts, S. P. M., Rodet, G., Settele, J., Steffan-Dewenter, I., Szentgyorgyi, H., Tscheulin, T., Westphal, C., Woyciechowski, M. and Vaissiere, B. E. (2009) Landscape context and habitat type as drivers of bee diversity in European annual crops. *Agriculture Ecosystems & Environment.* **133** (1-2), 40-47.

Carreck, N. L. (2008) Are honey bees (*Apis mellifera* L.) native to the British Isles? *Journal of Apicultural Research and Bee World.* **47** (4), 318-322.

Carter, D.J. in Plant, C.W. (Ed.) (2001) The butterflies and moths (Lepidoptera) of Buckingham Palace Garden. *London Naturalist.* Part 2. **80** (Suppl.), 169-191.

Carvell, C., Meek, W. R., Pywell, R. F., Goulson, D. and Nowakowski, M. (2007) Comparing the efficacy of agri-environment schemes to enhance bumblebee abundance and diversity on arable field margins. *Journal of Applied Ecology.* **44** (1), 29-40.

Carvell, C., Meek, W. R., Pywell, R. F. and Nowakowski, M. (2004) The response of foraging bumblebees to successional change in newly created arable field margins. *Biological Conservation*. **118** (3), 327-339.

Carvell, C., Osborne, J. L., Bourke, A. F. G., Freeman, S. N., Pywell, R. F. and Heard, M. S. (2011) Bumble bee species' responses to a targeted conservation measure depend on landscape context and habitat quality. *Ecological Applications*. **21** (5), 1760-1771.

Chao, A., Chazdon, R. L., Colwell, R. K. and Shen, T. J. (2005) A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters*. **8** (2), 148-159.

Chao, A., Chazdon, R. L., Colwell, R. K. and Shen, T. (2006) Abundance-based similarity indices and their estimation when there are unseen species in samples. *Biometrics*. **62** (2), 361-371.

Chazdon, R.L., Colwell, R.K., Denslow, J.S. and Guariguata, M.R. (1998) Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of northeastern Costa Rica. In: Dallmeier, F. and Comiskey, J. (eds.) *Forest biodiversity research, monitoring and modeling. Conceptual background and Old World case studies*. Paris, France: The Parthenon Publishing Group. Page 309.

Chinery, M. (1989) *Butterflies and day-flying moths of Britain and Europe*. London: William Collins Sons and Co. Ltd.

Chinery, M. (2005) *Collins complete guide to British insects*. London: HarperCollins Publishers Ltd.

Christensen, N. L., Bartuska, A. M., Brown, J. H., Carpenter, S., D'Antonio, C., Francis, R., Franklin, J. F., MacMahon, J. A., Noss, R. F., Parsons, D. J., Peterson, C. H., Turner, M. G. and Woodmansee, R. G. (1996) The report of the ecological society of America committee on the scientific basis for ecosystem management. *Ecological Applications*. **6** (3), 665-691.

Christie, C. (2000) *The British country house in the eighteenth century*. Manchester, UK: Manchester University Press.

CJ Wildbird Food, Upton Magna, Shrewsbury, England.

Colla, S. R. and Packer, L. (2008) Evidence for decline in eastern North American bumblebees (Hymenoptera : Apidae), with special focus on *Bombus affinis* Cresson. *Biodiversity and Conservation*. **17** (6), 1379-1391.

Colwell, R.K. (2009) Biodiversity: Concepts, patterns, and measurement. In: Levin, S. (ed.) *The Princeton guide to ecology*. Princeton USA: Princeton University Press.

Colwell, R. K. (2012) *EstimateS 8.2 User's Guide* [online]. Available from: http://viceroy.eeb.uconn.edu/estimates/EstimateSPages/EstSUsersGuide/EstimateS UsersGuide.htm#Chao1 [Accessed 24 September, 2012].

Colwell, R. K. and Coddington, J. A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*. **345** (1311), 101-118.

Colyer, C. N. and Hammond, C. O. (1968) *Flies of the British Isles.* 2nd ed. London, England: Frederick Warne & Co Ltd.

Comba, L., Corbet, S. A., Barron, A., Bird, A., Collinge, S., Miyazaki, N. and Powell, M. (1999a) Garden flowers: Insect visits and the floral reward of horticulturally-modified variants. *Annals of Botany.* **83** (1), 73-86.

Comba, L., Corbet, S. A., Hunt, L. and Warren, B. (1999b) Flowers, nectar and insect visits: Evaluating British plant species for pollinator-friendly gardens. *Annals of Botany.* **83** (4), 369-383.

Corbet, S. A., Bee, J., Dasmahapatra, K., Gale, S., Gorringe, E., La Ferla, B., Moorhouse, T., Trevail, A., Van Bergen, Y. and Vorontsova, M. (2001) Native or exotic? Double or single? Evaluating plants for pollinator-friendly gardens. *Annals of Botany.* **87** (2), 219-232.

Costanza, R., dArge, R., deGroot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., ONeill, R. V., Paruelo, J., Raskin, R. G., Sutton, P. and vandenBelt, M. (1997) The value of the world's ecosystem services and natural capital. *Nature.* **387** (6630), 253-260.

Cowgill, S. E., Wratten, S. D. and Sotherton, N. W. (1993) The effect of weeds on the numbers of hoverfly (Diptera, Syrphidae) adults and the distribution and composition of their eggs in winter-wheat. *Annals of Applied Biology.* **123** (3), 499-515.

Crawshay, G. A. (1905) A large community of *Vespula vulgaris. Entomologist's Monthly Magazine.* **41**, 8-10.

Cussans, J., Goulson, D., Sanderson, R., Goffe, L., Darvill, B. and Osborne, J. L. (2010) Two bee-pollinated plant species show higher seed production when grown in gardens compared to arable farmland. *Plos One.* **5** (7), e11753.

Daily, G. C., Alexander, S., Ehrlich, P. R., Goulder, L., Lubchenco, J., Matson, P. A., Mooney, H. A., Postel, S., Schneider, S. H., Tilman, D. and Woodwell, G. M. (1997) Ecosystem services: Benefits supplied to human societies by natural ecosystems. *Issues in Ecology.* **2**, 2-15.

Danks, H. V. (1971) Nest mortality factors in stem-nesting aculeate Hymenoptera. *Journal of Animal Ecology.* **40** (1), 79-83.

Darlington, P. J. (1957) *Zoogeography: the geographical distribution of animals.* New York, USA: Wiley Publishing.

Darwin, C. (1862) *On the various contrivances by which British and foreign orchids are fertilised by insects.* London, England: John Murray.

Davies, Z. G., Fuller, R. A., Loram, A., Irvine, K. N., Sims, V. and Gaston, K. J. (2009) A national scale inventory of resource provision for biodiversity within domestic gardens. *Biological Conservation.* **142** (4), 761-771.

Dean, R. (The Red Beehive Company). e-mail to hilary.erenler@northampton.ac.uk 17 August 2012.

Defra. (2011) *Agriculture in the United Kingdom 2011.* Available online (http://www.defra.gov.uk/statistics/files/defra-stats-foodfarm-crosscutting-auk-auk2011-120709.pdf) [Accessed 4 November 2012].

Defra Environment Statistics Service. (2011) *Attitudes and Knowledge Relating to Biodiversity and the Natural Environment 2007 - 2011* (Report - available online, http://defra.gov.uk) [Accessed 5 May 2012].

Derraik, J. G. B., Closs, G. P., Dickinson, K. J. M., Sirvid, P., Barratt, B. I. P. and Patrick, B. H. (2002) Arthropod morphospecies versus taxonomic species: a case study with Araneae, Coleoptera, and Lepidoptera. *Conservation Biology.* **16** (4), 1015-1023.

Dias, B. S. F., Raw, A. and Imperatri-Fonseca, V. L. (1999) *International Pollinators Initiative: Saõ Paulo Declaration on Pollinators. Report on the recommendations of the workshop on the conservation and sustainable use of pollinators in agriculture with emphasis on bees.* Brasília, Brazil: Brazilian Ministry of the Environment (MMA).

Dicks, L. V., Corbet, S. A. and Pywell, R. F. (2002) Compartmentalization in plant-insect flower visitor webs. *Journal of Animal Ecology.* **71** (1), 32-43.

Diekotter, T., Kadoya, T., Peter, F., Wolters, V. and Jauker, F. (2010) Oilseed rape crops distort plant-pollinator interactions. *Journal of Applied Ecology.* **47** (1), 209-214.

Dipterists Forum *The Society for the Study of Flies (Diptera)* [online]. Available from: www.dipteristsforum.org.uk [Accessed 9 September, 2012].

Donovan, E. (1792) *The natural history of British insects explaining them in their several states, with the periods of their transformations, their food, and oeconomy together with the history of such minute insects as require investigation by the microscope, the whole illustrated by coloured figures, designed and executed from living specimens.* London, England: F & C Rivington.

Dormann, C. F., Fründ, J., Blüthgen, N. and Gruber, B. (2009) Indices, graphs and null models: Analyzing bipartite ecological networks. *The Open Ecology Journal.* **2**, 7-24.

Dormann, C. F., Gruber, B. and Fründ, J. (2008) Introducing the bipartite package: Analysing ecological networks. *R News.* **8** (2), 8-11.

Dormann, C. F., Schweiger, O., Augenstein, I., Bailey, D., Billeter, R., de Blust, G., DeFilippi, R., Frenzel, M., Hendrickx, F., Herzog, F., Klotz, S., Liira, J., Maelfait, J. P., Schmidt, T., Speelmans, M., van Wingerden, W. K. R. E. and Zobel, M. (2007) Effects of landscape structure and land-use intensity on similarity of plant and animal communities. *Global Ecology and Biogeography.* **16**, 774-787.

Dramstad, W. and Fry, G. (1995) Foraging activity of bumblebees (*Bombus*) in relation to flower resources on arable land. *Agriculture Ecosystems & Environment.* **53**, 123-135.

Dunnett, N. and Quasim, M. (2000) Perceived benefits to human well-being of urban gardens. *HorTechnology.* **10** (1), 40-45.

Dupont, Y. L., Padron, B., Olesen, J. M. and Petanidou, T. (2009) Spatio-temporal variation in the structure of pollination networks. *Oikos.* **118** (8), 1261-1269.

Dutton, R. (1949) *The English Country House.* 3rd ed. London, England: B.T. Batsford Ltd.

Dytham, C. (2011) *Choosing and using statistics: A biologist's guide*. Third ed. Chichester, UK: Blackwell Science.

Ebeling, A., Klein, A. M., Schumacher, J., Weisser, W. W. and Tscharntke, T. (2008) How does plant richness affect pollinator richness and temporal stability of flower visits? *Oikos*. **117** (12), 1808-1815.

Ebeling, A., Klein, A. and Tscharntke, T. (2011) Plant-flower visitor interaction webs: Temporal stability and pollinator specialization increases along an experimental plant diversity gradient. *Basic and Applied Ecology*. **12** (4), 300-309.

Ebert, A. (2011) Nectar for the taking: The popularization of scientific bee culture in England, 1609-1809. *Agricultural History*. **85** (3), 322-343.

EDINA. *OS Scale 1:25000 Raster Ordnance Survey, GB. © Crown Copyright* [online]. Available from: http://edina.ac.uk/digimap [Accessed 25 September, 2012].

Edwards, M. (2003) *An entomological survey of National Trust gardens* (Report for The National Trust). Sussex, England: Unpublished.

Edwards, M. and Jenner, M. (2009) *Field guide to the bumblebees of Great Britain and Ireland*. 2nd ed. England: Ocelli.

Edwards, R. (ed.) (1998) *Provisional atlas of the aculeate Hymenoptera of Britain and Ireland. Part 2*. Dorset: Biological Records Centre.

Elton, A., Harrison, B. and Wark, K. (1992) *Researching the country house: A guide for local historans*. London, England: B.T. Batsford Ltd.

Engels, J. (2001) Home Gardens - a genetic resources perspective. In: *Home gardens and in situ conservation of plant genetic resources in farming systems*. Rome, Italy: IPGRI.

ESRI. (2011) *ArcGIS Desktop: Release 10 Environmental Systems Research Institute* http://esriuk.com. [Accessed 6 June 2010].

Everaars, J., Strohbach, M. W., Gruber, B. and Dormann, C. F. (2011) Microsite conditions dominate habitat selection of the red mason bee (*Osmia bicornis*, Hymenoptera: Megachilidae) in an urban environment: a case study from Leipzig, Germany. *Landscape and Urban Planning*. **103**, 15-23.

Eversham, B. (2010) *Building and curating an insect collection* (unpublished notes).

Exeler, N., Kratochwil, A. and Hochkirch, A. (2010) Does recent habitat fragmentation affect the population genetics of a heathland specialist, *Andrena fuscipes* (Hymenoptera: Andrenidae)? *Conservation Genetics*. **11** (5), 1679-1687.

Faegri, F. and van der Pijl, L. (1966) *The principles of pollination ecology*. Oxford, England: Pergamon Press Ltd.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics*. **34**, 487-515.

Falk, S. J. (2011) *A survey of the bees and wasps of fifteen chalk grassland and chalk heath sites within the East Sussex South Downs*. Self-Published.

Fetridge, E. D., Ascher, J. S. and Langellotto, G. A. (2008) The bee fauna of residential gardens in a suburb of New York City (Hymenoptera: Apoidea). *Annals of the Entomological Society of America.* **101** (6), 1067-1077.

Field Studies Council (2005) *Guide to the butterflies of Britain: AIDGAP guide.* 2nd ed. Preston Montford, England: FSC.

Field Studies Council (2007) *Guide to the bees of Britain; AIDGAP guide.* Preston Montford, England: FSC.

Field, A. (2009) *Discovering statistics using SPSS.* 3rd ed. London, England: Sage Publications Ltd.

Fischer, J. and Lindenmayer, D. B. (2002) Treating the nestedness temperature calculator as a "black box" can lead to false conclusions. *Oikos.* **99** (1), 193-199.

Fisher, J. (1989) *The origins of garden plants.* London, England: Constable and Company Limited.

Fisher, R. A. (1930) *The genetical theory of natural selection.* Oxford, England: Clarendon Press.

Fitzpatrick, U., Murray, T. E., Paxton, R. J., Breen, J., Cotton, D., Santorum, V. and Brown, M. J. F. (2007) Rarity and decline in bumblebees - A test of causes and correlates in the Irish fauna. *Biological Conservation.* **136** (2), 185-194.

Fontaine, C., Collin, C. L. and Dajoz, I. (2008) Generalist foraging of pollinators: diet expansion at high density. *Journal of Ecology.* **96** (5), 1002-1010.

Fontaine, C., Dajoz, I., Meriguet, J. and Loreau, M. (2006) Functional diversity of plant-pollinator interaction webs enhances the persistence of plant communities. *Plos Biology.* **4** (1), 129-135.

Forup, M. L., Henson, K. S. E., Craze, P. G. and Memmott, J. (2008) The restoration of ecological interactions: plant-pollinator networks on ancient and restored heathlands. *Journal of Applied Ecology.* **45** (3), 742-752.

Fox, R., Brereton, T. M., Asher, J., Botham, M. S., Middlebrook, I., Roy, D. B. and Warren, M. S. (2012) *The state of the UK's butterflies 2011.* Dorset, England: Butterfly Conservation.

Frankie, G. W., Thorp, R. W., Hernandez, J., Rizzardi, M., Ertter, B., Pawelek, J. C., Witt, S. L., Schindler, M., Coville, R. and Wojcik, V. A. (2009) Native bees are a rich natural resource in urban California gardens. *California Agriculture.* **63** (3), 113-120.

Frankie, G. W., Thorp, R. W., Schindler, M., Hernandez, J., Ertter, B. and Rizzardi, M. (2005) Ecological patterns of bees and their host ornamental flowers in two northern California cities. *Journal of the Kansas Entomological Society.* **78** (3), 227-246.

Franzén, M. and Öckinger, E. (2012) Climate-driven changes in pollinator assemblages during the last 60 years in an Arctic mountain region in Northern Scandinavia. *Journal of Insect Conservation.* **16** (2), 227-238.

Free, J. B. and Williams, I. H. (1970) Preliminary investigations on occupation of artificial nests by *Osmia rufa* L (Hymenoptera, Megachilidae). *Journal of Applied Ecology.* **7** (3), 559-568.

Fründ, J., Linsenmair, K. E. and Blüthgen, N. (2010) Pollinator diversity and specialization in relation to flower diversity. *Oikos.* **119** (10), 1581-1590.

Fuentes-Montemayor, E., Goulson, D. and Park, K. J. (2011) The effectiveness of agri-environment schemes for the conservation of farmland moths: assessing the importance of a landscape-scale management approach. *Journal of Applied Ecology.* **48** (3), 532-542.

Galeano, J., Pastor, J. M. and Iriondo, J. M. (2009) Weighted-Interaction Nestedness Estimator (WINE): A new estimator to calculate over frequency matrices. *Environmental Modelling & Software.* **24** (11), 1342-1346.

Galluzzi, G., Eyzaguirre, P. and Negri, V. (2010) Home gardens: neglected hotspots of agro-biodiversity and cultural diversity. *Biodiversity and Conservation.* **19** (13), 3635-3654.

Garmin. Etrex 10 *Hand-held GPS* [online]. Available from: http://www.garmin.com/uk/ [Accessed 24 March, 2012].

Gaston, K. J., Smith, R. M., Thompson, K. and Warren, P. H. (2005) Urban domestic gardens (II): experimental tests of methods for increasing biodiversity. *Biodiversity and Conservation.* **14** (2), 395-413.

Gathmann, A. and Tscharntke, T. (2002) Foraging ranges of solitary bees. *Journal of Animal Ecology.* **71** (5), 757-764.

Gerber, H. S. and Klostermeyer, E. C. (1970) Sex control by bees: a voluntary act of egg fertilization during oviposition. *Science.* **167** (3914), 82-83.

GetMapping PLC. *Google Earth* [online]. Available from: www.googleearth.com [Accessed 21 September, 2012].

Ghazoul, J. (2006) Floral diversity and the facilitation of pollination. *Journal of Ecology.* **94** (2), 295-304.

Gibson, R. H., Knott, B., Eberlein, T. and Memmott, J. (2011) Sampling method influences the structure of plant-pollinator networks. *Oikos.* **120** (6), 822-831.

Gilbert, F., Rotheray, G., Emerson, P. and Zafar, R. (1994) The evolution of feeding strategies. *Linnean Society Symposium Series; Phylogenetics and Ecology.* **1** (1), 323-343.

Gillman, M. P. (2009) *An introduction to mathematical models in ecology and evolution: time and space.* 2nd ed. Chichester, UK: Wiley-Blackwell.

Girolami, V., Marzaro, M., Vivan, L., Mazzon, L., Greatti, M., Giorio, C., Marton, D. and Tapparo, A. (2012) Fatal powdering of bees in flight with particulates of neonicotinoids seed coating and humidity implication. *Journal of Applied Entomology.* **136** (1-2), 17-26.

Goddard, M. A., Dougill, A. J. and Benton, T. G. (2010) Scaling up from gardens: biodiversity conservation in urban environments. *Trends in Ecology & Evolution.* **25** (2), 90-98.

Gotelli, N.J. and Colwell, R.K. (2011) Estimating species richness. In: Magurran, A. R. and McGill, B. J. (eds.) *Biological Diversity: Frontiers in measurement and assessment.* Oxford: Oxford University Press.

Goulson, D. (2010) *Bumblebees - behaviour, ecology and conservation.* 2nd ed. Oxford: Oxford University Press.

Goulson, D., Hughes, W. O. H., Derwent, L. C. and Stout, J. C. (2002) Colony growth of the bumblebee, *Bombus terrestris*, in improved and conventional agricultural and suburban habitats. *Oecologia.* **130** (2), 267-273.

Goulson, D., Lepais, O., O'Connor, S., Osborne, J. L., Sanderson, R. A., Cussans, J., Goffe, L. and Darvill, B. (2010) Effects of land use at a landscape scale on bumblebee nest density and survival. *Journal of Applied Ecology.* **47** (6), 1207-1215.

Goulson, D., Lye, G. C. and Darvill, B. (2008) Decline and conservation of bumblebees. *Annual Review of Entomology.* **53**, 1-38.

Greenleaf, S. S. and Kremen, C. (2006) Wild bee species increase tomato production and respond differently to surrounding land use in Northern California. *Biological Conservation.* **133** (1), 81-87.

Greenleaf, S. S., Williams, N. M., Winfree, R. and Kremen, C. (2007) Bee foraging ranges and their relationship to body size. *Oecologia.* **153** (3), 589-596.

Gruber, B., Eckel, K., Everaars, J. and Dormann, C. F. (2011) On managing the red mason bee (*Osmia bicornis*) in apple orchards. *Apidologie.* **42** (5), 564-576.

Grundel, R., Frohnapple, K. J., Jean, R. P. and Pavlovic, N. B. (2011) Effectiveness of bowl trapping and netting for inventory of a bee community. *Entomological Society of America.* **40** (2), 374-380.

Hadley, A. S. and Betts, M. G. (2012) The effects of landscape fragmentation on pollination dynamics: absence of evidence not evidence of absence. *Biological Reviews.* **87** (3), 526-544.

Haenke, S., Scheid, B., Schaefer, M., Tscharntke, T. and Thies, C. (2009) Increasing syrphid fly diversity and density in sown flower strips within simple vs. complex landscapes. *Journal of Applied Ecology.* **46** (5), 1106-1114.

Hannon, L. E. and Sisk, T. D. (2009) Hedgerows in an agri-natural landscape: Potential habitat value for native bees. *Biological Conservation.* **142** (10), 2140-2154.

Harvey, P. R. (2001) The bees, wasps and ants (Hymenoptera: Aculeata) of Buckingham Palace Garden. In Plant, C.W. (Ed.) The natural history of Buckingham Palace Garden, London. *London Naturalist.* **80** (Suppl.), 269-278.

Hatfield, R. G. and LeBuhn, G. (2007) Patch and landscape factors shape community assemblage of bumblebees, *Bombus* spp. (Hymenoptera : Apidae), in montane meadows. *Biological Conservation.* **139**, 150-158.

Head, S., (2012) Living Gardens: Gardeners and wildlife gardening. RHS magazine, *The Garden* (September), pp. 68-71.

Hegland, S. J. and Boeke, L. (2006) Relationships between the density and diversity of floral resources and flower visitor activity in a temperate grassland community. *Ecological Entomology.* **31** (5), 532-538.

Hegland, S. J., Grytnes, J. A. and Totland, O. (2009) The relative importance of positive and negative interactions for pollinator attraction in a plant community. *Ecological Research.* **24** (4), 929-936.

Henle, K., Alard, D., Clitherow, J., Cobb, P., Firbank, L., Kull, T., McCracken, D., Moritz, R. F. A., Niemela, J., Rebane, M., Wascher, D., Watt, A. and Young, J. (2008) Identifying and managing the conflicts between agriculture and biodiversity conservation in Europe - A review. *Agriculture Ecosystems & Environment.* **124** (1-2), 60-71.

Hennig, E. I. and Ghazoul, J. (2011) Plant-pollinator interactions within the urban environment. *Perspectives in Plant Ecology Evolution and Systematics.* **13** (2), 137-150.

Herrera, C. M. (1988) Variation in mutualisms - the spatio-temporal mosaic of a pollinator assemblage. *Biological Journal of the Linnean Society.* **35** (2), 95-125.

Hessayon, D. G. (1993) *The tree and shrub expert.* 2nd ed. London. England: Transworld Publishers Ltd.

Hessayon, D. G. (1995) *The flower expert.* 2nd ed. London, England: Transworld Publishers.

Heward, J. and Taylor, R. (1996) *The country houses of Northamptonshire.* Swindon, England: Royal Commission on the Historic Monuments of England.

Hobbs, R., Arico, S., Aronson, J., Baron, J., Bridgewater, P., Cramer, V., Epstein, P., Ewel, J., Klink, C., Lugo, A., Norton, D., Ojima, D., Richardson, D., Sanderson, E., Valladares, F., Vila, M., Zamora, R. and Zobel, M. (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography.* **15** (1), 1-7.

Hogg, B. N., Bugg, R. L. and Daane, K. M. (2011) Attractiveness of common insectary and harvestable floral resources to beneficial insects. *Biological Control.* **56** (1), 76-84.

Holzschuh, A., Dormann, C. F., Tscharntke, T. and Steffan-Dewenter, I. (2011) Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination. *Proceedings of the Royal Society B-Biological Sciences.* **278** (1723), 1-8.

Holzschuh, A., Dudenhöffer, J. and Tscharntke, T. (2012) Landscapes with wild bee habitats enhance pollination, fruit set and yield of sweet cherry. *Biological Conservation.* **153**, 101-107.

Holzschuh, A., Steffan-Dewenter, I. and Tscharntke, T. (2010) How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? *Journal of Animal Ecology.* **79** (2), 491-500.

Hooper, T. (1991) *Guide to bees and honey.* 3rd ed. London, England: Blandford.

Hoverfly Recording Scheme *Dipterists' Forum National Recording Scheme for Hoverflies* [online]. Available from: www.hoverflyrecordingscheme.org.uk [Accessed 10 October, 2012].

Hunter, M. D. (2001) Multiple approaches to estimating the relative importance of top-down and bottom-up forces on insect populations: Experiments, life tables, and time-series analysis. *Basic and Applied Ecology.* **2** (4), 295-309.

Hunter, M. D., Varley, G. C. and Gradwell, G. R. (1997) Estimating the relative roles of top-down and bottom-up forces on insect herbivore populations: A classic study revisited. *Proceedings of the National Academy of Sciences of the United States of America.* **94** (17), 9176-9181.

IBM Corp. (2012) *SPSS: Version 20.* [online]. Available from: *http://www-01.ibm.com/software/analytics/spss/products/statistics/.* [Accessed 4 June 2010].

Ings, T. C., Montoya, J. M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C. F., Edwards, F., Figueroa, D., Jacob, U., Jones, J. I., Lauridsen, R. B., Ledger, M. E., Lewis, H. M., Olesen, J. M., van Veen, F. J. F., Warren, P. H. and Woodward, G. (2009) Ecological networks - beyond food webs. *Journal of Animal Ecology.* **78** (1), 253-269.

ITV. *Anglia News Report (29 May 2012): Farmers benefit from soaring prices of rapeseed oil* [online]. Available from: http://www.itv.com/news/anglia/2012-05-29/farmers-benefit-from-soaring-prices-of-rapeseed-oil/ [Accessed 22 September, 2012].

James, A., Pitchford, J. W. and Plank, M. J. (2012) Disentangling nestedness from models of ecological complexity. *Nature.* **487**, 227-230.

Jauker, F., Peter, F., Wolters, V. and Diekotter, T. (2012a) Early reproductive benefits of mass-flowering crops to the solitary bee *Osmia rufa* outbalance post-flowering disadvantages. *Basic and Applied Ecology.* **13**, 268-276.

Jauker, F., Bondarenko, B., Becker, H. C. and Steffan-Dewenter, I. (2012b) Pollination efficiency of wild bees and hoverflies provided to oilseed rape. *Agricultural and Forest Entomology.* **14** (1), 81-87.

Jauker, F., Diekoetter, T., Schwarzbach, F. and Wolters, V. (2009) Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. *Landscape Ecology.* **24** (4), 547-555.

Jenkins, D. A. and Matthews, R. W. (2004) Cavity-nesting hymenoptera in disturbed habitats of Georgia and South Carolina: Nest architecture and seasonal occurrence. *Journal of the Kansas Entomological Society.* **77** (3), 203-214.

Joint Committee for the Conservation of British Invertebrates (Invertebrate Link). (2002) A code of conduct for collecting insects and other invertebrates. *British Journal of Entomology and Natural History.* **15**, 1-6.

Jongman, R. H. G., Ter Braak, C. J. F. and Van Tongeren, O. F. R. (eds.) (1995) *Data analysis in community and landscape ecology.* Cambridge, England: Cambridge University Press.

Jordano, P. (1987) Patterns of mutualistic interactions in pollination and seed dispersal: Connectance, dependence asymmetries, and coevolution. *American Naturalist.* **129** (5), 657-677.

Jost, L., Chao, A. and Chazdon, R.L. (2011) Compositional similarity and β diversity. In: Magurran, A. R. and McGill, B. J. (eds.) *Biological Diversity: Frontiers in measurement and assessment.* New York, USA: Oxford University Press. pp. 66-84.

Kaiser-Bunbury, C. N., Memmott, J. and Mueller, C. B. (2009) Community structure of pollination webs of Mauritian heathland habitats. *Perspectives in Plant Ecology Evolution and Systematics.* **11** (4), 241-254.

Kareiva, P. (1990) Population-dynamics in spatially complex environments - theory and data. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences.* **330** (1257), 175-190.

Kearns, C. A. and Inouye, D. S. (1997) Pollinators, flowering plants, and conservation biology - Much remains to be learned about pollinators and plants. *Bioscience.* **47** (5), 297-307.

Kearns, C. A. and Oliveras, D. M. (2009) Environmental factors affecting bee diversity in urban and remote grassland plots in Boulder, Colorado. *Journal of Insect Conservation.* **13** (6), 655-665.

Keil, P., Biesmeijer, J. C., Barendregt, A., Reemer, M. and Kunin, W. E. (2011) Biodiversity change is scale-dependent: an example from Dutch and UK hoverflies (Diptera, Syrphidae). *Ecography.* **34** (3), 392-401.

Kevan, P. G. and Baker, H. G. (1983) Insects as flower visitors and pollinators. *Annual Review of Entomology.* **28**, 407-453.

Keys, J. (1780) *The practical bee-master.* London: The author.

Kimber, I. *UK Moths: A guide to the moths of Great Britain and Ireland* [online]. Available from: www.ukmoths.org.uk [Accessed 11 September, 2012].

King, M. (2002) *England's green unpleasant land? Why urgent action is needed to save England's wild flower grasslands.* London: Plantlife.

King, M. (2011) *Nature's Tapestry: The story of England's grasslands and why not all grass is green.* England: The Grasslands Trust. [Online]. Available:www.thegrasslands-trust.org [Accessed 1 September 2012].

Kirkpatrick, J., Daniels, G. and Davison, A. (2009) An antipodean test of spatial contagion in front garden character. *Landscape and Urban Planning.* **93** (2), 103-110.

Kleijn, D. and van Langevelde, F. (2006) Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. *Basic and Applied Ecology.* **7** (3), 201-214.

Klein, A. M., Steffan-Dewenter, I. and Tscharntke, T. (2003) Fruit set of highland coffee increases with the diversity of pollinating bees. *Proceedings of the Royal Society B-Biological Sciences.* **270**, 955-961.

Klein, A. M., Vaissiere, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C. and Tscharntke, T. (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B-Biological Sciences.* **274** (1608), 303-313.

Knight, M. E., Osborne, J. L., Sanderson, R. A., Hale, R. J., Martin, A. P. and Goulson, D. (2009) Bumblebee nest density and the scale of available forage in arable landscapes. *Insect Conservation and Diversity.* **2** (2), 116-124.

Krauss, J., Steffan-Dewenter, I. and Tscharntke, T. (2003) How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? *Journal of Biogeography.* **30** (6), 889-900.

Krebs, C. J. (1994) *Ecology: The experimental analysis of distribution and abundance.* 4th ed. USA: Harper Collins College Publishers.

Krebs, C. J. (2009) *Ecology.* 6th ed. San Francisco, USA: Pearson Benjamin Cummings.

Kremen, C. and Chaplin-Kramer, R. (2007) Insects as providers of ecosystem services: Crop pollination and pest control. In: Stewart, A. J. A., New, T. R. and Lewis, O. T. (eds.) *Insect Conservation Biology: The 22nd symposium of the Royal Entomological Society,* pp. 349-382. Oxford, England: CAB International.

Kremen, C. and Ricketts, T. (2000) Global perspectives on pollination disruptions. *Conservation Biology.* **14** (5), 1226-1228.

Kreyer, D., Oed, A., Walther-Hellwig, K. and Frankl, R. (2004) Are forests potential landscape barriers for foraging bumblebees? Landscape scale experiments with *Bombus terrestris* agg. and *Bombus pascuorum* (Hymenoptera, Apidae). *Biological Conservation.* **116** (1), 111-118.

Krombein, K. V. (1967) *Trap-nesting wasps and bees: Life histories, nests and associates.* Washington DC, USA: Smithsonian Press.

Krunic, M. and Stanisavljevic, L. (2006) Augmentation of managed populations of *Osmia cornuta* and *O. rufa* (Hymenoptera: Megachilidae) in Southeastern Europe. *European Journal of Entomology.* **103** (3), 695-697.

Krunic, M., Stanisavljevic, L., Pinzauti, M. and Felicioli, A. (2005) The accompanying fauna of *Osmia cornuta* and *Osmia rufa* and effective measures of protection. *Bulletin of Insectology.* **58** (2), 141-152.

Kwak, M.M., Velterop, O. and Boerrigter, E.J.M. (1996) Insect diversity and the pollination of rare plant species. In: Matheson, A., Buchmann, S. L., O'Toole, C., Westrich, P. and Williams, I. H. (eds.) *The conservation of bees,* pp. 115-124. London, England: Academic Press.

Kwak, M. M., Velterop, O. and van Andel, J. (1998) Pollen and gene flow in fragmented habitats. *Applied Vegetation Science.* **1** (1), 37-54.

Lagerlof, J., Stark, J. and Svensson, B. (1992) Margins of agricultural fields as habitats for pollinating insects. *Biotic Diversity in Agroecosystems.* **1** (1), 117-124.

Lander, T. A., Bebber, D. P., Choy, C. T. L., Harris, S. A. and Boshier, D. H. (2011) The Circe Principle explains how resource-rich land can waylay pollinators in fragmented landscapes. *Current Biology.* **21** (15), 1302-1307.

Lazaro, A. and Totland, O. (2010) Local floral composition and the behaviour of pollinators: attraction to and foraging within experimental patches. *Ecological Entomology.* **35** (5), 652-661.

Lepš, J. and Šmilauer, P. (2003) *Multivariate analysis of ecological data using CANOCO*. Cambridge, England: Cambridge University Press.

Leroy, P. D., Verheggen, F. J., Capella, Q., Francis, F. and Haubruge, E. (2010) An introduction device for the aphidophagous hoverfly *Episyrphus balteatus* De Geer (Diptera: Syrphidae). *Biological Control.* **54** (3), 181-188.

Littlejohn, D. (1997) *The fate of the English country house*. New York: Oxford University Press.

Liu, X. J., Zhang, L. A. and Hong, S. (2011) Global biodiversity research during 1900-2009: a bibliometric analysis. *Biodiversity and Conservation.* **20** (4), 807-826.

Loram, A., Thompson, K., Warren, P. H. and Gaston, K. J. (2008a) Urban domestic gardens (XII): The richness and composition of the flora in five UK cities. *Journal of Vegetation Science.* **19** (3), 321-330.

Loram, A., Warren, P. H. and Gaston, K. J. (2008b) Urban domestic gardens (XIV): The characteristics of gardens in five cities. *Environmental Management.* **42** (3), 361-376.

Loram, A., Warren, P., Thompson, K. and Gaston, K. (2011) Urban domestic gardens: The effects of human interventions on garden composition. *Environmental Management.* **48** (4), 808-824.

Lord, T. (2002) *The encyclopedia of planting combinations*. London, England: Octopus Publishing Group Ltd.

Lye, G. C., Park, K., Osborne, J., Holland, J. and Goulson, D. (2009) Assessing the value of Rural Stewardship schemes for providing foraging resources and nesting habitat for bumblebee queens (Hymenoptera: Apidae). *Biological Conservation.* **142** (10), 2023-2032.

MacArthur, R. H. and Wilson, E. O. (1967) *The theory of island biogeography*. New York, USA: Princeton University Press.

Maeta, Y. and Kitamura, T. (1974) *How to manage the Mame-Ko bee (Osmia cornifrons Radoszkowski) for pollination of fruit crops*. Nagaroshi, Japan: Ask Co Ltd.

Magurran, A.R. (2011) Measuring biological diversity in time (and space). In: Magurran, A. R. and McGill, B. J. (eds.) *Biological Diversity; Frontiers in measurement and assessment*. New York, USA: Oxford University Press. pp. 85-94.

Magurran, A. R. and McGill, B. J. (eds.) (2011) *Biological Diversity: Frontiers in measurement and assessment*. New York, USA: Oxford University Press.

Margules, C. R. and Pressey, R. L. (2000) Systematic conservation planning. *Nature.* **405**, 243-253.

Marren, P. (2000) *Where have all the flowers gone? A study of local extinctions as recorded in the county floras*. London, England: Plantlife.

Marren, P. (2001) 'What time hath stole away': Local extinctions in our native flora. *British Wildlife.* **12**, 305-310.

Matteson, K. C. and Langellotto, G. A. (2010) Determinates of inner city butterfly and bee species richness. *Urban Ecosystems.* **13** (3), 333-347.

Maurer, B.A. and McGill, B.J. (2011) Measurement of species diversity. In: Magurran, A. R. and McGill, B. J. (eds.) *Biological Diversity: Frontiers in measurement and assessment.* New York, USA: Oxford University Press Inc. pp. 55-65.

Mayer, C., Adler, L., Armbruster, W. S., Dafni, A., Eardley, C., Huang, S. Q., Kevan, P. G., Ollerton, J., Packer, L., Ssymank, A., Stout, J. C. and Potts, S. G. (2011) Pollination Ecology in the 21st Century: Key questions for future research. **3** (2), 8-23.

Maynard Smith, J. (1977) *Mathematical ideas in biology.* Cambridge, England: Cambridge University Press.

McCollin, D., Moore, L. and Sparks, T. (2000) The flora of a cultural landscape: environmental determinants of change revealed using archival sources. *Biological Conservation.* **92** (2), 249-263.

McGill, B.J. (2011) Species abundance distributions. In: Magurran, A. R. and McGill, B. J. (eds.) *Biological Diversity: Frontiers in measurement and assessment.* New York, USA: Oxford University Press. pp. 105-122.

McGill, B. J., Etienne, R. S., Gray, J. S., Alonso, D., Anderson, M. J., Benecha, H. K., Dornelas, M., Enquist, B. J., Green, J. L., He, F., Hurlbert, A. H., Magurran, A. E., Marquet, P. A., Maurer, B. A., Ostling, A., Soykan, C. U., Ugland, K. I. and White, E. P. (2007) Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters.* **10** (10), 995-1015.

Memmott, J., Craze, P. G., Waser, N. M. and Price, M. V. (2007) Global warming and the disruption of plant-pollinator interactions. *Ecology Letters.* **10** (8), 710-717.

Memmott, J. and Waser, N. M. (2002) Integration of alien plants into a native flower-pollinator visitation web. *Proceedings of the Royal Society of London Series B-Biological Sciences.* **269** (1508), 2395-2399.

Memmott, J., Waser, N. M. and Price, M. V. (2004) Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society B-Biological Sciences.* **271** (1557), 2605-2611.

Michener, C. D. (2007) *The bees of the world.* Second ed. Maryland, USA: The John Hopkins University Press.

Miotk, P. (1996) The naturalized garden - A refuge for animals? First results. *Zoologischer Anzeiger.* **235** (1-2), 101-116.

Mitchell, D. (2008) *A note on rising food prices.* Policy Research Working Paper 4682. Washington: World Bank.

Mittermeier, R. A., Myers, N., Thomsen, J. B., da Fonseca, G. A. B. and Olivieri, S. (1998) Biodiversity hotspots and major tropical wilderness areas: Approaches to setting conservation priorities. *Conservation Biology.* **12** (3), 516-520.

Morandin, L. A. and Winston, M. L. (2006) Pollinators provide economic incentive to preserve natural land in agroecosystems. *Agriculture Ecosystems & Environment.* **116** (3-4), 289-292.

Mowl, T. and Hickman, C. (2008) *The historic gardens of England: Northamptonshire.* Stroud, England: Tempus Publishing.

Munoz, A. A. and Cavieres, L. A. (2008) The presence of a showy invasive plant disrupts pollinator service and reproductive output in native alpine species only at high densities. *Journal of Ecology.* **96** (3), 459-467.

Musgrave, T. (2009) *The head gardeners: Forgotten heroes of horticulture.* London, England: Aurum Press Limited.

Natural England. (2010) *Lost Life: England's lost and threatened species.* [online]. Available: http://publications.naturalengland.org.uk/publication/32023 [Accessed 1 November 2011].

NBKA (Northamptonshire Beekeepers' Association). *NBKA Home page* [online]. Available from: http://www.northantsbees.org.uk/ [Accessed 28 January, 2010].

NERC. (2009) *£10 million initiative to tackle bee and pollinator decline* [online]. Available from: http://www.nerc.ac.uk/press/releases/2009/10-bees.asp [Accessed 31 August, 2012].

NERC (CEH) (2011) *Countryside Survey: Land Cover Map 2007.*

NHBS website. *Butterfly net* [online]. Available from: http://www.nhbs.com/standard_butterfly_net_tefno_163233.html [Accessed 18 September, 2012].

NHM (Natural History Museum). *The 'big six' bumblebees in the UK* [online]. Available from: http://www.nhm.ac.uk/research-curation/research/projects/bombus/bumblebeeid.html [Accessed 17 October, 2012].

O'Brien, D. M., Boggs, C. L. and Fogel, M. L. (2003) Pollen feeding in the butterfly *Heliconius charitonia*: isotopic evidence for essential amino acid transfer from pollen to eggs. *Proceedings of the Royal Society B-Biological Sciences.* **270** (1533), 2631-2636.

Öckinger, E., Dannestam, A. and Smith, H. G. (2009) The importance of fragmentation and habitat quality of urban grasslands for butterfly diversity. *Landscape and Urban Planning.* **93** (1), 31-37.

Odum, H.T. (1962) Ecological tools and their use. In: Waggoner, P. E. and Ovington, J. D. (eds.) *Man and the Ecosystem: Proceedings of the Lockwood conference on the suburban forest and ecology.* Connecticut, USA: The Connecticut Agricultural Experiment Station. pp. 57-75.

Oertli, S., Müller, A. and Dorn, S. (2005) Ecological and seasonal patterns in the diversity of a species-rich bee assemblage (Hymenoptera : Apoidea : Apiformes). *European Journal of Entomology.* **102** (1), 53-63.

Olesen, J. M., Bascompte, J., Dupont, Y. L. and Jordano, P. (2007) The modularity of pollination networks. *Proceedings of the National Academy of Sciences of the United States of America.* **104** (50), 19891-19896.

Oliver, I. and Beattie, A. J. (1996) Invertebrate morphospecies as surrogates for species: A case study. *Conservation Biology.* **10** (1), 99-109.

Ollerton, J., (2012) The importance of native pollinators. *The Plantsman,* (June), pp. 86-89.

Ollerton, J. and Erenler, H. E. (2013) *Examining the Perfect for Pollinators Scheme: From plant provision and sales by the horticultural industry to plant selection by consumers*. In prep.

Ollerton, J., Killick, A., Lamborn, E., Watts, S. and Whiston, M. (2007) Multiple meanings and modes: on the many ways to be a generalist flower. *Taxon.* **56** (3), 717-728.

Ollerton, J., Winfree, R. and Tarrant, S. (2011) How many flowering plants are pollinated by animals? *Oikos.* **120** (3), 321-326.

Ollerton, J., Price, V., Armbruster, W. S., Memmott, J., Watts, S., Waser, N. M., Totland, O., Goulson, D., Alarcón, R., Stout, J. C. and Tarrant, S. (2012) Overplaying the role of honey bees as pollinators: a comment on Aebi and Neumann (2011). *Trends in Ecology & Evolution.* **27** (3), 141-2.

Ordnance Survey *British national grid* [online]. Available from: http://www.ordnancesurvey.co.uk/oswebsite/gi/nationalgrid/nghelp1.html [Accessed 20 September, 2012].

Osborne, J. L., Clark, S. J., Morris, R. J., Williams, I. H., Riley, J. R., Smith, A. D., Reynolds, D. R. and Edwards, A. S. (1999) A landscape-scale study of bumblebee foraging range and constancy, using harmonic radar. *Journal of Applied Ecology.* **36** (4), 519-533.

Osborne, J. L., Martin, A. P., Carreck, N. L., Swain, J. L., Knight, M. E., Goulson, D., Hale, R. J. and Sanderson, R. A. (2008a) Bumblebee flight distances in relation to the forage landscape. *Journal of Animal Ecology.* **77** (2), 406-415.

Osborne, J. L., Martin, A. P., Shortall, C. R., Todd, A. D., Goulson, D., Knight, M. E., Hale, R. J. and Sanderson, R. A. (2008b) Quantifying and comparing bumblebee nest densities in gardens and countryside habitats. *Journal of Applied Ecology.* **45** (3), 784-792.

Osborne, J. L., Williams, I. H. and Corbet, S. A. (1991) Bees, pollination and habitat change in the European community. *Bee World.* **72** (3), 99-116.

O'Toole, C. (2002) *The Red Mason Bee - Osmia rufa: All you need to know.* 2nd ed. Leicestershire, England: Osmia Publications Ltd.

O'Toole, C., (2011) Mason bees as managed pollinators of orchard crops. *Bee World,* (March), pp. 5-8.

Owen, J. (2010) *Wildlife of a garden: A thirty-year study.* Peterborough, UK: Royal Horticultural Society.

Owen, J. (1981) Trophic variety and abundance of hoverflies (Diptera, Syrphidae) in an English suburban garden. *Holarctic Ecology.* **4** (3), 221-228.

Owen, J. (1983) The most neglected wildlife habitat of all. *New Scientist.* **97** (1339), 9-11.

Palmer, M. W. (1990) The estimation of species richness by extrapolation. *Ecology.* **71** (3), 1195-1198.

Partap, U., Partap, T. and He, Y. H. (2001) Pollination failure in apple crop and farmers' management strategies in Hengduan Mountains, China. *Proceedings of the*

Eighth International Pollination Symposium on Pollination: Integrator of Crops and Native Plant Systems. pp. 225-230.

Pawelek, J. C., Frankie, G. W., Thorp, R. W. and Przybylski, M. (2009) Modification of a community garden to attract native bee pollinators in urban San Luis Obispo, California. *Cities and the Environment.* **2** (1), 1-20.

Peet, R. K. (1974) The measurement of species diversity. *Annual Review of Ecology and Systematics.* **5**, 285-307.

Pereira, H. M., Leadley, P. W., Proenca, V., Alkemade, R., Scharlemann, J. P. W., Fernandez-Manjarres, J. F., Araujo, M. B., Balvanera, P., Biggs, R., Cheung, W. W. L., Chini, L., Cooper, H. D., Gilman, E. L., Guenette, S., Hurtt, G. C., Huntington, H. P., Mace, G. M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R. J., Sumaila, U. R. and Walpole, M. (2010) Scenarios for global biodiversity in the 21st century. *Science.* **330** (6010), 1496-1501.

Pitts-Singer, T. L. and Cane, J. H. (2011) The alfalfa leafcutting bee, *Megachile rotundata*: The world's most intensively managed solitary bee. *Annual Review of Entomology.* **56**, 221-237.

Plant, C. W. (2001) Hoverflies (Diptera: Syrphidae) in Buckingham Palace Garden. In Plant, C.W. (Ed.) The natural history of Buckingham Palace Garden, London. *London Naturalist.* **80** (suppl.), 259-267.

Pocock, M. J. O., Evans, D. M. and Memmott, J. (2012) The robustness and restoration of a network of ecological networks. *Science.* **335** (6071), 973-977.

Pollard, E. (1977) Method for assessing changes in abundance of butterflies. *Biological Conservation.* **12** (2), 115-134.

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O. and Kunin, W. E. (2010) Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution.* **25** (6), 345-353.

Potts, S. G., Petanidou, T., Roberts, S., O'Toole, C., Hulbert, A. and Willmer, P. (2006) Plant-pollinator biodiversity and pollination services in a complex Mediterranean landscape. *Biological Conservation.* **129** (4), 519-529.

Potts, S. G., Vulliamy, B., Dafni, A., Ne'eman, G. and Willmer, P. (2003) Linking bees and flowers: How do floral communities structure pollinator communities? *Ecology.* **84** (10), 2628-2642.

Potts, S. G., Vulliamy, B., Roberts, S., O'Toole, C., Dafni, A., Ne'eman, G. and Willmer, P. G. (2004) Nectar resource diversity organises flower-visitor community structure. *Entomologia Experimentalis Et Applicata.* **113** (2), 103-107.

Power, E. R. (2005) Human-nature relations in suburban gardens. *Australian Geographer.* **36** (1), 39-53.

Preszler, R. W. and Price, P. W. (1988) Host quality and sawfly populations - a new approach to life table analysis. *Ecology.* **69** (6), 2012-2020.

Primack, R. B. (1985) Longevity of individual flowers. *Annual Review of Ecology and Systematics.* **16**, 15-37.

Proctor, M. C. F., Yeo, P. and Lack, A. (1996) *The Natural History of Pollination.* Portland, USA: Timber Press.

Prŷs-Jones, O. E. and Corbet, S. A. (2011) *Bumblebees. Naturalists' Handbooks 6 (Ecology and Identification).* 3rd ed. Exeter, England: Pelagic Publishing.

Pyke, G. H. (1984) Optimal Foraging Theory - a critical review. *Annual Review of Ecology and Systematics.* **15**, 523-575.

R Development Core Team *R: A Language and Environment for Statistical Computing* [online]. Available from: http://www.r-project.org/ [Accessed 2 July, 2012].

Rathcke, B. J. and Jules, E. S. (1993) Habitat fragmentation and plant pollinator interactions. *Current Science.* **65** (3), 273-277.

Raven, S. (2012) *Sarah Raven's Bees, Butterflies and Blooms* [online]. Available from: http://www.sarahraven.com/beesbutterfliesblooms [Accessed 9 November, 2012].

Raw, A. (1972) The biology of the solitary bee *Osmia rufa* (L) (Megachilidae). *Transactions of the Royal Entomological Society of London.* **124** (3), 213-229.

RHS (2012a) *Plants for Pollinators* [online]. Available from: http://www.rhs.org.uk/Gardening/Sustainable-gardening/Plants-for-pollinators [Accessed 9 November, 2012].

RHS (2012b) *Royal Horticultural Society (Home page)* [online]. Available from: http://www.rhs.org.uk [Accessed 1 August, 2012].

Riley, C. V. (1892) *Directions for collecting and preserving insects.* Washington, USA: US National Museum (Bulletin No 39, part F).

Roberts, S. P. M. and Dean, R. (2012) *Information Sheet No 4: Red mason bee (Osmia bicornis)* [online]. BWARS (Bees, Wasps and Ants Recording Society) and Hymettus Ltd. Available from: www.bwars.com [Accessed 5 August, 2012].

Rosenheim, J. A. (1990) Density-dependent parasitism and the evolution of aggregated nesting in the solitary Hymenoptera. *Annals of the Entomological Society of America.* **83** (3), 277-286.

Rotheray, G. and Gilbert, F. (2011) *The natural history of hoverflies.* Ceredigion, Wales: Forrest Text.

Roubik, D. W. (1992) *Ecology and natural history of tropical bees.* Cambridge, England: Cambridge University Press.

Roy, D. B., Hill, M. O. and Rothery, P. (1999) Effects of urban land cover on the local species pool in Britain. *Ecography.* **22** (5), 507-517.

Roy, D. B. and Sparks, T. H. (2000) Phenology of British butterflies and climate change. *Global Change Biology.* **6** (4), 407-416.

Ryckewaert, P., Razanamaro, O., Rasoamanana, E., Rakotoarimihaja, T., Ramavovololona, P. and Danthu, P. (2011) Sphingidae as likely pollinators of Madagascar's baobabs. *Bois Et Forets Des Tropiques.* **307**, 55-68.

Salisbury, A. (2012) The future of gardening for wildlife. *RHS: The Garden*. (September), 69-70.

Samnegard, U., Persson, A. S. and Smith, H. G. (2011) Gardens benefit bees and enhance pollination in intensively managed farmland. *Biological Conservation*. **144** (11), 2602-2606.

Santamaria, L. and Rodriguez-Girones, M. A. (2007) Linkage rules for plant-pollinator networks: Trait complementarity or exploitation barriers? *Plos Biology*. **5** (2), 354-362.

Sattler, T., Duelli, P., Obrist, M. K., Arlettaz, R. and Moretti, M. (2010) Response of arthropod species richness and functional groups to urban habitat structure and management. *Landscape Ecology*. **25** (6), 941-954.

Saunders, D. A., Hobbs, R. J. and Margules, C. R. (1991) Biological consequences of ecosystem fragmentation - a Review. *Conservation Biology*. **5** (1), 18-32.

Schaffers, A. P., Raemakers, I. P., Sykora, K. V. and Ter Braak, C. J. F. (2008) Arthropod assemblages are best predicted by plant species composition. *Ecology*. **89** (3), 782-794.

Schueepp, C., Herrmann, J. D., Herzog, F. and Schmidt-Entling, M. H. (2011) Differential effects of habitat isolation and landscape composition on wasps, bees, and their enemies. *Oecologia*. **165** (3), 713-721.

Schweiger, O., Musche, M., Bailey, D., Billeter, R., Diekoetter, T., Hendrickx, F., Herzog, F., Liira, J., Maelfait, J., Speelmans, M. and Dziock, F. (2007) Functional richness of local hoverfly communities (Diptera, Syrphidae) in response to land use across temperate Europe. *Oikos*. **116** (3), 461-472.

Seidelmann, K. (1999) The function of the vestibulum in nests of a solitary stem-nesting bee, *Osmia rufa* (L.). *Apidologie*. **30**, 19-29.

Seidelmann, K. (2006) Open-cell parasitism shapes maternal investment patterns in the Red Mason bee *Osmia rufa*. *Behavioral Ecology*. **17** (5), 839-848.

Seidelmann, K., Ulbrich, K. and Mielenz, N. (2010) Conditional sex allocation in the Red Mason bee, *Osmia rufa*. *Behavioral Ecology and Sociobiology*. **64** (3), 337-347.

Sekita, N. and Yamada, M. (1993) Use of *Osmia cornifrons* for pollination of apples in Aomori Prefecture, Japan. *Jarq-Japan Agricultural Research Quarterly*. **26** (4), 264-270.

Shaw, P. J. A. (2003) *Multivariate statistics for the environmental sciences*. London, England: Hodder Arnold.

Siegel, S. and Castellan, N. J. (1988) *Non-parametric statistics for the behavioural sciences*. 2nd ed. New York: McGraw-Hill.

Silva. ClinoMaster *Model 70498* [online]. Available from: http://silva.se/products/proffessional/clinomaster [Accessed 24 March, 2012].

Smith, R. M., Thompson, K., Hodgson, J. G., Warren, P. H. and Gaston, K. J. (2006a) Urban domestic gardens (IX): Composition and richness of the vascular plant flora, and implications for native biodiversity. *Biological Conservation*. **129** (3), 312-322.

Smith, R. M., Gaston, K. J., Warren, P. H. and Thompson, K. (2006b) Urban domestic gardens (VIII): environmental correlates of invertebrate abundance. *Biodiversity and Conservation.* **15** (8), 2515-2545.

Smith, R. M., Warren, P. H., Thompson, K. and Gaston, K. J. (2006c) Urban domestic gardens (VI): environmental correlates of invertebrate species richness. *Biodiversity and Conservation.* **15** (8), 2415-2438.

Söderström, B., Svensson, B., Vessby, K. and Glimskar, A. (2001) Plants, insects and birds in semi-natural pastures in relation to local habitat and landscape factors. *Biodiversity and Conservation.* **10** (11), 1839-1863.

Sokal, R. R. and Rohlf, F. J. (1981) *Biometry.* Second ed. New York: W.H. Freeman and Company.

Spradbury, J. P. (1973) *Wasps: An account of the biology and natural history of social and solitary wasps.* London, UK: Sidgewick and Jackson.

Stace, C. A. (1997) *New flora of the British Isles.* 2nd ed. Cambridge: Cambridge University Press.

Steffan-Dewenter, I. and Leschke, K. (2003) Effects of habitat management on vegetation and above-ground nesting bees and wasps of orchard meadows in Central Europe. *Biodiversity and Conservation.* **12** (9), 1953-1968.

Steffan-Dewenter, I., Munzenberg, U., Burger, C., Thies, C. and Tscharntke, T. (2002) Scale-dependent effects of landscape context on three pollinator guilds. *Ecology.* **83** (5), 1421-1432.

Steffan-Dewenter, I., Potts, S. G. and Packer, L. (2005) Pollinator diversity and crop pollination services are at risk. *Trends in Ecology & Evolution.* **20** (12), 651-652.

Steffan-Dewenter, I. and Schiele, S. (2008) Do resources or natural enemies drive bee population dynamics in fragmented habitats? *Ecology.* **89** (5), 1375-1387.

Steffan-Dewenter, I. and Tscharntke, T. (2001) Succession of bee communities on fallows. *Ecography.* **24** (1), 83-93.

Stelzer, R. J., Chittka, L., Carlton, M. and Ings, T. C. (2010) Winter active bumblebees (*Bombus terrestris*) achieve high foraging rates in urban Britain. *Plos One.* **5** (3), e9559.

STEP Status and Trends of European Pollinators *STEP home* [online]. Available from: www.step-project.net [Accessed 31 August, 2012].

Stoate, C., Boatman, N. D., Borralho, R. J., Carvalho, C. R., de Snoo, G. R. and Eden, P. (2001) Ecological impacts of arable intensification in Europe. *Journal of Environmental Management.* **63** (4), 337-365.

Stone, G. N. and Willmer, P. G. (1989) Warm-up rates and body temperatures in bees - the importance of body size, thermal regime and phylogeny. *Journal of Experimental Biology.* **147**, 303-328.

Strohm, E. (2011) How can cleptoparasitic drosophilid flies emerge from the closed brood cells of the Red Mason bee? *Physiological Entomology.* **36** (1), 77-83.

Stubbs, A. E. and Falk, S. J. (2002) *British Hoverflies: An illustrated identification guide*. 2nd ed. Reading, England: BENHS (British Entomological and Natural History Society).

Su, J. C., Debinski, D. M., Jakubauskas, M. E. and Kindscher, K. (2004) Beyond species richness: Community similarity as a measure of cross-taxon congruence for coarse-filter conservation. *Conservation Biology*. **18** (1), 167-173.

Sutherland, J. P., Sullivan, M. S. and Poppy, G. M. (1999) The influence of floral character on the foraging behaviour of the hoverfly, *Episyrphus balteatus*. *Entomologia Experimentalis Et Applicata*. **93** (2), 157-164.

Tarrant, S. (2010) *The potential of restored landfill sites to support pollinating insects*. The University of Northampton. Ph.D. thesis, unpublished.

Tarrant, S., Ollerton, J., Rahman, M. L., Tarrant, J. and McCollin, D. (2012) Grassland restoration on landfill sites in the East Midlands, United Kingdom: An evaluation of floral resources and pollinating insects. *Restoration Ecology*. In press.

Taylor, P. D., Fahrig, L., Henein, K. and Merriam, G. (1993) Connectivity is a vital element of landscape structure. *Oikos*. **63** (3), 571-573.

Ter Braak, C. J. F. and Šmilauer, P. (2002) *CANOCO reference manual and CanoDraw for Windows user's guide: Software for canonical community ordination (version 4.5)*. New York, USA: Ithaca.

Ter Braak, C. J. F. and Šmilauer, P. (2011) *CANOCO for Windows version 4.52* (Copyright 1997-2003). Biometris, Plant Research International, Wangeningan, Netherlands.

The National Trust. (2012a) [online]. Available from: www.thenationaltrust.org.uk [Accessed 30 August, 2012].

The National Trust. (2012b) *Annual Report 2011-12*. [online]. Available from: www.thenationaltrust.org.uk [Accessed 1 November 2012].

Thomas, K. (1984) *Man and the natural world: Changing attitudes in England 1500-1800*. London, England: Penguin Books Limited.

Thompson, C. (2012) *Honey bee problem nearing a 'critical point': Unusual honey bee die offs have become so severe that some US bee keepers will qualify for disaster relief funds* [online]. Available from: http://www.guardian.co.uk/environment/2012/jan/13/honeybee-problem-critical-point [Accessed 13 March, 2012].

Thompson, K., Hodgson, J. G., Smith, R. M., Warren, P. H. and Gaston, K. J. (2004) Urban domestic gardens (III): Composition and diversity of lawn floras. *Journal of Vegetation Science*. **15** (3), 373-378.

Tommasi, D., Miro, A., Higo, H. A. and Winston, M. L. (2004) Bee diversity and abundance in an urban setting. *Canadian Entomologist*. **136** (6), 851-869.

Torchio, P. F. and Tepedino, V. J. (1980) Sex-ratio, body size and seasonality in a solitary bee, *Osmia lignaria* Propinqua Cresson (Hymenoptera, Megachilidae). *Evolution*. **34** (5), 993-1003.

Trivers, R. L. and Willard, D. E. (1973) Natural selection of parental ability to vary sex-ratio of offspring. *Science.* **179** (4068), 90-92.

Tscharntke, T., Gathmann, A. and Steffan-Dewenter, I. (1998) Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. *Journal of Applied Ecology.* **35** (5), 708-719.

Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I. and Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. *Ecology Letters.* **8** (8), 857-874.

Tylianakis, J. M., Tscharntke, T. and Lewis, O. T. (2007) Habitat modification alters the structure of tropical host-parasitoid food webs. *Nature.* **445** (7124).

UKBMS. (2010a) *UK Butterfly Monitoring Scheme G1: Monitoring butterfly numbers by the transect method - summary information for recorders* [online]. Available from: http://www.ukbms.org/Downloads/UKBMS%20G1%20Transect%20monitoring%20summary.pdf [Accessed 5 March, 2010].

UKBMS. (2012b) *UK Butterfly Monitoring Scheme G2: Field guidance notes for butterfly transects* [online]. Available from: http://www.ukbms.org/Downloads/UKBMS%20G2%20Transect%20field%20guidance%20%20notes.pdf [Accessed 5 March, 2010].

UKCIP *UK Climate Impacts Programme* [online]. Available from: www.ukcip.org.uk [Accessed 12 September, 2012].

Ulrich, W. (2012) *NODF - a FORTRAN program for nestedness analysis Version 2.0 (September 2012)* [online]. Available from: http://www.home.umk.pl/~ulrichw/Downloads/NODFManual.pdf [Accessed 1 November, 2012].

Ulrich, W. and Almeida-Neto, M. (2012) On the meanings of nestedness: back to the basics. *Ecography.* **35**, 865-871.

Ulrich, W., Almeida-Neto, M. and Gotelli, N. J. (2009) A consumer's guide to nestedness analysis. *Oikos.* **118** (1), 3-17.

Ulrich, W. and Gotelli, N. J. (2007) Null model analysis of species nestedness patterns. *Ecology.* **88** (7), 1824-1831.

UNEP-WCMC. (2011) *UK National Ecosystem Assessment: Synthesis of the key findings.* Cambridge, England: UNEP-WCMC.

United Nations. (2011) *World Population Prospects: The 2010 Revision (Published 3 May 2011)* [online]. Available from: www.unpopulation.org [Accessed 3 May, 2011].

vanEngelsdorp, D. and Meixner, M. D. (2010) A historical review of managed honey bee populations in Europe and the United States and the factors that may affect them. *Journal of Invertebrate Pathology.* **103**, S80-S95.

Varley, G. C., Gradwell, G. R. and Hassell, M. P. (1975) *Insect Population Ecology - an analytical approach.* 2nd ed. Oxford, United Kingdom: Blackwell Scientific Publications.

Vazquez, D. P., Melian, C. J., Williams, N. M., Blüthgen, N., Krasnov, B. R. and Poulin, R. (2007) Species abundance and asymmetric interaction strength in ecological networks. *Oikos.* **116** (7), 1120-1126.

Vicens, N. and Bosch, J. (2000) Pollinating efficiency of *Osmia cornuta* and *Apis mellifera* (Hymenoptera: Megachilidae, Apidae) on 'Red Delicious' Apple. *Environmental Entomology.* **29** (2), 235-240.

Walker, K. J. (2003) One species lost every year? An evaluation of plant extinctions in selected British vice-counties since 1900. *Watsonia.* **25**, 359-374.

Walker, K. J. and Preston, C. D. (2006) Ecological predictors of extinction risk in the flora of lowland England, UK. *Biodiversity and Conservation.* **15** (6), 1913-1942.

Walther, B. A. and Morand, S. (1998) Comparative performance of species richness estimation methods. *Parasitology.* **116**, 395-405.

Warder, J. (1720) *The True Amazons: Or, the monarchy of bees. Being a new discovery and improvement of these wonderful creatures.* 4th ed. London: John Pemberton.

Warton, J. (1822) *The Works of Alexander Pope with notes and illustrations.* Volume III. London: Richard Priestley.

Waser, N.M. (2006) Specialization and generalization in plant-pollinator interactions: A historical perspective. In: Waser, N. M. and Ollerton, J. (eds.) *Plant-pollinator interactions: From specialization to generalization*, pp. 3-17. Chicago, USA: University of Chicago Press.

Waser, N. M. and Ollerton, J. (eds.) (2006) *Plant-pollinator interactions: From specialization to generalization.* Chicago, USA: University of Chicago Press.

Waser, N. M., Chittka, L., Price, M. V., Williams, N. M. and Ollerton, J. (1996) Generalization in pollination systems, and why it matters. *Ecology.* **77** (4), 1043-1060.

Watanabe, M. E. (2008) Colony collapse disorder: Many suspects, no smoking gun. *Bioscience.* **58** (5), 384-388.

Weiner, C. N., Werner, M., Linsenmair, K. E. and Blüthgen, N. (2011) Land use intensity in grasslands: Changes in biodiversity, species composition and specialisation in flower visitor networks. *Basic and Applied Ecology.* **12** (4), 292-299.

Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, N., Petanidou, T., Potts, S. G., Roberts, S. P. M., Szentgyorgyi, H., Tscheulin, T., Vaissiere, B. E., Woyciechowski, M., Biesmeijer, J. C., Kunin, W. E., Settele, J. and Steffan-Dewenter, I. (2008) Measuring bee diversity in different European habitats and biogeographical regions. *Ecological Monographs.* **78** (4), 653-671.

Westphal, C., Steffan-Dewenter, I. and Tscharntke, T. (2003) Mass flowering crops enhance pollinator densities at a landscape scale. *Ecology Letters.* **6** (11), 961-965.

Westphal, C., Steffan-Dewenter, I. and Tscharntke, T. (2006) Bumblebees experience landscapes at different spatial scales: possible implications for coexistence. *Oecologia.* **149** (2), 289-300.

Westrich, P. (1998) *Habitat requirements of British bees and wasps.* Cardiff, UK: International Bee Research Association.

Westrich, P. (1996) Habitat requirements of central European bees and the problems of partial habitats. *Linnean Society Symposium Series; the Conservation of Bees.* **18**, 1-15.

Whitehorn, P. R., O'Connor, S., Wackers, F. L. and Goulson, D. (2012) Neonicotinoid pesticide reduces bumble bee colony growth and queen production. *Science.* **336** (6079), 351-352.

Wiegert, R. G. and Owen, D. F. (1971) Trophic structure, available resources and population density in terrestrial versus aquatic ecosystems. *Journal of Theoretical Biology.* **30**, 69-81.

WikiMedia Commons (2005) *Alexander Pope's house at Twickenham* (From an original painting at Orleans House Gallery, Richmond). Published with kind permission from the Richmond Borough Art Collection, Orleans House Gallery, Richmond. [online]. Available from: http://commons.wikimedia.org/wiki/File:Twickenham.png. [Accessed 12th September 2012].

Wilkaniec, Z. and Giejdasz, K. (2003) Suitability of nesting substrates for the cavity-nesting bee *Osmia rufa. Journal of Apicultural Research.* **42** (3), 29-31.

Williams, N. M., Cariveau, D., Winfree, R. and Kremen, C. (2011) Bees in disturbed habitats use, but do not prefer, alien plants. *Basic and Applied Ecology.* **12** (4), 332-341.

Wilson, C. A. (ed.) (2003) *The country house kitchen garden 1600-1950.* Gloucestershire, England: Sutton Publishing Limited.

Wilson, E. O. (2001) *The diversity of life.* London, England: Penguin Books.

Winemiller, K. O. (1989) Must connectance decrease with species richness? *American Naturalist.* **134** (6), 960-968.

Winfree, R., Williams, N. M., Dushoff, J. and Kremen, C. (2007) Native bees provide insurance against ongoing honey bee losses. *Ecology Letters.* **10** (11), 1105-1113.

Wratten, S. D., Gillespie, M., Decourtye, A., Mader, E. and Desneux, N. (2012) Pollinator habitat enhancement: Benefits to other ecosystem services. *Agriculture Ecosystems & Environment.* **159**, 112-122.

WWF. *World Wildlife Fund - Tigers: Challenges and threats* [online]. Available from: http://www.wwf.org.uk/what_we_do/safeguarding_the_natural_world/wildlife/tigers/?gclid=CN7P1PTr1rQCFSHHtAodmRkAeA&pc=ALD004002 [Accessed 7 January, 2012].

Yamamura, K. (1999) Key-factor/key-stage analysis for life table data. *Ecology.* **80** (2), 533-537.

Yeates, D. K. and Wiegmann, B. M. (eds.) (2005) *The evolutionary biology of flies.* New York, USA: Columbia University Press.

Yeo, P. F. and Corbet, S. A. (1995) *Solitary wasps.* 2nd ed. Slough: The Richmond Publishing Co. Ltd.

Zmyslony, J. and Gagnon, D. (1998) Residential management of urban front-yard landscapes: A random process? *Landscape and Urban Planning.* **40** (4), 295-307.

Appendix I

Details of the 17 properties used for the study. Garden descriptions and access details correct as at January 2013.

ALTHORP

Address: Althorp House, Althorp, Northamptonshire, NN7 4HQ

House original build date: 1508

Architect: Unknown. Remodelled in 1650 by Dorothy, the widow of the 1st Earl of Sunderland. Additions by Henry Holland in 1786[1]

Original owner: Sir John Spencer

Garden designer/Landscape architect: André Le Nôtre[2]

Notable events in the garden's history:

- 1707 *Britannia Illustrata* engraving shows that part of Althorp's formal gardens were given over to vegetables, fruit trees and grass, and that formal tree-lined avenues radiated from it[1]
- 'Brownian' alterations, including the filling in of the moat, proposed by Henry Holland following the 1787 plans of Samuel Lapidge ('Capability' Brown's chief assistant)
- 'Capability' Brown believed to have visited Althorp in 1780 to offer advice about future changes to the landscape[1]
- W.M. Teulon added terraces in the 1860s[1]
- Lake known as 'Round Oval' refilled in 1868 with summerhouse, later to be dedicated to the memory of Diana, Princess of Wales, moved there in 1926[2]
- Late 1990s planting work by Dan Pearson[1]

Current garden:

Description

Mowl and Hickman (2008) describe the present-day garden at Althorp as 'gently elegant, but essentially bland'. The gardens are dominated by tightly mown grass and there is limited floral variety in the few beds and borders present.

During the 2010 sampling season, major restoration work was taking place. As a result the borders to the west of the main house were not fully maintained. The borders to the north-west of the Stable Block (containing *Buddleja* sp., *Digitalis ferruginea* and *Rosa rugosa*) were particularly popular with flower-visiting insects.

Public access

Private house. The gardens are open each day during the months of July and August.

Present owner: The Right Honourable Charles Spencer (9th Earl Spencer)

Website: http://www.althorp.com/

---

[1] Mowl and Hickman (2008)
[2] Hall (1994)

BOUGHTON

Address: Boughton House, Kettering, Northamptonshire, NN14 1BJ

House original build date: Late 17th century house built on Tudor foundations[1]

Architect/design: The design ideas of Ralph, the 1st Duke of Buccleuch, gained during his ambassadorial duties at the court of Louis XIV, heavily influenced the design of Boughton House[2]

Original owner: 1st Duke of Montagu (Montagu ancestors owned the Estate from 1528)[1]

Garden designer/Landscape architect: Ralph Montagu employed Leonard van der Meulan as a gardener early in the eighteenth century. The garden design is attributed to Charles Bridgeman[1]

Notable events in the garden's history:

- Design of garden influenced by Duke Ralph[3]. Series of canals, lakes and avenues laid out over 100 acres. The design included parterres, fountains and woodland
- After the death of the 2nd Duke in 1749 the estate passed through the female line. For almost 200 years 'benign neglect became the norm' as nature reclaimed the terraces and waterways silted up.[4]
- Management plan drawn up at the end of the twentieth century to restore areas of the estate, clean up silted ponds and re-plant lime avenues
- 'Orpheus', commissioned by the present Duke of Buccleuch and created between 2007-2009 is the first new landscape feature at the estate for 300 years[1]

Current garden:

Description

The garden consists of a mix of components including an extensive walled garden with a sensory area that is open to the public, ponds fringed with native plants, a dower garden (previously the private woodland garden of David Scott and Valerie Finnis) and the Duke's own garden. All areas were accessed for sampling during the current project.

Public access

Private house. Gardens open daily throughout August.

Present owner: The 10th Duke of Buccleuch, Richard Walter John Montagu Douglas Scott

Website: http://www.boughtonhouse.org.uk

---

[1] The Dicamillo Companion
[2] Burton (1994)
[3] Heward and Taylor (1996)
[4] Boughton House website

CANONS ASHBY

Address: Canons Ashby, Daventry, Northamptonshire, NN11 3SD

House original build date: 1550[1]

Architect/design: The Dryden family built the current house on the site originally used by Sir John Cope. (Cope's original house reportedly used masonry from the nearby fallen priory[2]). In the mid-seventeenth century Sir John Dryden re-did much of the house in the Jacobean style[3]

Original owner(s): The Dryden family

Garden designer/Landscape architect: Edward Dryden[3]

Notable events in the garden's history:

- Edward Dryden laid out the formal garden in the 18th century[3]
- Plans of the garden were published in an 1885 book *History of Gardening* written by Alice Amherst and in H. Inigo Triggs' *Formal Gardens in England and Scotland* (1902). This publication went on to have significant influence on Edwardian garden design[3]
- After 1948 the house became unoccupied and the garden overgrown
- The house was gifted to the National Trust by the Dryden family in 1980 and was eventually reopened in 1984[2]
- Canons Ashby received > 50,000 visitors in 2011/12[4]

Current garden:

Description

A compact garden comprising formal flower beds with annual bedding, a herb border, and semi-wild area. The 2010 sampling took place prior to the major 2011 restoration project in the lower garden.

Public access

Open several days a week depending on season.

Present owner: The National Trust

Website: http://www.nationaltrust.org.uk/canons-ashby-house/

---

[1] The Dicamillo Companion
[2] The National Trust (Canons Ashby) website
[3] Hall (1994)
[4] The National Trust website

COTON MANOR

Address: Coton Manor, Coton, Northamptonshire, NN6 8RQ

House original build date: 17th century[1]

Architect: unknown

Original owner: unknown

Garden designer/Landscape architect:

The current design reflects the work, skill and knowledge of the present owners, Ian and Susie Pasley-Tyler

Notable events in the garden's history:

- Prior to WWII when Ian Pasley-Tyler's parents moved into the property there were no formal gardens. The area surrounding the house was used for cattle grazing[2]
- In 1990 Ian and Susie Pasley-Tyler started creating the garden
- The wildflower meadow was sown in 1994[3]

Current garden:

Description

This compact garden contains many elements including beds, borders, water gardens, a beech wood (with bluebells in spring), a herb garden, a fruit area and semi-wild patches, including a wildflower meadow.

Public access

Tuesday to Saturday from March to September

Present owners: Ian and Susie Pasley-Tyler

Website: http://www.cotonmanor.co.uk/

---

[1] The Dicamillo Companion
[2] Alexander-Sinclair (2011)
[3] Coton Manor website

COURTEENHALL

Address: The Estate Office, Courteenhall, Northamptonshire, NN7 2QD

House original build date: 1793[1]

Architect: Samuel Saxon[1]

Original owner: Sir William Wake[2]

Garden designer/Landscape architect: Humphry Repton 1790s[2]

Notable events in the garden's history:

- Gardens designed by Humphry Repton, the last great landscape architect of the 18th century[2]
- In 2008 an area of the garden was sown with wildflowers[3]

Current garden:

Description

This garden is comprised of many smaller components that include an arboretum, a pond and a wildflower area. Additionally there is a traditional walled garden which contains perennial borders, fruit trees and a large vegetable growing area.

Public access

Private house and garden. The gardens are not open to the public although private weddings occasionally take place there.

Present owners: Charles and Joan Wake

Website: http://www.courteenhall.co.uk/

---

[1] The Dicamillo Companion
[2] Courteenhall website
[3] D. Wilkes (pers. comm.)

EASTON NESTON

Address: Easton Neston, Towcester, Northamptonshire

House original build date: 1699-1702[1]

Architect: Possibly William Talman or Nicholas Hawksmoor. Design executed and altered by Hawksmoor. Additions (including chimneys) by William Kent in 1735[2]

Original owner: Sir William Fermor[1]

Garden designer/Landscape architect: John Raffield (entrance gate and screen to the park in 1820s)[1]

Notable events in the garden's history:

- Canal (known as the Long water) designed by Hawksmoor (date unknown)

Current garden:

Description

The garden is comprised of formal areas with ponds, fountains and yew hedges which adjoin a very large walled kitchen garden containing an orchard, vegetable and soft fruit growing areas plus new beds and borders (planted in 2009). Large tree-lined avenues radiate out from the house. Nearby a less formal pond with native planting at its edge exists.

Public access

Private house and garden. Not open to the public.

Present owner: Mr Leon Max

Website: None

---

[1] Harris (1979)
[2] The Dicamillo Companion

FARNBOROUGH HALL

Address: Farnborough Hall, Farnborough, Warwickshire, OX17 1DU

House original build date: mid 18th century

Architect: Sanderson Miller[1]

Original owner: Holbech family acquired the Farnborough Estate in 1684[1]

Garden designer/Landscape architect: Sanderson Miller in 18th century.

Notable events in the garden's history:

- William Holbech lead the design of the garden using ideas gained during his 'grand tour' in the late 18th century
- Three quarters of a mile terrace walk created (date unknown). Terrace passes an ionic building and leads to an obelisk[1]
- The National Trust acquired the property in 1960, but it is still run and occupied by the Holbech family.

Current garden:

Description

The main garden is approached from a long drive leading up to the house. Two borders with mirrored planting extend to the door of the property. The long terrace walk is tightly mown and bordered on one side by tall trees. At a lower level, a series of borders, including a rose garden, lead down to a pool.

Public access

Wednesday and Saturday afternoons only (Apr – Sep.).

Present owner: The National Trust. The house continues to be occupied by the Holbech family.

Website: http://www.nationaltrust.org.uk/farnborough-hall/

---

[1] The National Trust (Farnborough) website

HOLDENBY HOUSE

Address: Holdenby House, Estate Office, Holdenby, Northamptonshire, NN6 8DJ

House original build date: 1583[1]

Architect/designer: unknown, but the house was commissioned by Sir Christopher Hatton to be the largest private house at the time[2]

Original owner: Sir Christopher Hatton

Garden designer/Landscape architect: unknown

Notable events in the garden's history[2,3]:

- In 1647 Charles I was self-imprisoned for five months within the confines of the house and gardens following his defeat in the Civil War. King Charles' Walk, his favourite part of the Elizabethan garden, has been incorporated into the present-day garden
- Holdenby bought by Captain Adam Baynes in 1650 who demolished all but the kitchen wing (now the main house)
- House and gardens pass back to the Crown in 1660. Subsequently purchased by The Duke of Marlborough (1709). Passed down through the female line to the Lowthers (present owners)
- James Lowther initiates restoration and replanting of the garden from 1979 onwards

Current garden:

Description

Several distinct areas make up this garden, which almost completely surrounds the house. There are formal beds and borders (including the silver border), a kitchen garden, an Elizabethan garden, a pond garden and nearby woodland. The original walled garden is now the site of a commercial falconry centre.

Public access

Private house. Access to gardens on Sundays (Apr. – Sep.)

Present owners: James and Karen Lowther

Website: http://www.holdenby.com/

---

[1] The Dicamillo Companion
[2] Holdenby website
[3] Holdenby brochure

KELMARSH HALL

Address: Kelmarsh Hall, Kelmarsh, Northamptonshire, NN6 9LY

House original build date: 1728-32[1]

Architect: Built by Francis Smith of Warwick to a James Gibb design. Additions (entrance lodges) made by James Wyatt in 1778[1,2]

Original owner: House built for William Hanbury

Garden designer/Landscape architect: unknown

Notable events in the garden's history:

- Estate purchased by Richard Naylor in 1864 for its potential as a hunting ground[2]
- Nancy Lancaster laid out the gardens in the 1930s during the time she lived there as a lessee with Ronald Tree. Norah Lindsay and Geoffrey Jellicoe assisted Lancaster with designs[2]

Current garden:

Description

The current garden is a medley of herbaceous borders, rose gardens and beds. The walled garden (containing a huge array of flowers as well as extensive vegetable beds) is unusual in that it is triangular in shape.

Public access

Open Tuesdays, Wednesdays, Thursdays and Sundays from April to September

Present owner: The Kelmarsh Trust (Charitable Trust)

Website: http://www.kelmarsh.com/

---

[1] Mowl and Hickman (2008)
[2] Kelmarsh website

KIRBY HALL

Address: Kirby Hall, off Kirby Lane, Corby, Northamptonshire, NN17 3EN

House original build date: 1570-75[1]

Architect: Inigo Jones[1]

Original owner: Sir Humphrey Stafford

Garden designer/Landscape architect Principally designed by Christopher IV

Notable events in the garden's history:

- During the 1680s Christopher IV, who was a noted horticulturalist, created what his brother later described as 'Ye finest garden in England'[2]
- At their peak in 1700 the gardens covered almost 15 acres. Parterres extended to a stream, and beyond that a 'wilderness' was visible[3]
- Following the death of Sir Christopher Hatton IV in 1706 the gardens fell into decline. His son felled areas of woodland to pay off his debts[3]
- By 1810 the gardens and house were described as 'unaccountably neglected and fast going to ruin and decay'[3]
- During the 1930s the property became the responsibility of the Office of Works. Photographs from the 1950s show extensive rose planting[3]
- In 1984 English Heritage took over the property and started a garden renovation programme

Current garden:

Description

Two borders (the last remaining flower beds) have been populated with plants befitting the time of the garden's heyday. However, the remainder of the garden comprises over-mown, grass-dominated areas. These include the area occupied by the original parterres as well as others that extend to the property boundary.

Public access

Mondays, Thursdays, Fridays, Saturdays and Sundays from April to November

Present owner: English Heritage

Website: http://www.english-heritage.org.uk/daysout/properties/kirby-hall/

[1] The Dicamillo Companion
[2] Burton (1994)
[3] English Heritage (Kirby) Printed Information

LAMPORT HALL

Address: Lamport Hall Preservation Trust Limited, Lamport Hall, Lamport, Northamptonshire, NN6 9HD

House original build date: 1655

Architect: John Webb (1654)[1]

Original owner: Sir Justinian Isham (although Lamport manor had been in the family since 1560)[2]

Garden designer/Landscape architect: Gardens originally planned out by Gilbert Clerke in 1655[3] and laid out in 1677[1]

Notable events in the garden's history:

- In 1857 Charles Isham planted Irish yews to make Eagle Walk (a trail leading to caged eagles) and created the rockery which represents the earliest alpine garden in the UK. He placed small figures on this rocky face which are recognised today as the world's first gnomes[3]
- In the early part of the twenty-first century the walled garden was replanted with wide blocks of herbaceous perennials

Current garden:

Description

Iron gates dating to 1700 remain in the garden, as does Eagle Walk and a very large walled garden. The latter contains an unusual layout of herbaceous perennials, many of which could be described as candidates for prairie planting. Other beds and borders contain an interesting mix of plants of various heights, colours and flowering times, most of which receive some shelter from nearby walls. A long south-west facing border of lavender adjoins grazing pasture. In 2010 the orchard had limited ground flora as a result continuous mowing and the application of herbicides around tree bases. This changed in 2011 when a more relaxed approach to management was taken.

Public access

Wednesday and Thursday afternoons, April to October

Present owner: Lamport Hall Preservation Trust (charitable trust)

Website: http://www.lamporthall.co.uk/

---

[1] British History website
[2] Heward and Taylor (1996)
[3] Lamport website

LOIS WEEDON HOUSE

Address: Lois Weedon House, Lois Weedon, Nr. Towcester, Northamptonshire

House original build date: Queen Anne style – but believed to have been built in 1904 for the Speaker of the House of Commons[1]

Architect: unknown

Original owner: unconfirmed

Garden designer/Landscape architect: unknown

Notable events in the garden's history: None documented

Current garden:

Description

This garden has a real cottage-garden feel to it. As well as possessing formal beds and borders, there are terraces that lead down to a large pond together with shady walks. A ha-ha separates the garden from grazing land on the estate. The walled garden has wide south and east facing flower borders within it, together with areas where soft fruit is grown.

Public access

This is a private house and garden. It opens twice a year to raise money for charity under the National Garden Scheme[2]

Present owners: Sir John and Lady Greenaway

Website: None

---

[1] South Northants website
[2] National Garden Scheme website

STEANE PARK

Address: Steane Park Garden, Brackley, Northamptonshire, NN13 6DP

House original build date: The late medieval and 16th century house no longer exists. Only the service end survives. The complete building is known from a drawing by Tillemans dating to 1719[1]

Architect: unknown

Original owner: Possibly built by Baron William Morley or his son Henry[1]

Garden designer/Landscape architect: unknown

Notable events in the garden's history:

- In 1752 the house was in ruins and is believed to have been dismantled soon after that date. Any existing garden areas are likely to have been abandoned
- The surviving part of the house was sold to a Captain Alcock in 1890. The remodelling and extensions are attributed to him. It is possible that parts of the garden came into existence at this time[1]

Current garden:

Description

The design of the current garden and the diversity of compartments and plants it contains can be attributed to the present owners, in particular Lady Connell. The garden has many beds and borders together with a vegetable patch, a large pond, a wildflower meadow and a bog garden. Semi-wild areas are allowed to flourish which encourages native plants to establish and flower.

Public access

This is a private house and garden. Group visits to the garden are possible by appointment.

Present owners: Sir Michael and Lady Connell

Website: http://www.steanepark.co.uk/

---

[1] Heward and Taylor (1996)

SULGRAVE MANOR

Address: Sulgrave Manor, Manor Road, Sulgrave, Northamptonshire, OX17 2SD

House original build date: 1540[1]

Architect: unknown

Original owner: Lawrence Washington[2]

Garden designer/Landscape architect: Early garden designers unknown. In the 1920s Sir Reginald Blomfeld designed the garden[3]

Notable events in the garden's history:

- From the late 18th century to 1914 Sulgrave was used as a farmstead and all traces of the previous garden were lost[2]
- Herbaceous borders, a knot garden with traditional herbs and the orchard were laid out in 1920[2]
- Garden first opened to the public in 1921[3]
- Garden became the National Garden of the Herb Society in 1997 and includes beds containing herbs both taken to and brought from the Americas[4]

Current garden:

Description

In addition to the area designated for the Herb Society, the garden has an orchard, several flower borders and a Tudor vegetable garden. Native flowering plants are plentiful in areas that are left as semi-wild, in particular where the composting takes place.

Public access

Weekends from noon and Tuesdays – Fridays from 2pm (April – Oct)

Present owner: Sulgrave Manor Trust (charitable trust)

Website: http://www.sulgravemanor.org.uk/

---

[1] The Dicamillo Companion
[2] Sulgrave website
[3] Sulgrave brochure
[4] The Herb Society

UPTON HOUSE

Address: Upton House and Gardens, Nr. Banbury, Oxfordshire, OX15 6HT

House original build date: Known to be a manor house in 1452, it was rebuilt in the 20 years after that. Sir Rushout Cullen made extensive changes on purchasing it in 1695[1]

Architect: House remodelled by Percy Morley-Horder in 1927-29 for the 2nd Viscount Bearsted

Original owner: Sir Rushout Cullen

Garden designer/Landscape architect: unknown

Notable events in the garden's history:

- Lord Bearsted bought the property in 1927. Lady Bearsted employed Kitty Lloyd-Jones to re-design the gardens which included the creation of a bog garden[2]

Current garden:

Description

The gardens at Upton comprise a number of borders close to the house followed by a series of wide terraces, each supported by stone walls, which contain a range of woody plants, herbaceous perennials (including the National Collection of Asters) and edible plants. These terraces lead down to a large pond. There is a separate bog garden, a semi-wild area planted with hazel, a herb garden and woodland walks. The orchard is tightly mown, as are all the lawn areas.

Public access

Open every day 11am – 5pm (except Thursdays)

Present owner: The National Trust

Website: http://www.nationaltrust.org.uk/upton-house/

---

[1] The National Trust (Upton House) website
[2] The National Trust (2009)

WADDESDON MANOR

Address: Waddesdon Manor, Waddesdon, Buckinghamshire, HP18 0JH

House original build date: 1874-89

Architect: G.H. Destailleur[1]

Original owner: Baron Ferdinand de Rothschild

Garden designer/Landscape architect: Elie Lainé (1870s)[1]

Notable events in the garden's history:

- House built on a cleared and levelled hilltop. Trees hauled into position to create a mature setting in the shortest time possible[1]
- During the second World War potatoes were grown on the large parterre at the front of the house[2]
- James de Rothschild died without an heir in 1957 and the house and gardens were left to The National Trust.
- In 1995 the parterre was restored to its Victorian glory by the current Lord Rothschild's daughter, Beth Tommasini[1]
- The rose garden, planted with 600 roses, was created in 2000. It is a tribute to the rose garden originally laid out by Miss Alice de Rothschild who inherited the estate in 1898 from her brother
- Waddesdon Manor was The National Trust's fifth most visited property in 2011/12, with more than 339 000 people touring the house and gardens[3]

Current garden:

Description

The gardens at Waddesdon are dominated by routes leading to and from the main house. Formal carpet bedding is a feature of the famous parterre (in 2010, five thousand Begonias were planted). Annuals are used on round beds along the drive leading to the house and there is an extensive collection of David Austin roses in the recently created rose garden. The woodland walks are extensively managed although some native ground flora is present.

Public access

Wednesday to Friday and weekends from March to December

Present owner: The National Trust

Website: http://www.nationaltrust.org.uk/waddesdon-manor/

---

[1] Harris (1979)
[2] Paul Farnell, Waddesdon Manor Head Gardener (pers. comm.)
[3] The National Trust (2012)

WREST PARK

Address: Wrest Park, Silsoe, Luton, Bedfordshire, MK45 4HR

House original build date: Present house is a re-build dating to 1839[1]. The original house was demolished having been owned by the de Gray's since 1260[2]

Architect: Thomas de Grey, 2nd Earl de Grey (amateur architect)[2]

Original owner: John De Grey first owned Wrest Park in the 1260s[2]

Garden designer/Landscape architect: de Grey family, Thomas Archer and 'Capability' Brown[2]

Notable events in the garden's history:

- Creation of the 18th century canal with Baroque-style garden pavilion (designed by Thomas Archer and built 1709-11)[3]
- Henry, duke of Kent inherited the formal gardens and added a designed woodland around it between 1710 and 1740[2]
- Jemima, marchioness Grey employed 'Capability' Brown to soften the formal lines created by her Grandfather[2]
- Old house demolished and a new house designed by Thomas, Earl de Grey built north of the original property in 1839. The gardens were redesigned at the same time using the French style of large parterres and benefited from the addition of an orangery and Italian garden[2]
- In 2006 Wrest Park passed into the hands of English Heritage[1]
- In 2011 a new restoration project started in the garden. The description below reflects the gardens as they were when sampled in 2010.

Current garden:

Description

A very formal garden. Few flower resources available in the Italian garden with the parterre dominated by red pelargoniums. The woodland walks are heavily managed and the lawn areas are tightly mown.

Public access

Open weekends only (Nov. to Apr.) then every day apart from Tuesdays and Wednesdays.

Present owner: English Heritage

Website: http://www.english-heritage.org.uk/daysout/properties/wrest-park/

---

[1] English Heritage (Wrest Park) website
[2] English Heritage Information Boards
[3] Girouard (1984)

Appendix I References

Alexander-Sinclair, J. (2011). An instinct for beauty. [Online] Available: http://www.worldreviewer.com/member/jamesas/ (Accessed 24/9/2012)

Boughton House: The English Versaille (2010) In-house brochure produced by The Living Landscape Trust. Available from Boughton House, Kettering, Northamptonshire

Boughton House website. [Online] Available: http://www.boughtonhouse.org.uk (Accessed 23/9/2012)

British History website. Parishes: Langport with Hanging Houghton [online] Available: http://www.british-history.ac.uk (Accessed 24/9/2012)

Burton, N. (1994) *English Heritage from the air*. 2nd ed. London, England: Sidgwick and Jackson Limited.

Coton Manor website. [Online] Available: http://www.cotonmanor.co.uk (Accessed 23/9/2012)

Courteenhall website. [online] Available: http://www.courteenhall.co.uk (Accessed 23/9/2012)

English Heritage (Kirby) Information Boards documenting the creation of the gardens. Available to view at Kirby House, Northamptonshire

English Heritage (Wrest Park) Information Boards documenting the creation of the house and gardens. Available to view at Wrest Park, Bedfordshire

English Heritage (Wrest Park) website [online] Available: http://www.english-heritage.org.uk/daysout/properties/wrest-park/ (Accessed 25/9/2012)

Farnell, P. Head gardener at Waddesdon Manor. (Personal communication to hilary.erenler@northampton.ac.uk) April, 2010

Girouard, M. (1984) *Historic Houses of Britain*. 2nd ed. London, England: Peerage Books.

Harris, J. (1979) *The Artist and the Country House: A History of Country House and Garden View Painting in Britain 1540 – 1870*. Philip Wilson for Sotheby Parke Bernet. London, England

Heward, J. and Taylor, R. (1996) *The Country Houses of Northamptonshire*. Swindon, England: Royal Commission on the Historic Monuments of England.

Holdenby brochure (undated) *Holdenby (House, Gardens, Falconry)* Produced by AH Jolly Ltd, Yelvertoft, Northamptonshire

Holdenby website [online] Available: http://www.holdenby.com (Accessed 23/9/2012)

Kelmarsh Hall website [online] Available: http://www.kelmarsh.com (Accessed 23/9/2012)

Appendix I References (continued)

Lamport Hall website [online] Available: http://www.lamporthall.co.uk (Accessed 24/9/2012)

Mowl, T. Hickman, C. (2008) *The historic gardens of England: Northamptonshire.* Stroud, England: Tempus Publishing.

National Garden Scheme. NGS gardens open for charity [online] Available: http://www.ngs.org.uk (Accessed 24/9/2012)

South Northants County Council. Village descriptions: Weedon Lois. [online] Available: http://www.southnorthants.gov.uk/Weedon_Lois_VDS.pdf (Accessed 24/9/2012)

Sulgrave Manor (2010) *The Birthplace of George Washington's Ancestors.* In-house brochure. Available from Sulgrave Manor, Northamptonshire

Sulgrave Manor website [online] Available: http://www.sulgravemanor.org.uk/ (Accessed 25/9/2012)

The Dicamillo Companion to British and Irish Country Houses [online] Available: http://www.dicamillocompanion.com (Accessed 24/9/2012)

The Herb Society website [online] Available: http://www.herbsociety.org.uk/ (Accessed 24/9/2012)

The National Trust website. Canons Ashby [online] Available: http://www.nationaltrust.org.uk/canons-ashby-house/ (Accessed 25/9/2012)

The National Trust website. Upton House and Gardens [online] Available: http://www.nationaltrust.org.uk/upton-house/ (Accessed 25/9/2012)

The National Trust (2009) A Fortune Well Spent? Leaflet documenting aspects of Upton House and Gardens. Available at Upton House, Oxfordshire

The National Trust (2012) *Annual Report 2011-12* [online] Available: http://www.nationaltrust.org.uk/about-us/annual-reports/ (Accessed 25/9/2012)

Wilkes, D. Head gardener at Courteenhall. (Personal communication to hilary.erenler@northampton.ac.uk) June 2010

Appendix II

Abbreviations used in the thesis

AL – Althorp Estate

APG – Angiosperm Phylogeny Group

BAP – Biodiversity Action Plan

BB – Bumblebees

BBCT – Bumblebee Conservation Trust

BDM – Butterflies and day-flying moths

Beds. - Bedfordshire

BOU – Boughton House

BPG – Buckingham Palace Garden

Bucks. - Buckinghamshire

BWARS – Bees, Wasps and Ants Recording Society

CA – Canons Ashby

CHALL - Courteenhall

CM – Coton Manor

DCA – Detrended correspondence analysis

Defra – Department of the Environment, Food and Rural Affairs

ECDF(s) – Empirical cumulative distribution function(s)

EN – Easton Neston

FAR – Farnborough Hall

F - Flies

HF - Hoverflies

HOL – Holdenby House

IPI – Insect Pollinator Initiative

KEL – Kelmarsh Hall

KIR – Kirby Hall

LAM – Lamport Hall

LW – Lois Weedon House

NBKA – Northamptonshire Beekeepers' Association

NERC – Natural Environment Research Council

NGO – Non-governmental organisation

NGS – National Garden Scheme

NHM – Natural History Museum

NODF – Nestedness Metric based on Overlap and Decreasing Fill

Northants. - Northamptonshire

NT – National Trust

OSR – Oilseed rape

Pers. comm. – Personal communication

Pers. obs. – Personal observation

RAD(s) – Rank abundance distribution(s)

RDA – Redundancy analysis

REGWQ – Ryan, Einot, Gabriel, Welsch Q (*post hoc* test)

SAD(s) – Species abundance distribution(s)

SB – Solitary bees

SOCW – Social wasps

SOLW – Solitary wasps

ST – Steane Park

STEP – Status and Trends of European Pollinators

SUL – Sulgrave Manor

UK – United Kingdom

UKBMS – UK Butterfly Monitoring Scheme

UKCIP – UK Climate Impacts Programme

UN – United Nations

UNEP-WCMC – UN Environment Programme - World Conservation Monitoring Centre

UP – Upton House

USA – United States of America

WAD – Waddesdon Manor

Warks. – Warwickshire

WINE – Weighted-Interaction Nestedness Estimator

WNODF – Weighted Nestedness Metric based on Overlap and Decreasing Fill

WR – Wrest Park

Appendix III

Summary of the seven key non-parametric species richness estimators available. After Colwell and Coddington (1994), Chazdon *et al.* (1998) and Gotelli and Colwell (2011).

Name of estimator	Suitable for abundance (A) or incidence (I) data	Description
ACE Abundance-based coverage estimator	A	Estimator based on species with ≤ 10 individuals in a sample
ICE Incidence-based coverage estimator	I	Estimator based on species found in ≤ 10 samples
Chao 1	A	Estimates the number of species in a sample based on the number of rare species present. Uses singletons and doubletons for abundance data
Chao 2	I	Estimates the number of species in a sample based on the number of occurrences of rare species. Uses 'uniques' or duplicates for incidence data
Jack 1 First-order jack knife	A	Estimate based on the number of species that occur *only* in one sample.
Jack 2 Second-order jack knife	I	Estimate based on the number of species that occur only in one sample and, in addition, those that occur only in two samples
Boot Bootstrap	I	Bootstrap method based on the proportion of samples containing each species

Appendix IV

List of the 20 National Trust gardens surveyed by Edwards (2003).

National Trust Property	Postcode	County
Alfriston Clergy House	BN26 5TL	Sussex
Anglesey Abbey	CB25 9EJ	Cambridgeshire
Batemans	TN19 7DS	Sussex
Chartwell	TN19 1PS	Kent
Claremont	KT10 9JG	Surrey
Clivedon	SL6 0JA	Berkshire
Emmets	TN14 6BA	Kent
Ham House	TW10 7RS	Surrey
Hinton Ampner	SO24 0LA	Hampshire
Ickworth	IP29 5QE	Surrey
Igtham Mote	TN15 0NT	Kent
Nymans	RH17 6EB	Sussex
Polesden Lacey	RH5 6BD	Surrey
Scotney	TN3 8JN	Kent
Sheffield Park	TN22 3QX	Sussex
Sissinghurst	TN17 2AB	Kent
Stowe	MK18 5DG	Buckinghamshire
Uppark	GU31 5QR	Hampshire
The Vynne	RG24 9HL	Hampshire
Wimpole	SG8 0BW	Cambridgeshire

Appendix V

Dunn-Šidák method for adjusting the significance level (α) when making multiple comparisons (Sokal and Rohlf, 1981).

$$\alpha' = 1 - (1 - 0.05)^{1/k}$$

where k = the number of comparisons

Example: 6 independent tests

$1 - (1 - 0.05)^{1/6}$

$1 - (0.95)^{0.1667}$

$1 - 0.9915$

$\alpha = 0.0085$

Appendix VI

List of insect species recorded in 2010 and 2011.

Bumblebees	**2010**	**2011**
Bombus barbutellus (Kirby, 1802)	1	1
Bombus campestris (Panzer, 1801)	1	1
Bombus hortorum (Linnaeus, 1761)	1	1
Bombus hypnorum (Linnaeus, 1758)	1	1
Bombus lapidarius (Linnaeus, 1758)	1	1
Bombus lucorum senso latu	1	1
Bombus pascuorum (Scopoli, 1763)	1	1
Bombus pratorum (Linnaeus, 1761)	1	1
Bombus ruderarius (Müller, 1776)	1	1
Bombus ruderatus (Fabricius, 1775)	1	1
Bombus rupestris (Fabricius, 1793)	1	1
Bombus sylvestris (Lepeletier, 1832)	1	1
Bombus terrestris (Linnaeus, 1758)	1	1
Bombus vestalis (Geoffroy, 1785)	1	1

Solitary bees		
Andrena bicolor Fabricius, 1775	1	1
Andrena bucephala Stephens, 1846	1	0
Andrena carantonica Pérez, 1902	1	1
Andrena chrysosceles (Kirby, 1802)	1	1
Andrena cineraria (Linnaeus, 1758)	1	1
Andrena dorsata (Kirby, 1802)	1	1
Andrena flavipes Panzer, 1799	1	1
Andrena fulva (Müller, 1776)	1	0
Andrena haemorrhoa (Fabricius, 1781)	1	1
Andrena labialis (Kirby, 1802)	1	0
Andrena nigroaenea (Kirby, 1802)	1	1
Andrena nitida (Müller, 1776)	1	1
Andrena semilaevis Pérez, 1903	1	1
Andrena subopaca Nylander, 1848	1	0
Andrena wilkella (Kirby, 1802)	1	0
Anthidium manicatum (Linnaeus, 1758)	1	1
Anthophora furcata (Panzer, 1798)	0	1
Anthophora plumipes (Pallas, 1772)	1	1
Anthophora quadrimaculata (Panzer, 1798)	1	1
Chelostoma campanularum (Kirby, 1802)	0	1
Colletes daviesanus Smith, 1846	1	1
Halictus rubicundus (Christ, 1791)	1	1
Halictus tumulorum (Linnaeus, 1758)	0	1
Hylaeus communis Nylander, 1852	1	1
Hylaeus hyalinatus Smith, 1842	1	1

Lasioglossum albipes (Fabricius, 1781)	1	0
Lasioglossum calceatum (Scopoli, 1763)	1	1
Lasioglossum lativentre (Schenck, 1853)	0	1
Lasioglossum leucopus (Kirby, 1802)	0	1
Lasioglossum malachurum (Kirby, 1802)	1	1
Lasioglossum morio (Fabricius, 1793)	0	1
Lasioglossum smeathmanellum (Kirby, 1802)	1	1
Megachile centuncularis (Linnaeus, 1758)	1	1
Megachile ligniseca (Kirby, 1802)	1	1
Megachile versicolor Smith, F. 1844	0	1
Megachile willughbiella (Kirby, 1802)	1	1
Melecta albifrons (Forster, 1771)	1	1
Nomada fabriciana (Linnaeus, 1767)	1	1
Nomada flava Panzer, 1798	1	1
Nomada goodeniana (Kirby, 1802)	1	1
Nomada marshamella (Kirby, 1802)	1	0
Nomada panzeri Lepeletier, 1841	1	0
Nomada ruficornis (Linnaeus, 1758)	0	1
Osmia bicolor (Schrank, 1781)	1	0
Osmia bicornis (Linnaeus, 1758)	1	1
Osmia caerulescens (Linnaeus, 1758)	1	1
Osmia leaiana (Kirby, 1802)	0	1
Sphecodes ephippius (Linnaeus, 1787)	1	0
Sphecodes geoffrellus (Kirby, 1802)	0	1
Sphecodes monilicornis (Kirby, 1802)	0	1
Species A – K[1]	1	0

Social wasps

Dolichovespula media (Retzius, 1783)	1	1
Dolichovespula norwegica (Fabricius, 1781)	1	0
Dolichovespula saxonica (Fabricius, 1793)	0	1
Dolichovespula sylvestris (Scopoli, 1763)	1	1
Vespa crabro Linnaeus, 1758	1	1
Vespula germanica (Fabricius, 1793)	1	1
Vespula vulgaris (Linnaeus, 1758)	1	1

Solitary wasps

Agrypon tenuitarsum Kiss, 1926	0	1
Amblyteles armatorius (Forster, 1771)	0	1
Ancistrocerus gazella (Panzer, 1798)	1	1
Ancistrocerus nigricornis (Curtis, 1826)	1	0
Ancistrocerus parietinus (Linnaeus, 1758)	1	1
Ancistrocerus parietum (Linnaeus, 1758)	0	1
Anoplius caviventris (Aurivillius, 1907)	0	1
Cerceris rybyensis (Linnaeus, 1771)	1	1
Chrysis ignita (Linnaeus, 1758)	0	1
Crossocerus dimidiatus (Fabricius, 1781)	1	0

Crossocerus elongatulus (Vander Linden, 1829)	0	1
Ectemnius continuus (Fabricius, 1804)	1	0
Gasteruption jaculator (Linnaeus, 1758)	0	1
Mellinus arvensis (Linnaeus, 1758)	1	0
Philanthus triangulum (Fabricius, 1775)	1	0
Probolus concinnus Wesmael, 1853	0	1
Sapyga quinquepunctata (Fabricius, 1781)	0	1
Symmorphus gracilis (Brullé, 1832)	1	1
Trypoxylon attenuatum Smith, 1851	0	1

Butterflies and day-flying moths

Adela rufimitrella Scopoli, 1763	1	0
Aglais urticae (Linnaeus, 1758)	1	1
Anthocharis cardamines (Linnaeus, 1758)	1	1
Aphantopus hyperantus (Linnaeus, 1758)	1	1
Autographa gamma (Linnaeus, 1758)	1	0
Cacoecimorpha pronubana Hübner 1799	1	0
Callistege mi Clerck, 1759	1	0
Celastrina argiolus (Linnaeus, 1758)	1	1
Chrysoteuchia culmella (Linnaeus, 1758)	1	1
Gonepteryx rhamni (Linnaeus, 1758)	1	1
Inachis io (Linnaeus, 1758)	1	1
Lycaena phlaeas (Linnaeus, 1761)	1	0
Macroglossum stellatarum (Linnaeus, 1758)	1	0
Maniola jurtina (Linnaeus, 1758)	1	1
Ochlodes venata (Bremer & Grey, 1852)	1	1
Oidaematophorus lithodactyla (Treitschke, 1833)	1	0
Pammene regiana Zeller, 1849	1	0
Pararge aegeria (Linnaeus, 1758)	1	1
Pieris brassicae (Linnaeus, 1758)	1	1
Pieris napi (Linnaeus, 1758)	1	1
Pieris rapae (Linnaeus, 1758)	1	1
Polygonia c-album (Linnaeus, 1758)	1	1
Polyommatus icarus (Rottemburg, 1758)	1	1
Pyrausta aurata (Scopoli, 1753)	1	1
Pyronia tithonus (Linnaeus, 1758)	1	1
Satyrium w-album (Knoch, 1782)	1	0
Thymelicus sylvestris (Poda, 1761)	1	0
Vanessa atalanta (Linnaeus, 1758)	1	1
Vanessa cardui (Linnaeus, 1758)	1	0
Xanthorhoe montanata (Denis & Schiffermüller, 1775)	1	1
Zygaena filipendulae (Linnaeus, 1758)	1	0

Flies

Bombylius major Linnaeus, 1758	1	1
Conops quadrifasciata De Greer, 1776	1	0
Phasia hemiptera (Fabricius, 1794)	1	0

Sicus ferrugineus (Linnaeus, 1761)	0	1
Tachina fera (Linnaeus, 1761)	1	1

Hoverflies

Anasimyia lineata (Fabricius, 1787)	1	0
Baccha elongata (Fabricius, 1775)	1	1
Cheilosia albitarsis (Meigen, 1822)	1	0
Cheilosia illustrata (Harris, 1780)	1	0
Cheilosia pagana (Meigen, 1822)	1	0
Cheilosia proxima (Zetterstedt, 1843)	1	1
Cheilosia ranunculi Doczkal, 2000	1	0
Cheilosia vulpina (Meigen, 1822)	1	0
Chrysogaster solstitialis (Fallén, 1817)	1	0
Criorhina berberina (Fabricius, 1805)	1	0
Dasysyrphus albostriatus (Fallén, 1817)	1	1
Dasysyrphus tricinctus (Fallén, 1817)	1	0
Epistrophe eligans (Harris, 1780)	1	1
Epistrophe grossulariae (Meigen, 1822)	1	1
Episyrphus balteatus (De Greer, 1776)	1	1
Eristalis arbustorum (Linnaeus, 1758)	1	1
Eristalis intricarius (Linnaeus, 1758)	1	0
Eristalis nemorum (Linnaeus, 1758)	0	1
Eristalis pertinax (Scopoli, 1763)	1	1
Eristalis tenax (Linnaeus, 1758)	1	1
Eumerus funeralis Meigen, 1822	1	1
Eupeodes corollae (Fabricius, 1794)	1	0
Eupeodes latifasciatus (Macquart, 1829)	1	1
Eupeodes luniger (Meigen, 1822)	1	1
Eupeodes nielseni (Dušek & Láska, 1976)	0	1
Ferdinandea cuprea (Scopoli, 1763)	1	1
Helophilus pendulus (Linnaeus, 1758)	1	1
Heringia vitripennis (Meigen, 1822)	1	1
Leucozona latinaria (Müller, 1776)	1	0
Leucozona lucorum (Linnaeus, 1758)	1	0
Melangyna labiatarum (Verrall, 1901)	1	0
Melangyna umbellatarum (Fabricius, 1794)	1	0
Melanostoma mellinum (Linnaeus, 1758)	1	1
Melanostoma scalare (Fabricius, 1794)	1	1
Merodon equestris (Fabricius, 1794)	1	1
Myathropa florea (Linnaeus, 1758)	1	1
Neoascia podagrica (Fabricius, 1775)	1	1
Parhelophilus frutetorum (Fabricius, 1775)	1	0
Parasyrphus punctulatus (Verrall, 1873)	0	1
Platycheirus albimanus (Fabricius, 1781)	1	1
Platycheirus clypeatus (Meigen, 1822)	1	0
Platycheirus manicatus (Meigen, 1822)	1	1
Platycheirus peltatus (Meigen, 1822)	1	1
Platycheirus scutatus (Meigen, 1822)	1	1
Platycheirus splendidus Rotheray, 1998	1	0

Platycheirus sticticus (Meigen, 1822)	1	0
Platycheirus tarsalis (Schummel, 1837)	1	0
Rhingia campestris (Meigen, 1822)	1	1
Rhingia rostrata (Linnaeus, 1758)	1	0
Riponnensia splendens (Meigen, 1822)	1	0
Scaeva pyrastri (Linnaeus, 1758)	1	1
Sphaerophoria scripta (Linnaeus, 1758)	1	1
Syritta pipiens (Linnaeus, 1758)	1	1
Syrphus rectus Osten Sacken, 1875	1	0
Syrphus ribesii (Linnaeus, 1758)	1	1
Syrphus torvus Osten Sacken, 1875	1	0
Syrphus vitripennis Meigen, 1822	1	1
Volucella bombylans (Linnaeus, 1758)	1	1
Volucella inanis (Linnaeus, 1758)	1	0
Volucella pelluscens (Linnaeus, 1758)	1	1
Volucella zonaria (Poda, 1761)	0	1
Xanthandrus comtus (Harris, 1780)	0	1
Xanthogramma pedissequum (Harris, 1776)	1	1
Xylota segnis (Linnaeus, 1758)	1	1

Honeybee

Apis mellifera[2] Linnaeus, 1758	1	1

---

[1] Eleven solitary bee species (Species A - Species K) remained unidentified from the 2010 sampling session (see explanation in Chapter 2 – Identification of species).

[2] *Apis mellifera mellifera* may also have been present but this was not treated as a distinct species for the purposes of this study (see Chapter 2 – Hymenoptera, honey bees).

Appendix VII

List of plant families and genera recorded from the 17 gardens in 2010.

Plant families

Acanthaceae
Adoxaceae
Alstromeriaceae
Amaranthaceae
Amaryllidaceae
Anacardiaceae
Apiaceae
Apocynaceae
Aquifoliaceae
Araceae
Araliaceae
Aristolochiaceae
Asparagaceae
Asteraceae
Balsaminaceae
Begoniaceae
Berberidaceae
Betulaceae
Boraginaceae
Brassicaceae
Buxaceae
Calceolariaceae
Campanulaceae
Cannaceae
Caprifoliaceae
Caryophyllaceae
Celastraceae
Cistaceae
Cleomaceae
Colchicaceae
Commelinaceae
Convolvulaceae
Cornaceae
Crassulaceae
Cucurbitaceae
Cupressaceae
Cyperaceae
Dioscoreaceae
Eleagnaceae
Equisetaceae
Ericaceae
Escalloniaceae

Euphorbiaceae
Fabaceae
Fagaceae
Garryaceae
Geraniaceae
Grossulariaceae
Gunneraceae
Hydrangeaceae
Hypericaceae
Iridaceae
Juncaceae
Lamiaceae
Lauraceae
Liliaceae
Linaceae
Lythraceae
Magnoliaceae
Malvaceae
Myrsinaceae
Myrtaceae
Oleaceae
Onagraceae
Orchidaceae
Orobanchaceae
Oxalidaceae
Paeoniaceae
Papaveraceae
Phrymaceae
Pittosporaceae
Plantaginaceae
Plumbaginaceae
Poaceae
Polemoniaceae
Polygonaceae
Portulacaceae
Primulaceae
Ranunculaceae
Rhamnaceae
Rosaceae
Rubiaceae
Rutaceae
Salicaceae

Sapindaceae
Saxifragaceae
Scrophulariaceae
Solanaceae
Staphyleaceae
Tamaricaceae
Taxaceae
Thymelaeaceae
Tropaeolaceae
Urticaceae
Verbenaceae
Violaceae
Xanthorrhoeaceae
Zingiberaceae

TOTAL = 98 families

Plant genera

Abelia
Abutilon
Acacia
Acanthus
Acer
Achillea
Acidanthera
Aconitum
Aegopodium
Agapanthus
Agastache
Agave
Ageratum
Agrimonia
Agrostemma
Ajuga
Alcea
Alchemilla
Alliaria
Allium
Alstroemeria
Alternathera
Althaea
Alyssum
Amaranthus
Amaryllis
Amsonia
Anagallis
Anaphalis
Anchusa
Anemone
Anethum
Angelica
Antennaria
Anthemis
Anthriscus
Antirrhinum
Apium
Apocynum
Aquilegia
Aralia
Arbutus
Arctium
Argemone
Argyranthemum
Aristolochia

Armeria
Arnica
Artemisia
Arum
Aruncus
Asarina
Asclepias
Asparagus
Asphodeline
Asphodelus
Aster
Astilbe
Astrantia
Aubretia
Aucuba
Aurinia
Ballota
Baptisia
Begonia
Bellis
Berberis
Bergenia
Borago
Brassica
Brunnera
Bryonia
Buddleja
Bupleurum
Buxus
Calamintha
Calceolaria
Calendula
Caltha
Calystegia
Campanula
Canna
Capsella
Cardamine
Carex
Caryopteris
Catanache
Ceanothus
Centaurea
Centranthus
Cephalaria
Cerastium

Ceratostigma
Cerinthe
Cestrum
Chaenomeles
Chamerion
Chelidonium
Chelone
Chenopodium
Choisya
Chrysanthemum
Cichorium
Cimicifuga
Circaea
Cirsium
Cistus
Clematis
Cleome
Clerodendron
Cnicus
Colchicum
Conium
Convallaria
Convolvulus
Coreopsis
Cornus
Corylus
Cosmos
Cotinus
Cotoneaster
Crambe
Crassula
Crataegus
Crocosmia
Curcubita
Cyclamen
Cymbalaria
Cynara
Cynoglossum
Cyperus
Cytisus
Dactylorhiza
Dahlia
Daphne
Dasiphora
Daucus
Delphinium

Deutzia
Dianthus
Dicentra
Digitalis
Dipsacus
Doronicum
Echinacea
Echinops
Echium
Eleagnus
Epilobium
Epimedium
Equisetum
Eremurus
Erica
Erigeron
Erodium
Eruca
Eryngium
Erysimum
Escallonia
Eucomis
Euonymus
Eupatorium
Euphorbia
Exochorda
Felicia
Filipendula
Foeniculum
Forsythia
Frageria
Fremontodendron
Fritillaria
Fuchsia
Galega
Galium
Gaura
Gazania
Genista
Geranium
Gerbera
Geum
Gillenia
Gladiolus
Glechoma
Glycyrrhiza

Gunnera
Hebe
Hedera
Hedychium
Helenium
Helianthemum
Helianthus
Helichrysum
Heliotropium
Helleborus
Hemerocallis
Heracleum
Hesperis
Heuchera
Hibiscus
Hieracium
Hosta
Hyacinthoides
Hyacinthus
Hydrangea
Hypericum
Hyssopus
Ilex
Impatiens
Inula
Iochroma
Iris
Jasminum
Juncus
Juniperus
Kirengeshoma
Knautia
Kniphofia
Kolkwitzia
Laburnum
Lamiastrum
Lamium
Lantana
Lapsana
Lathyrus
Lavandula
Lavatera
Leonurus
Leucanthemum
Levisticum
Liatris

Ligularia
Ligustrum
Lilium
Limonium
Linaria
Linum
Lobelia
Lobularia
Lonicera
Lotus
Lunaria
Lupinus
Luzula
Lychnis
Lycopus
Lysimachia
Lythrum
Macleaya
Magnolia
Mahonia
Malus
Malva
Mandragora
Matricaria
Matthiola
Mecanopsis
Melilotus
Melissa
Mentha
Mercurialis
Millium
Mimulus
Monarda
Monardella
Montia
Morina
Muscari
Myosotis
Myrrhis
Myrtus
Narcissus
Nectaroscordum
Nemesia
Nepeta
Nicandra
Nicotiana

Nigella
Oenothera
Olearia
Omphalodes
Onopordum
Origanum
Ornithogalum
Osteospermum
Oxalis
Ozothamnus
Paeonia
Papaver
Parahebe
Pelargonium
Penstemon
Perovskia
Persicaria
Petasites
Petroselinum
Petunia
Phacelia
Phaseolus
Philadelphus
Phlomis
Phlox
Phygelius
Physalis
Picris
Pittosporum
Plantago
Poa
Polemonium
Polygonum
Portulaca
Potentilla
Primula
Prunella
Prunus
Pseudofumaria
Pulicaria
Pulmonaria
Pulsatilla
Pycnanthemum
Pyrus
Ranunculus
Rhazya

Rheum
Rhinanthus
Rhodochiton
Rhododendron
Ribes
Ricinus
Rodgersia
Romneya
Rosa
Rosmarinus
Rubus
Rudbeckia
Ruta
Salix
Salvia
Sambucus
Sanguisorba
Santolina
Sanvitalia
Saponaria
Satureja
Saxifraga
Scabiosa
Scilla
Scrophularia
Sedum
Sempervivum
Senecio
Sidalcea
Silene
Silphium
Silybum
Sisymbrium
Sisyrinchium
Skimmia
Solanum
Solidago
Sonchus
Spiraea
Stachys
Staphylea
Stellaria
Stephanandra
Succisa
Symphoricarpos
Symphyotrichum

Symphytum
Syringa
Tagetes
Tamarix
Tamus
Tanacetum
Taraxacum
Taxus
Teucrium
Thalictrum
Thermopsis
Thymus
Tiarella
Tilia
Tithonia
Torilis
Trachystemon
Tradescantia
Tricyrtis
Trifolium
Tripleurospermum
Triteleia
Tropaeolum
Tulipa
Urtica
Vaccinium
Valeriana
Verbascum
Verbena
Veronica
Veronicastrum
Vestia
Viburnum
Vicia
Vinca
Viola
Weigela
Wisteria
Yucca
Zantedeschia
Zinnia

TOTAL = 409 genera

Appendix VIII

Example of the calculation of k values according to life stages (Table 6.3) using the methods of Varley et al., (1975) and Yamamura (1999). The example is for Lamport, nest 3 (LAM 3).

	Stage	Mortality/loss factor	Initial number (I)	Number lost (L)	Mortality ($d = L/I$)	Survival ($s = 1-d$)	k-value [$-\ln(s)$]
$k1$	constructed cell	developmental failure	197	41	0.208	0.792	0.233
$k2$	O. bicornis cell	parasitism by Cacoxenus indagator	156	5	0.032	0.968	0.033
$k3$	O. bicornis cell	parasitism by other parasites	151	1	0.007	0.993	0.007
$k4$	cocoon	loss to Monodontomerus obscurus	150	2	0.013	0.987	0.013
$k5$	adult within cocoon	removal of males	148	104	0.703	0.297	1.213
$k6$	adult available to emerge	death prior to emergence	44	7	0.159	0.841	0.173
K	emerged adult female		37				
	TOTAL		**160**		**1.122**	**4.878**	**1.672**

278

Appendix IX

Post hoc test used to assess differences between mean ranks for eight properties (each with three nests) using the method of Siegel and Castellan (1988).

$$|\overline{R_u} - \overline{R_v}| \geq z_{a/k(k-1)} \sqrt{\frac{N(N+1)}{12}\left(\frac{1}{n_u} + \frac{1}{n_v}\right)}$$

where:

$|\overline{R_u} - \overline{R_v}|$ is the magnitude of the differences between mean ranks of groups 1 and 2 (the groups being compared)

$z_{a/k(k-1)}\sqrt{\frac{N(N+1)}{12}\left(\frac{1}{n_u} + \frac{1}{n_v}\right)}$ is the critical difference

$z_a = 0.05$

k = total number of samples

N = number of groups used in analysis

n_u = number of nests in the first group being compared

n_v = number of nests in the second group being compared

Appendix X

Solitary bee families and genera other than *O. bicornis* found in occupied tubes.

Property	Nest no.	Family, genus
BOU	3	Megachilidae, *Osmia*
CHALL	1, 2	Colletidae, *Hylaeus*
FAR	1	Megachilidae, *Osmia*
FAR	2,3	Colletidae, *Hylaeus*
KEL	1	Megachilidae, *Osmia*
KEL	2,3	Megachilidae, *Megachile*
LW	1	Megachilidae, *Megachile*, Colletidae, *Hylaeus*
LW	2	Megachilidae, *Megachile, Osmia*; Colletidae, *Hylaeus*