School of Life Sciences,
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USING CITIZEN SCIENCE TO MONITOR BUMBLEBEE POPULATIONS

May 2016

Leanne Maura Casey

A degree submitted for the degree of Doctor of Philosophy

Bumblebees are important pollinators of crops and wildflowers and are currently in global decline. The main drivers of decline include agricultural intensification, climate change, invasive species, pesticides, parasites and pathogens and it is thought that these multiple stressors act together to impact populations. However, their relative importance is unknown and there are wide knowledge gaps in relation to the current status of species populations and their response to environmental variables such as climate, habitat and land use change.

Citizen science offers a potential method of collecting data at a broad enough scale to measure species population responses to environmental stressors and it has successfully been applied to other taxa, particularly UK birds and butterflies. This thesis investigates the use of citizen science to address the current knowledge gaps in the status of UK bumblebee populations by analysing volunteer-collected data on current distribution and abundance trends in relation to habitat and climate change. Results are compared to previous studies to infer long-term changes in population dynamics.

The value of applying citizen science methods to bumblebee monitoring is highlighted, revealing evidence for decline of some common species and the recent retraction of rare species to their climatic optima. The main findings reveal a potential impact of climate on the distribution of winter-active bumblebees. They also indicate that, while urban parks and gardens provide refuge for bumblebees in an otherwise impoverished landscape, urbanisation may favour short-tongued generalist species over long-term specialists. The outcomes of this thesis have important management implications for UK bumblebee populations including the need for reassessment of the conservation status of *B. soroeensis* and the sympathetic management of urban parks and gardens for long-tongued specialists through the provision of suitable forage material.

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SUMMARY ABSTRACT

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of *B. soroeensis* and the sympathetic management of urban parks and gardens for long-

tongued specialists through the provision of suitable forage material.

DECLARATION

I hereby declare that this thesis has not been and will not be, submitted in whole or in part to another University for the award of any other degree. It has been composed by myself and embodies the results of my own research. Where appropriate, I have acknowledged the nature and extent of work carried out in collaboration with others.

Signature:

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Leanne Maura Casey

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Chapter 1

GENERAL INTRODUCTION

1.1 Loss of biodiversity and the threat to associated ecosystem services

The Convention on Biological Diversity officially defined biodiversity as "diversity of life at a genetic, ecosystem and species level" and also described it as "the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems" (United Nations, 1992). It encompasses the entire biological hierarchy from alleles to kingdoms while also including the diversity of interactions at each level of organisation (Sarker and Margules, 2002). The appearance of the term "biodiversity" in scientific journals increased dramatically following the ratification of the Convention on Biological Diversity in Rio de Janeiro in 1992 as scientists faced the challenging task of quantifying the diversity of life on earth and understanding the processes that govern it. Conflict arises regarding conceptualisation of the term and in relation to methods of measuring biodiversity and its importance (Eiswerth and Haney, 2001; Moonen and Barberi, 2008). This has led to difficulty in the practical application of the term for purposes such as policy-making and landscape planning and management (Moonen and Barberi, 2008; Sarker and Margules, 2002) which is further constrained by the requirement for cost and time effective approaches to measurement (Buchs, 2003, Hilty and Merenlender, 2000). As a solution, indicator taxa are often used as a proxy to measure diversity and ecosystem functioning (Gaston, 1996, Buchs, 2003). These are often charismatic "flagship" taxa (Gaston, 1996), for example Thomas (2005) demonstrated that extinction rates in British butterflies,

which are very well monitored as a result of their visibility and popularity, are similar to those in a range of other insect groups. This led to him suggesting that similar monitoring schemes be extended to other popular insects, including bumblebees, which could also act as indicators for lesser-known taxa.

Despite the challenges that exist in monitoring biodiversity, major developments have been made in describing the association between species diversity and ecosystem processes and in identifying functionally important species (Loreau et al., 2001; Hooper et al., 2005; Balvanera et al., 2006; Magurran, 2013). High levels of biodiversity generally lead to better ecosystem functioning (Balvenera et al., 2006; Hooper et al., 2005) and delivery of ecosystem services, defined as any benefit that humans derive from ecosystems (Mace et al., 2012; MA, 2005). These services are vital to our survival, providing healthy fertile soils, clean air, clean water, disease and pest regulation, climate regulation, and food and fibre production along with cultural and aesthetic benefits (Mace et al., 2012). It is therefore of great concern that we are losing biodiversity at an alarming rate with knock on consequences for ecosystem functioning, the provision of ecosystem services and human wellbeing (Mace et al., 2012; Balvanera et al., 2006; Hooper et al., 2005; MA, 2005; Loreau et al., 2001). It has been estimated that biodiversity is declining a thousand times faster than at rates found in the fossil record due to the impact of humans on the planet in the form of habitat destruction, over-exploitation, pollution and ecosystem alteration (Frankham et al., 2004; MA, 2005). The Millennium Ecosystem Assessment (2005) estimated that over 60% of global ecosystem services were already overused or deteriorating as a result of this decline. Rates of biodiversity loss are set to accelerate in response to the inevitable increase in human population density (Visconti et al., 2015). This threat may be exacerbated by the spatial

congruence between people and biodiversity with research showing that humans tend to occupy areas of high species richness for a wide range of taxonomic groups (see Luck, 2007 for review) and that almost one fifth of the global human population resides within biodiversity hotspots (Cincotta et al., 2000; Gaston and Spicer, 2013). Drastic global action needs to be undertaken if we are to halt biodiversity loss and protect the ecosystem services on which we depend. Previous global targets set by the Convention on Biological Diversity to slow biodiversity loss by 2010 have not been met, and indicators that measure metrics that relate to human benefits from biodiversity are all still in decline (Collen et al., 2015). In response to an international recognition of urgent need for further action, the United Nations set up the Intergovernmental Panel on Biodiversity and Ecosystem Services (IPBES), modelled after the influential Intergovernmental Panel on Climate Change). The recent 2016 IPBES report warns of global declines in pollinators and calls for an increase in monitoring of these functionally important taxa in order to protect associated ecosystems and pollination services (Schmeller and Bridgewater, 2016).

1.2 Ecosystem pollination services threatened by pollinator declines

Pollination can be defined as the deposition of pollen from a male anther on to the female stigma of a flower (Faegri and Van der Pijl, 2013)). Pollinators act as vectors of pollen transfer, facilitating sexual reproduction in flowering plants. Traditionally, plant-animal pollination interactions were thought to have evolved during the Cretaceous period coinciding with an explosive diversification of angiosperms (Grimaldi, 1999; Kearns and Inouye, 1997). However, Ren et al. (2009) have recently challenged this evolutionary timeline by providing evidence to suggest that pollination of non-

angiosperms by lacewings occurred prior to this during the Mesozoic period with biotic pollination becoming the dominant angiosperm strategy by the late Cretaceous (Ollerton and Coulthard, 2009). The original pollinators are thought to have been generalised insects such as beetles, anthophilic Diptera, sphecid wasps and primitive moths with the Order Diptera being the most pivotal in early angiosperm pollination (Grimaldi, 1999). A recent study involving the collation and analysis of global data on pollination vectors estimated that 87.5% of angiosperms are animal pollinated, ranging from 78% in temperate zones to 94% in tropical communities (Ollerton et al., 2011). Although geographical bias is inherent to this type of global study, for example in this case there is an entire lack of data from Northern Africa, these figures are based on the most comprehensive dataset that currently exists. A diverse range of insect species of the Orders Hymenoptera, Diptera, Lepidoptera and Coleoptera pollinates these extant entomophilous species. In plant-animal pollination, the primary goal for the plant is the efficient transfer of pollen while the pollinator aims for optimal acquisition of food resources. This conflict of interest leads to both parties exerting selective pressure driving the co-evolution of plants and their pollinators. As plant reproductive success relies on efficient pollen transfer, plants have evolved traits to attract suitable pollinators, which in turn drive the co-evolution of specialist pollinator traits and behaviour suitable for optimal foraging (Bronstein et al., 2006).

Pollination services are critical for maintaining ecosystems and biodiversity through this long-established relationship that has evolved between wild plants and their pollinators. Pollination also has an economic value and provides benefits to human health through crop production. The global production of crops that depend on pollinators is an industry worth up to US$577 billion annually (IPBES, 2016). These include food crops along with

crops that provide biofuels (e.g. canola and palm oils), fibres (e.g. cotton), medicines, forage for livestock, and construction materials (IPBES, 2016). Many crop species require insect pollination to give sufficient yields (Stoddard and Bond, 1987; Williams et al., 1987; Free, 1993; Goulson, 2003; Klein et al., 2007). It is estimated that over 75% of human food crops rely at least in part on pollination (IPBES, 2016) with over a third of all crops using insects as vectors (McGregor, 1976; Corbet et al., 1991; Klein et al., 2007; Williams, 1995). Pollinated food crops include fruit, vegetables, nuts, seed and oils which are highly nutritious dietary sources of vitamins and minerals that are essential for human well-being (Daily and Karp, 2015). Pollinator decline could lead to significant global health burdens from both non-communicable diseases and micronutrient deficiencies (Smith et al., 2015)

There is widespread concern that we may be nearing a "pollination crisis" due to global declines in pollinator species in response to habitat degradation, agricultural intensification, pesticide use, parasites and pathogens, invasive species and climate change that threaten biodiversity, ecosystem health and pollination services (Holden, 2006; Gross, 2008; Goulson et al., 2015; IPBES, 2016). Conflict exists regarding the use of the term "pollination crisis" with some scientists challenging its validity due to a lack of global data on pollinator declines across a wide range of taxonomic groups and little evidence for declines in crop production (Ghazoul, 2005; 2015). However, while there is an overall paucity of global data on pollinator populations, highlighting the need for widespread monitoring (Ghazoul, 2015; Goulson et al., 2015; IPBES, 2016), analyses of existing datasets do reveal a concerning trend towards decline across several continents and numerous taxonomic groups. In Europe studies have revealed declines in wild bees (Kosier et al., 2007; Nieto et al., 2014), honeybees (Potts et al., 2010), hoverflies

(Biesmeijer et al., 2006) butterflies (Fox et al., 2015), moths (Fox et al., 2013) and wasps (Ollerton et al., 2014). In Asia there is evidence for declines in the wild bee populations of China (Xie et al., 2008; Williams et al., 2009) and Japan (Matsumara et al., 2004; Inoue et al., 2008). North (Grixti et al. 2009, Cameron et al. 2011, Burkle et al. 2013) and South (Morales et al., 2013; Schmid-Hempel et al., 2014) American populations of wild bees are also showing evidence for decline as are South African populations (Pauw, 2007). In addition, a recent global assessment of the red list index for bird and mammal pollinators reveals deterioration in their status with most species moving towards, rather than away from, extinction (Regan et al., 2015). While more studies are needed to quantify the impact of these pollinator declines on crop production, there is some evidence to suggest that crop yields are affected by changes in associated pollinator populations (Aizen and Harder 2009; Garibaldi et al., 2013; Tylianakis, 2013). Aizen et al. (2008) did not reveal a decrease in crop production, however their analysis of a long term FAO dataset highlighted the fact that cultivated crops have become more pollinator dependant and they warned that if this trend continues, declining pollinator populations may not meet the demand for crop pollination. Ghazoul (2005) argues that many food crops do not depend on pollinators including those that are wind-pollinated, such as rice, wheat and maize or self-pollinated such as lentils peas and soya. However, studies have recently shown that crops that do depend on pollinators are particularly important for human health, containing essential vitamins and minerals (Free 1993; Klein et al., 2007; Eilers et al., 2011; Vanbergen et al., , 2013) and that micronutrient deficiencies in areas where they are unavailable due to a reduction in dietary variety and an overdependence on food staples (Smith et al., 2015).

Conserving a high diversity of pollinators is important for effective conservation of plant communities and crop production through functional complementarity, whereby different species specialise in pollinating flowers on different parts of the plant at different times throughout the flowering season and have different responses to environmental perturbations (Blüthgen and Klein, 2011; Fründ et al., 2013; Brosi, 2016 but see Kleijn et al., 2015). It is therefore of great concern that the recent assessment of pollinators by IPBES highlights that, in many cases, over forty percent of insect pollinators are threatened at a local level (IPBES, 2016). The report also highlights substantial gaps in our knowledge of insect pollinator population dynamics which make a global assessment of decline impossible. Researchers emphasise an urgent need for effective monitoring of pollinator species in order to inform management strategies and conserve the critical ecosystem service of pollination (IPBES, 2016; Goulson, 2015).

1.3 Declines in bumblebees, a functionally important pollinator taxon

Wild bees are important pollinators of native plants with a large number of wild flowers specialised to depend upon them for reproduction (Corbet et al., 1991; Osborne et al., 1991; Kwak et al, 1991a and 1991b; Rathcke and Jules, 1993; Goulson 2003; Biesmeijer et al., 2006; Johnson, 1996; Johnson and Steiner 2000; Kenta et al., 2007). They display spatial complementarity through different preferences for plant species, varieties or foraging locations making them particularly efficient pollinators (Hoehn et al. 2008; Brittain, Kremen & Klein 2013). They also play a significant economic role in global crop production, providing $150 billion annually (Gallai et al, 2009). Wild bees offer insurance against changes in the abundance of managed stocks and in many cases produce a higher crop yield (Garibaldi et al. 2013; Woodcock et al. 2013).

Bumblebees (*Bombus* spp.) are highly valued wild pollinators of crops (Corbet et al.*,* 1991) and wildflowers (Osborne and Williams, 1996). Bumblebee physiology and behaviour are such that they are particularly efficient at collecting pollen. Their plump, hairy body increases the likelihood of coming into contact with plant reproductive parts while foraging and provides a suitable surface for pollen to adhere to (Stanghellini et al., 1997 and 1998; Thompson and Goodell, 2001). Unlike other pollinators, they are partially endothermic, producing body heat by rapid muscle contraction (Heinrich, 1979) and their thick pile of setae provides insulation allowing them to be active at times of the day and in weather conditions during which most other pollinators are unable to forage (Corbet et al., 1993; Goulson, 2003). Due to their ability to withstand inclement weather conditions, they emerge earlier and hibernate later than most other pollinators, providing pollination services throughout most of the flowering season (Goulson, 2003). They are also polymorphic both within and between species, allowing them to exploit a diverse range of flowers comprised of different shapes and sizes (Sladen, 1912; Goulson, 2003; Peat et al., 2005). Bumblebees are also one of few pollinators specialised for buzz pollination, a rapid contraction of the flight muscles that produces vibrations to release large quantities of pollen from the anthers of certain plants that are dependent on it for reproduction, such as members of the Solanaceae family (Goulson 2003; Van den Eijende et al., 1991). Finally, bumblebee populations are comprised of both specialist and generalist pollinators with long-tongued bumblebees specialising on flowers with deep corollas, such as members of the Fabaceae family and short-tongued generalists pollinating a more diverse array of plant taxa (Goulson, 2003, Goulson and Darvill, 2004) increasing their overall efficiency as pollinators.

Bumblebees have undergone serious declines in recent decades in North America, Europe and Asia (Kosier et al., 2007; Colla and Packer, 2008; Grixti et al., 2009; Williams and Osborne, 2009; Goulson et al., 2008; Cameron et al., 2011; Williams et al., 2009). In North America, some Bombus species have been declining gradually over a number of decades (Colla and Packer, 2008; Grixti et al., 2009; Williams and Osborne, 2009) whereas others have undergone precipitous declines over short time-spans, for example since late 1990s, *B. terricola* and *B. occidentalis* have disappeared from much of their range and *B. franklini* has become extinct (Williams and Osborne, 2009; Goulson, 2015). In Japan, declines in native Bombus spp. have been observed recently (Matsumara et al., 2004; Inoue et al., 2008) and in China, declines have been reported from the lowland area of the Sichuan Basin (Williams et al., 2009). Substantial range contractions have occurred in European bumblebee species in recent decades with some local extinctions and four species have disappeared entirely from the continent (Williams, 1982; Kozier et al. 2007; Williams and Osborne, 2009; Goulson et al., 2008, 2015). In the UK, two species (*B. cullumanus* and *B. subterraneus*) have been driven to extinction in recent decades and analysis of historical distribution maps highlights severe range contractions in six out of twenty-four extant species (*B. ruderatus*, *B. humilis*, *B. muscorum*, *B. distinguendus*, *B. sylvarum* and *B. ruderarius*) which led to their protected status under the UK Biodiversity Action Plan (1992-12) (Williams, 1982; Goulson, 2003; Goulson et al., 2008). A further four species, *B. jonellus*, *B. monticola*, *B.rupestris*, and *B. soroeensis* are thought to be rare or declining (Williams and Osborne, 2009). Range dynamics of these species, however, has not been quantified since the early 1980s and more up-to-date information is needed to assess their current status. Additionally, while some UK species (*B. terrestris, B. lapidarius, B. lucorum, B. pascuorum* and *B. pratorum*) are

thought to have remained common based on the available distribution maps, there is an entire lack of information on bumblebee abundances and we do not know whether they are less abundant than formerly and if they are currently in decline (Goulson, 2015). Citizen science surveys could potentially fill these knowledge gaps by providing a cost-effective means of long-term bumblebee population monitoring over a broad geographical scale (Goulson et al., 2015; IPBES, 2016). The value of citizen science in monitoring bumblebee populations is explored in this thesis using long-term UK bumblebee datasets.

1.4 Citizen science

1.4.1 History of citizen science

Citizen science can be defined simply as the engagement of non-professional volunteers in scientific research or more formally as 'a method of integrating public outreach and scientific data collection locally, regionally, and across large geographical scales' (Cooper et al., 2007). The scope of citizen science is far-reaching with projects existing across areas as diverse as astronomy, molecular science, conservation biogeography, computer science and ecology (Dickinson et al., 2010)

Members of the public have been actively participating in citizen science for centuries. In 1874, the British government funded the Transit of Venus project to measure the Earth's distance to the Sun which engaged the admiralty in collecting data all over the world (Ratcliff, 2008; Dickinson et al, 2010). Amateur ornithologists have been collecting data on the migration timing of bird species in Finland since 1749 (Greenwood, 2007). In 1900 the Audubon Society launched the first Christmas Bird Count across the US and Canada which has been running ever since, providing the longest time-series of animal

population monitoring and resulting in the publication of over 350 scientific papers on bird population dynamics, community ecology, biogeography and census methods (Devictor et al., 2010; Silvertown, 2009). Modern-day science also incorporates historical collections collected by amateur naturalists and stored in museums and herbaria to investigate species distribution and phenological changes over time (Miller-Rushing et al., 2012)

In recent years citizen science has gained greater attention among the scientific community, particularly in the field of ecology due to the urgent need for broad-scale species monitoring in the face of current rates of biodiversity loss and threats to ecosystems services (Silvertown, 2009; Dickinson et al., 2010). Developments in technology in the age of the World Wide Web have increased the visibility, functionality, and accessibility of citizen science projects. For example, E-bird, launched in 2002 by the Cornell Lab of Ornithology and the National Audubon Society collects five million bird observations monthly from amateur ornithologists who submit records to an online central database, which is then used to analyse changes in species distribution and abundance (Sullivan et al., 2014; E-bird, 2016). Online support, feedback and training can now easily be given to large numbers of volunteers, improving levels of enjoyment and motivation which in turn improves the consistency of participation and data provision (Rottman et al., 2012). Scientific and technological research into increasing the efficiency of collecting, storing and analysing large volumes of data that varies in quality and consistency, including the use of online systems that flag up unusual records and the use of rigorous statistical approaches, has also led to major developments in this field (Dickenson et al., 2010; Miller-Rushing et al., 2012; Isaac et al., 2014).

1.4.2 Reconnecting people with nature with mutual benefits for biodiversity and human wellbeing

Recent studies have highlighted the importance of human interaction with nature for both biodiversity conservation (Miller, 2005) and human health (Dallimer et al., 2012; Berman et al., 2008; Ulrich et al., 1991; Parson et al., 1998). In light of these findings, it is of concern that human beings are becoming increasingly disconnected from the natural environment due to a combination of global biodiversity loss combined with rapid urbanisation.

Urbanisation has led to some of the most profound land use changes globally and is considered one of the main drivers of species decline and biodiversity loss (McKinney, 2002, 2006). A recent analysis of IUCN Red List Data by Maxwell et al. (2016) placed urbanisation as the third greatest driver of biodiversity decline after agricultural activity and over-exploitation. While expanding urban environments are associated with a loss of biodiversity overall, this relationship is complex with certain taxa increasing in diversity in urban areas (McKinney et al., 2008). Pollinator studies reflect this complexity with some investigations highlighting urban environments as a potential ecological refuge for pollinators in an otherwise impoverished landscape (Goulson et al., 2002, Goulson et al., 2010, Osborne et al., 2008) while others reveal a negative association between urbanisation and pollinator diversity (Bates et al., 2011; Hernandez et al., 2009; Arhne et al, 2009; Geslin et al., 2013). It is clear that further monitoring and research is needed to elucidate the potential impact of expanding urban environments on populations (McKinney 2008; Fox, 2013).

Over half of the world's population now lives in urban areas with >80% of UK citizens residing in towns and cities and these figures are expected to rise by 2030 (United Nations Population Division, 2014). Miller (2005) highlights the current relevance of Pyle's (1978) "extinction of experience" whereby urbanisation leads to biotic homogenisation which triggers a response of apathy towards nature in city inhabitants. This apathy leads to a lack of biodiversity protection and a more depauperate natural environment which deepens isolation from nature further. Regional efforts are being made to reconnect human beings with nature through the protection and provision of green spaces in urban environments, environmental education programmes and involving the public directly in conservation activities (Dearborn and Kark, 2010; Miller 2005, 2006). However, given the current rates of urban sprawl, more widespread change is needed in order to protect our connection with nature and motivate people to conserve our remaining wilderness areas.

Citizen science offers a platform to reconnect human beings with nature while collecting much needed large-scale information on ecological trends in an affordable manner (Dickinson et al. 2010; Tulloch et al., 2013). Studies have shown that individuals taking part in a citizen science project report a better connectedness with nature leading to a desire to protect and conserve it (Koss, 2010; Stepenuck and Green 2015; Gooch, 2005). These realizations by participants foster a positive attitude towards environmental protection leading to associated behavioural change such as an increase in political activity linked to nature conservation and changes in land-owner's management techniques (Stepenuck and Green 2015). Volunteers also benefit from better physical health and fitness linked to an increase in activity and nature access (Pillemer et al., 2010) and also improved emotional health with individuals reporting feelings of

enjoyment, empowerment and pride linked to their participation (Koss, 2010; Stepenuck and Green 2015; Gooch, 2005). Socialising with other volunteers while working on a common goal led to a reported increased in the mental wellbeing of individual volunteers (Pillemer et al., 2010; Stepenuck and Green 2015; Gooch, 2005). Citizen science projects are also an effective environmental education tool with volunteers acquiring ecological knowledge, scientific literacy and an ability to think more scientifically through training, participatory learning and social learning (Dickinson et al., 2010; Trumbull et al., 2000; Bonney et al., 2009; Stepenuck and Green 2015). This increased community-level connectedness, awareness and motivation has the potential to effect positive changes to natural resource management and policies (Stepenuck and Green 2015).

1.4.3 Citizen science as an ecological monitoring tool

The value of using citizen science in ecological monitoring has been emphasised in recent decades in light of the current need to monitor broad-scale species population dynamics in relation to environmental stressors and mitigate against global biodiversity losses (Dickinson et al., 2010; Silvertown 2009). The use of volunteers allows data to be collected on a scale that would otherwise be impossible. There are many examples of citizen science projects across a wide range of taxa that have produced valuable information on species population trends in relation to environmental stressors such as habitat degradation, climate change and invasive species (Dickinson et al., 2010; Devictor et al., 2010; Silvertown, 2009).

In the UK, birds and butterflies are particularly well monitored by citizen science surveys (Pollard and Yates, 1993; Bibby, 2003; Silvertown, 2009). The British Trust for

Ornithology (BTO) launched Garden BirdWatch in 1994 and there are now more than 14, 000 citizen scientists recording weekly maximum counts of common bird species that visit their gardens (Plummer et al., 2015). The survey has been highly successful from an ecological perspective, leading to scientific publications revealing bird species responses to habitat and land-use change (Chamberlain et al., 2004; McKenzie et al., 2007; Chamberlain et al., 2007; Ockendon et al., 2009), climate change (Plummer et al., 2015) and disease (Lawson et al., 2012). It has recently been extended to incorporate other taxa with volunteers additionally monitoring mammals (Toms and Newson, 2006) and bees (D. Goulson, pers. comm.). The UK Butterfly Monitoring Scheme (UKBMS) was established in 1974 and volunteers have since collected butterfly abundance data on weekly transects for 71 species (Pollard and Yates, 1993). This long-term data has produced valuable information on species population trends in relation to changes in habitats (Warren et al., 2001; Oliver et al., 2010; Oliver et al., 2012) and climate (Warren et al., 2001; Pateman et al., 2012; Pearce-Higgins et al., 2015). Public surveys have also generated useful data on UK bumblebee nesting ecology but these tend to be small in spatial and temporal scale (Fussell and Corbet, 1992 a, b; Osborne et al., 2007; Lye et al., 2012). However, they highlight the potential of using citizen science as an ecological tool for monitoring bumblebee populations.

Despite the magnitude of valuable information that can be derived from ecological citizen science projects, challenges exist in ensuring data quality and using this practice as a valid means of scientific investigation. Fortunately this is an area of active research that has produced tested guidelines regarding the use of standardised methodology, data management and statistical techniques (Dickinson et al., 2010; Silvertown., 2009; Isaac et al., 2014) and once these are adhered to, citizen science data has been shown

to yield similar results to those collected by specialists (Delaney et al., 2008; Devictor et al., 2010; Newman et al., 2010; Fuccillo et al., 2015).

1.5 Aims and objectives

Bumblebees are in global decline and there is an urgent need to understand the population dynamics of these important pollinators in relation to environmental stressors; however, there is a paucity of data that is required to assess species populations. The most comprehensive distribution dataset exists for the UK and this has revealed severe range contractions for a number of species between 1960 and 1980 (Williams, 1982). However, it has not been analysed since and information on the current range dynamics of these species is lacking. There is also an entire lack of data on bumblebee abundances so that, while certain species are widespread and appear common, we do not know if they are declining in abundance. Bumblebees are charismatic, popular insects suitable for citizen science monitoring which has the potential to collect distribution and abundance data on the scale required to monitor species trends in relation to environmental variables. The aim of this thesis is to fill in the knowledge gaps in UK bumblebee population dynamics using data collected by volunteers.

Specific objectives are:

1.   To assess the efficacy of different types of training on the identification of bumblebee species by volunteers (Chapter 2)

2.   To assess the use of already-existing citizen science datasets to elucidate drivers of bumblebee population change (Chapters 3, 4, 5, 6)

3. To investigate the effect of environmental variables on the distribution of winter-active bumblebees in the UK using volunteer-derived data (Chapter 3).

4. To use historic citizen science data to investigate whether UK bumblebee species that underwent range contractions in the past have suffered further contractions in recent years (Chapter 4) and to assess population change in common species (Chapters 4, 5, 6)

5. To investigate climatic-associations of UK bumblebees by modelling historic data and to ascertain whether declining species are moving towards their climatic optima (Chapter 4)

6. To assess habitat-associations of UK bumblebees using citizen science distribution (Chapter 4) and abundance data (Chapters 5, 6)

Chapter 2

EVALUATING TRAINING METHODS FOR VOLUNTEERS OF CITIZEN-SCIENCE
MONITORING SCHEMES: A COMPLEX VERSUS A SIMPLE APPROACH.

2.1 Abstract

Citizen science is revolutionising the field of ecology, generating powerful volunteer derived datasets that enable the detection of species' population changes over a broad geographical scale. Despite concern regarding the accuracy of citizen science monitoring data, very little attention is currently directed at the training of volunteers in species identification. Here, the efficacy of two different training sessions of equal duration is evaluated in improving bumblebee identification skills of volunteers (n=122). In a simple training session, volunteers were introduced to the seven most common UK bumblebee species and in a contrasting complex session a further eleven species were included. Volunteers were assessed using pre- and post- training quizzes from which improvement scores were calculated. Training method profoundly influenced the ability of volunteers to identify bumblebee species. Simple training led to a vast improvement in the identification of the common UK bumblebee species and some improvement in the identification of other species. In contrast, volunteers in the complex training session became worse at identifying the common species and showed little improvement in identifying other species. Findings highlight the importance of considering methods of training for volunteers of citizen science monitoring schemes and have implications for such schemes worldwide.

2.2 Introduction

The involvement of non-professional volunteers in scientific enquiry, sometimes known as "citizen science" has becoming increasingly widespread, particularly during the past decade (Dickinson et al., 2010). It is not a new phenomemon; one of the earliest citizen science projects has been running since 1900 (National Aubedon Society's Christmas Bird Count; Chapman 1900). Citizen science is being successfully employed in a variety of scientific fields including computer science, geography, astronomy and archaeology; however, it is currently most influential in ecology (Dickinson et al., 2010). Species monitoring programmes, in particular, have benefited from citizen science. The involvement of volunteers in these programmes has enabled data collection on the broad geographical scale required to detect species range shifts and changes in population trends over time. This has led to an increase in our knowledge of how populations respond to environmental change and powerful volunteer-derived datasets are revealing population responses to climate and habitat change for a wide range of taxa (butterflies: Roy and Sparks, 2000; Warren et al., 2001; birds: Newson et al., 2009; Renwick et al., 2012; amphibians: Lepage et al. 1997; plants: Cleland et al., 2007). Other benefits of citizen science projects include scientific education of the public through volunteer training and feedback (Bonney et al., 2009).

One of the major challenges associated with citizen science is ensuring sufficient data quality (Silvertown 2009; Dickinson et al., 2010). Citizen science data is often "mined" for data subsets that are likely to be of higher quality and statistical methods accounting for observer error can also be applied. However, dealing with citizen science data at the analysis stage is notoriously complicated, requiring rigorous statistical techniques (Bonney et al., 2009), and efforts should be made to eliminate observer errors as much as possible during data collection. Strategies suggested to address the issue of data

quality at the data collection stage of long-term monitoring surveys include the provision of adequate training for volunteers (Dickinson et al., 2010) as well as the development of rigorous, standardised protocols (Silvertown 2009; Dickinson et al., 2010; Matteson et al., 2012).

Training provided to volunteers varies greatly between citizen science schemes. Some offer none, while others offer online training (e.g. Invasive Species Survey in USA, Graham et al., 2007), group training by an experienced recorder, or the opportunity to spend time with professional scientists in the field (e.g. UK Butterfly Monitoring Survey, UK Moth Counts, Fox et al., 2011). Some studies have attempted to quantify the quality of citizen science data collected following training, by comparing data collected by volunteers to those collected by professional scientists (e.g. Brandon et al., 2003; Bell 2007; Kremen et al., 2010). For example, Newman et al. (2010) describe poor performance of volunteers in identification of invasive weeds following online training, when compared to trained scientists. Given the large volumes of data now being collected by citizen scientists from numerous countries, it is remarkable how little attention has been given to attempting to assess which type of training is most effective. There is an urgent need to compare training techniques, and to assess their relative merits in enhancing the identification skills of volunteers.

Here a simple experiment designed to inform delivery of indoor training sessions for the identification of UK bumblebees is described. When designing such a presentation for beginners in bumblebee identification, it is not clear how much information to include. How many of the 24 UK species should be covered? The literature suggests that inclusion of too much information may reduce learning (Sweller 1988; Mayer et al. 2001), but how

much is too much? The improvement in identification skills of two groups of volunteers was assessed. Volunteers were subjected to two contrasting training sessions of equal duration, one in which only a small number of common bumblebees are included, and the second in which a large number of both common and rare species were introduced. This study also examines how individual bee species differ in the accuracy with which they are identified, and how the different training types improve this accuracy.

2.3 Methods

A total of 122 volunteers took part in the study. Volunteers were recruited by advertising a "BeeWalk Training Day" at The Cooperative Company Supermarkets across the UK as The Cooperative Company sponsored the study along with The Bumblebee Conservation Trust. The "BeeWalk Training Day" involved a bumblebee identification training session on arrival and a bumblebee walk on which identification skills could be practiced in the afternoon. Volunteers that attended training days most likely represent a subset of the general population with an existing interest in natural history, however this is likely to be the case for individuals participating in any species monitoring programme. None of the volunteers had previous experience in identification or recording of bumblebees (*Bombus* spp.). Volunteers were divided into two treatment groups. 65 volunteers received a "simple" form of bumblebee identification training and 57 volunteers received "complex" training. Training was delivered in a series of five sessions with each volunteer attending one session; three for the simple treatment and two for the complex treatment. Both training types involved a 30 minute indoor presentation on identification of UK bumblebees. In both treatments volunteers were taught the basics of bumblebee anatomy, how to distinguish bumblebees from other Hymenoptera, how

to distinguish between males, queens and workers and how to separate true social bumblebee species from the cuckoo bumblebee species (subgenus *Psithyrus*) that mimic them. A box containing pinned specimens of the seven most common bumblebees was passed around during the presentation and the same specimens were used for each treatment and each training session. In the "simple" form of training volunteers were introduced to seven of the most common bumblebee species in the UK (Table 2.1). In the complex form of training a further 11 species were introduced (Table 2.1). In both treatments the key distinguishing features of each species were explained using diagrams and photographs. Towards the end of the training session, volunteers were shown photographs of the species that had been described and were invited to determine the identity of each in an informal group setting.

The effect of training on volunteer ability to identify bumblebee species was tested using pre- and post- training quizzes. The pre-training quiz was carried out when volunteers first arrived and the post-training quiz was carried out directly after identification training to ensure that other activities, such as the bumblebee walk, did not influence results. Each quiz consisted of 19 bumblebee photographs comprising 14 species (Table 2.1). Post-training quiz photographs differed from those used in the pre-training quiz but photographs were similar in terms of the visibility of key species traits. The order of species was randomised for both quizzes. Photographs were projected onto a white screen for one minute and volunteers were asked to identify each species. In both pre- and post-training quizzes, volunteers were provided with a colour bumblebee identification guide (BBCT, 2010). An improvement score was calculated for each volunteer by subtracting the total number of questions they answered correctly in the

post-training quiz from the total number of correct answers in their corresponding pre-

training quiz.

Table 2.1 Species described in the "simple" and "complex" training types and quantity of each species included in quizzes.

Species	Simple Training	Complex Training	Quantity
*Bombus terrestris**	√	√	2
*Bombus lucorum**	√	√	2
*Bombus hortorum**	√	√	1
*Bombus lapidarius**	√	√	2
*Bombus pratorum**	√	√	2
*Bombus pascuorum**	√	√	2
*Bombus hypnorum**	√	√	1
Bombus jonellus	x	√	1
Bombus distinguendus	x	√	2
Bombus ruderarius	x	√	1
Bombus sylvarum	x	√	1
Bombus monticola	x	√	1
Bombus vestalis	x	√	0
Bombus sylvestris	x	√	0
Bombus rupestris	x	√	1
Bombus barbutellus	x	√	0
Bombus campestris	x	√	0
Bombus bohemicus	x	√	0

* the seven common species included in both training types.

In order to assess the effect of training type on the ability of volunteers to identify bumblebee species, a series of generalized linear models (GLM) were run in R Statistical Software Version 2.12.2 (R Development Core Team, 2011). Results from training sessions were pooled within each treatment since analysis of variance (ANOVA) showed no difference in improvement scores between sessions for the complex and simple training type (simple: $F_{2,62}$= 3.48, P>0.05; complex: $F_{1,55}$= 0.17, P>0.05). ANOVA also showed no effect of gender on improvement score for both treatments (simple: $F_{1,62}$= 0.06, P>0.05; complex: $F_{1,55}$= 2.69, P>0.05) and this variable was excluded from subsequent models. For each model, improvement score was fitted as the response variable with training type and pre-training score included as fixed factors. Three

separate models were run; one which included all species, one for the six most common species and one for the eight less common species.

To investigate whether or not the effect of training on volunteer identification skills differed according to bumblebee species, a generalized linear mixed model (GLMM) was run in R (lmer package) using binary data (correct/incorrect) derived from post-training scores as the response variable. For simplicity, only photographs of female bumblebees were considered. Fixed factors included species and training type. Each individual volunteer was assigned an identification code and codes were included in the model as a random effect.

2.4 Results

2.4.1 Training effects on improvement scores

All species

Of the 19 questions asked per person, the average before training score was 6.4 ±0.3 answered correctly (33.7%). Following training, on average 10.5 ±0.4 were answered correctly (55.3%) resulting in an average improvement score of 4.1 ±0.3 (21.6%). For the simple treatment, an average of 6.7 ±0.4 (35.3%) questions were answered correctly before training and this increased to 13.3 ±0.4 (70%) following training, giving an improvement score of 6.6 ±0.4 (34.7%) (Fig. 2.1a). By contrast, individuals receiving the complex treatment scored a mean of 6.0 ±0.3 (31.6%) before receiving training and 7.4 ±0.4 (39%) afterwards, resulting in a lower improvement score of 1.4 ±0.4 (7.4%) (Fig. 2.1a). Training type had a significant effect on improvement score (GLM: $F_{1,120}$= 124.98, P<0.001; Table 2.2). Pre-training score also had a significantly negative effect on improvement score (GLM: $F_{1,119}$= 28.51, P<0.001; Table 2.2).

Table 2.2 Effects of training type and pre-training quiz scores on improvement scores based on general linear models. The training x pre-score interaction did not contribute significantly in each model, and so was removed.

	d.f	Effect	F	*P*
All species				
Training	120	+ve	124.98	<0.001
Pre-score	119	-ve	28.51	<0.001
Seven most common species				
Training	120	+ve	215.9	<0.001
Pre-score	119	-ve	59.58	<0.001
Seven less common species				
Training	120	+ve	4.2	<0.05
Pre-score	119	-ve	23.65	<0.001
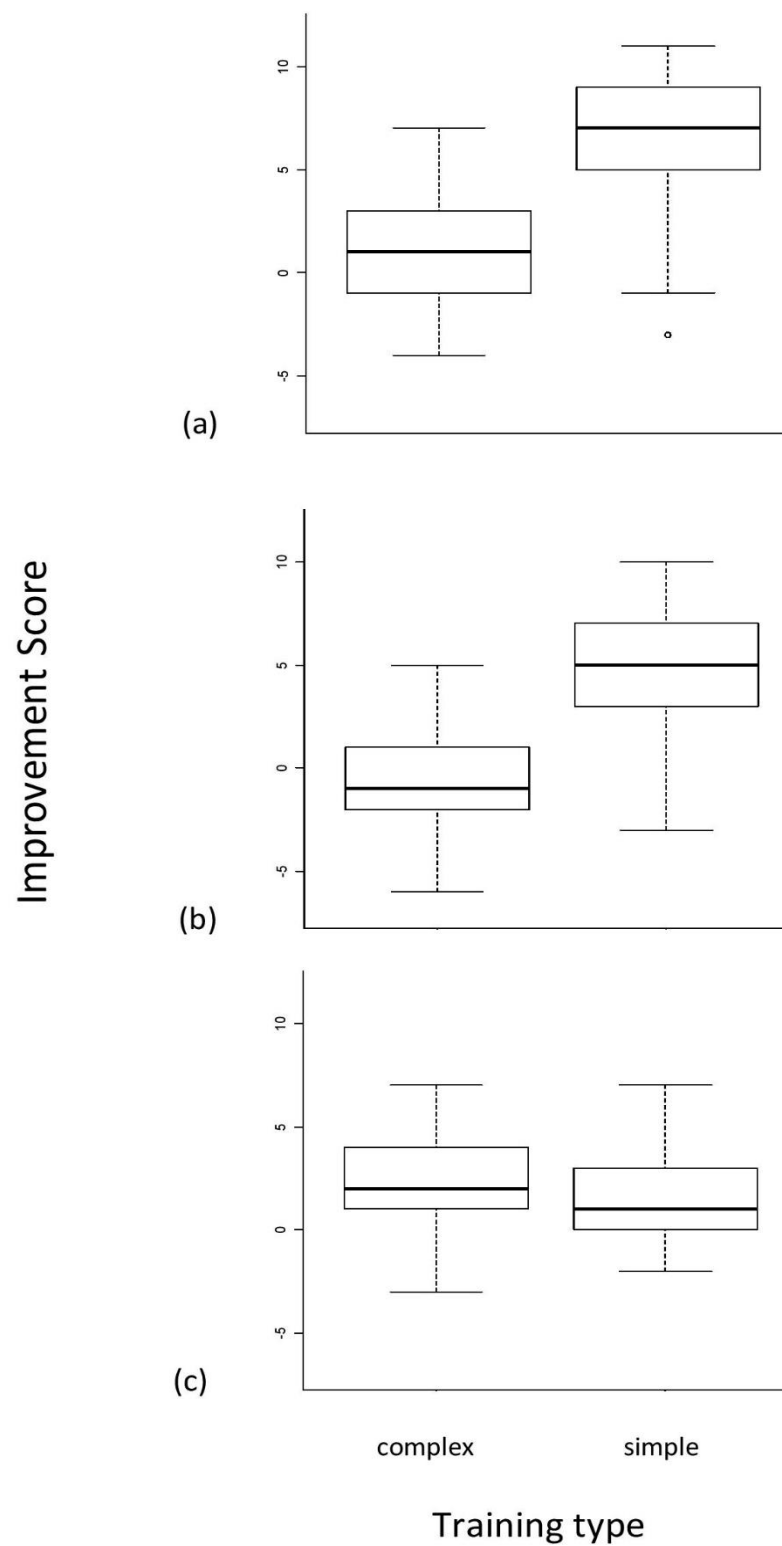
Fig. 2.1 Improvement scores in the complex and simple treatments for (a) all species (b) the seven most common species and (c) the seven less common species.

Seven most common species

Of the 12 questions on the seven most common species asked per person, the average number answered correctly (grouping all participants) was 4.5 ±0.2 (37.5%) before training and 6.8 ±0.3 (56.7%) after training resulting in an average improvement score of 2.3 (±0.4) (19.2%). For the participants who received simple training, improvement score increased by an average of 5.1 ±0.4 (42.5%). The scores of those who received the complex training decreased by an average of 0.8 ±0.3 (6.6%) (GLM: $F_{1,120}$= 215.9, P<0.001; Table 2.2, Fig 2.1b). Pre-training score has a significantly negative effect on improvement score (GLM: $F_{1,119}$= 59.58, P<0.001; Table 2.2).

Seven less common species

Of the 19 photos included in the quizzes, seven were of the less common species. Grouping all participants, the average number of pre-training questions answered correctly was 2 ±0.1 (28.6%). Following training 3.7 ±0.2 (52.9%) were answered correctly, resulting in an average improvement score of 1.7 ±0.2 (24.3%). For the simple treatment, the average improvement score was 1.4 ±0.2 (20%) compared with 2.1 ±0.3 (30%) following complex training (GLM: $F_{1,120}$= 4.2, P<0.05; Table 2.2, Fig. 2.1c). Again, pre-training score negatively affects improvement score (GLM: $F_{1,119}$= 23.65, P<0.001; Table 2.2).

2.4.2 Species analysis

A complex interaction between species, training type and pre/post score shows that improvement in identification following training differs according to both bumblebee species and training type (GLMM: χ^2_{13}= 65.86, P<0.001; Fig. 2.2). Because of this strong

three-way interaction, the effects of individual explanatory variables and their two-way interactions could not be independently assessed. It is clear that species differed in how easy they are to identify. For example, prior to training *B. pascuorum* was rarely correctly identified (5/122 correct questions) whereas *B. hypnorum* was often identified correctly (91/122) (Fig. 2.2). The three-way interaction demonstrates that the effect of training, and of training type, varies from species to species. For example, the identification of *B. pascuorum* improves greatly in the simple treatment but improves very little in the complex treatment (Fig. 2.2). Conversely, *B. monticola* shows no improvement in the simple treatment (in which this species is not mentioned) but only a marginal improvement in the complex treatment (Fig. 2.2).
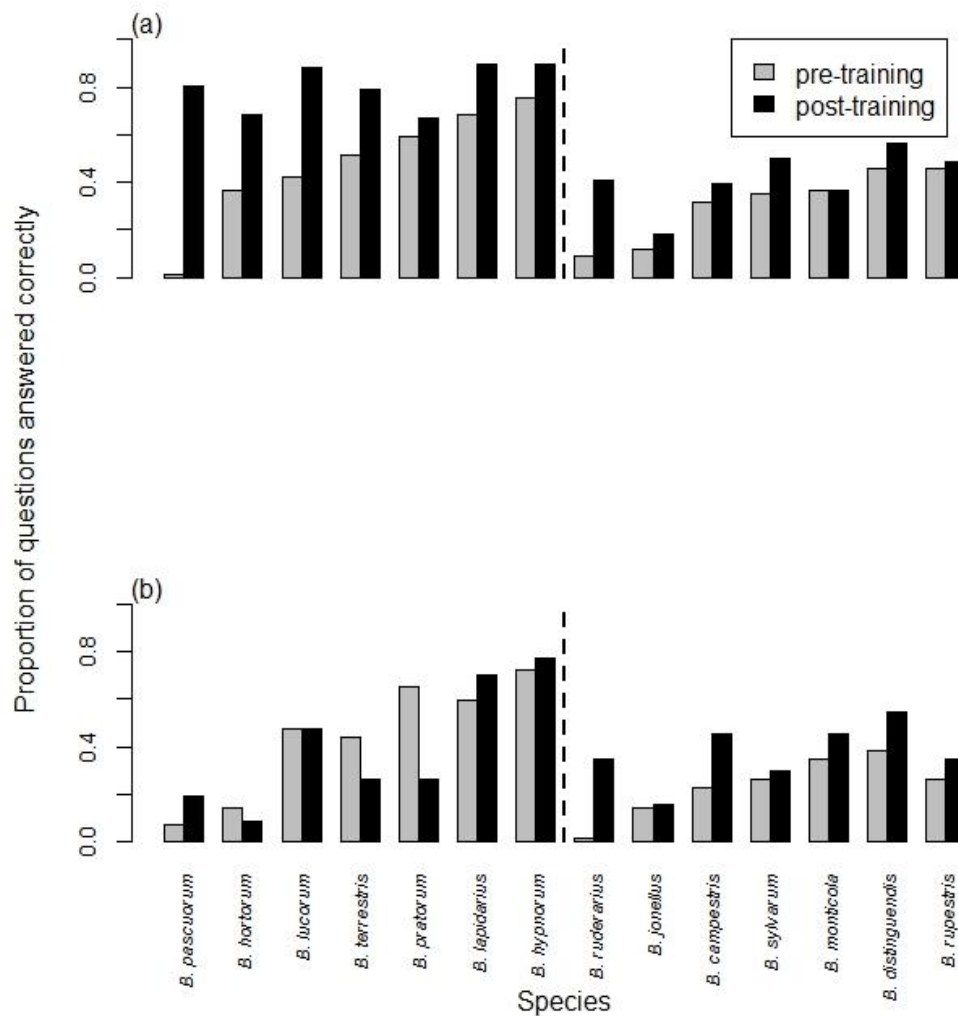
Fig. 2.2 Proportion of questions answered correctly in pre- and post- training quizzes for each species for (a) simple and (b) complex training type. A dashed line separates the seven most common species (left) from the seven less common species.

2.5 Discussion

This study reveals a number of interesting aspects of the efficacy of species identification training for citizen scientists. Overall, a simple 30 min indoor training session improved the ability of a mixed group of adults to identify bumblebees to species from photographs (from 33.7 to 55.3% of answers correct). However, training type had a profound influence on the efficacy of training. Simple training which focussed on just 7

species resulted in a much greater improvement in scores than complex training which included 18 species within the same length of training session. Volunteers given the simple training became much better at identifying the seven common species on which the training focussed, but also improved a little in identifying species not included in their training. In contrast, volunteers given the complex training got worse at identifying the seven common species, and only a little better at identifying the less common species.

In the simple training, volunteers had more time to focus on the basic steps required to separate males from females, true bumblebees from cuckoos and queens from workers. They were also introduced to a smaller suite of species with which they had time to become familiar. Subsequently, in the post-training test they may have been able to recognise unfamiliar traits as belonging to a species outside of this group, which they could attempt to identify using the field guide provided. This may explain why they improved in their ability to identify species not included in the training session.

In the complex treatment, it seems that the volunteers were exposed to too many species within the set timeframe. It has long been established that humans have a limited capacity to store information in their short term memory (Miller 1956), and that if information is presented too quickly then they are unable to process it and transfer it accurately to long-term memory (Pastore, 2012). If cognitive load is too high, because too much information or too many types of information are presented, then learning is impaired (Sweller 1988; Mayer et al., 2001). High cognitive loads can even lead to stress and high blood pressure (Fredericks et al., 2005). The challenge for those designing training sessions is to work out the optimum load.

It was unsurprising that the simple training was more effective in improving the identification of the seven most common bumblebees considering that these species were the focus of the training session. It is interesting, however, that volunteers who were given the complex training actually became worse at identifying the seven common species. This, again, is presumably because of the high information load of the complex treatment. Volunteers exposed to the complex training were perhaps more likely to confuse common species with similar rare species.

In general, volunteer scores in the pre-training quiz influenced their post-training scores (Table 2.2). If volunteers received high scores in the quiz prior to training they tended to have a lower improvement score than those who did less well. This is presumably simply because volunteers who were naturally more skilful at identifying species using the field guide alone had less room for improvement in their identification skills.

There were interesting differences between bumblebee species in the accuracy with which they were identified pre-training, and in the response of volunteers to the different training approaches. Some species are distinctive, and hence were usually identified correctly without any training; for example, *B. hypnorum* is the only species with a combination of a ginger thorax and a distinctive white tail. Improvement in identification differed between training types and also according to species. The simple treatment led to a general improvement, with higher scores for 13 of the 14 species included in the test (and remaining unchanged for *B. monticola*). Improvement in this treatment was particularly marked for two common species, *B. pascuorum* and *B. lucorum* (Figure 2.2). In contrast, the influence of receiving the complex training varied greatly across species, with improvements in some and declines in others. For example,

the accuracy of identification of *B. pascuorum* remained low, and scores for *B. lucorum* did not change. Accuracy declined markedly in two common species, *B. pratorum* and *B. terrestris*. It is likely that the simple treatment led to a marked improvement in some common species since these were at the focus of the training session. In contrast, volunteers in the complex treatment would not have been as familiar with common species' traits and were more likely to confuse these species with other species which were introduced during the training session.

Overall, this study suggests that initial training sessions for volunteer recorders are more effective if they are kept simple and focus on a small number of common species. By doing so, a fairly high level of accuracy was achieved in identification of common bumblebee species (70%). These common species are likely to comprise the vast majority of bees seen in most locations in the UK, suggesting that simple citizen science-based recording schemes targeted at gathering information on the abundance of the common species could produce data of moderate accuracy. Of course subsequent training sessions could be used to improve skills and one would hope that keen recorders would hone their identification skills further through practice. Also, volunteers leaving simple training sessions with a higher degree of confidence in the common species may feel more encouraged to develop their species identification skills and commit to long term monitoring surveys.

When assessing training requirements for a citizen science project, it is important to consider tradeoffs between time invested in volunteer training and logistics of training provision, including financial and geographical limitations. Tulloch et al. (2013) investigated the effect of time invested by British Trust for Ornithology (BTO) staff and

volunteers in gathering species data for bird monitoring programmes on the number of citations of the resulting published data. They found that increasing time investment does not necessarily lead to higher quality data and underlined the importance of identifying a "benefit threshold", a point at which further investment produces significantly fewer gains. They also found that a longitudinal project, similar to BeeWalk, whereby volunteers used long-term fixed sites, was more costly to manage but ultimately produced more benefits in terms of scientific knowledge and output than short-term cross-sectional schemes. This is to be due to the ability of longitudinal projects to measure the impact of environmental change on both the distribution and abundance of populations over time. Many of these projects used a tiered approach with regional, experienced volunteer coordinators training new recruits and assessing data quality (Pollard and Yates, 1993, Bell et al., 2008). This approach requires high initial investment that produces long term gains both in terms of scientific output and project sustainability (Pollard and Yates, 1993; Tulloch et al., 2013). While the current study showed that a short training session leads to an increase in the ability of volunteers to identify seven common species of bumblebee, it is unknown whether further investment in training provision will lead to an increase in knowledge of bumblebee population dynamics. Studies of bird species identification by secondary school pupils have shown that if anymore than 6-8 species are introduced in a single 45 min class, species identification accuracy decreases as does retention of information learned when assessed 6-8 weeks later (Randler and Bogner, 2002; Randler and Bogner, 2006; Randler 2008). This evidence coupled with the results from this training study suggests that bumblebee monitoring volunteers should initially focus on common species in one short training session since it has been shown to be effective. More species could be

introduced in an advanced training session after volunteers have completed one season of monitoring, allowing individuals to familiarise themselves with the common species before introducing rarer ones. Online systems, programmed to provide feedback on key species characteristics could also be used to supplement and reinforce information learned through direct training. This has already been shown to be effective in improving the accuracy of bumblebee identification by volunteers using photographs (Wal et al., 2016) but it has yet to be applied to monitoring schemes. As bumblebee monitoring projects progress, experienced, regional volunteers with advanced training could manage and train new recruits, forming a tiered approach similar to BMS (Pollard and Yates, 1993). This would help to reduce tradeoffs due to financial and geographical limitations and further engage volunteers through direct training and feedback at regional level. The finding that species differ in the ease with which they can be identified is not surprising but is important. If we can quantify the frequency with which particular species are identified accurately, and which species are most commonly mistaken for one another, then we can apply confidence limits to data collected by citizen scientists. We can also adjust subsequent training sessions to focus on the species that are most frequently misidentified. Identification tests based on photographs provide a simple means by which the accuracy of individual recorders can be quantified and monitored over time. Such tests could readily be delivered online and could help to keep recorders engaged, providing them with feedback on their performance, as well as providing scientists with regular updates on the quality of the data being provided by each volunteer. Unfortunately, it was not possible, in this particular study, to include more information on individual volunteer profiles, such as age and education, due to a request by The Cooperative Company to refrain from requesting private details from

individuals at training events. However, future training sessions could include requests for this information so that these variables are incorporated into analyses in order to investigate their potential effect on learning.

These findings have broad relevance to any citizen science scheme that requires volunteers to identify organisms. Many such schemes have been launched in recent years (Conrad and Hilchey, 2011) but little attention has been paid to determining the optimum type of training to offer, and often the accuracy of records obtained remains unclear. Of course this study is small in scope, and involves only two contrasting treatments, but we hope that our work will stimulate further studies in this area.

Chapter 3

USE OF CITIZEN SCIENTISTS TO MAP THE SPREAD OF WINTER-ACTIVE BUMBLEBEES IN GREAT BRITAIN

3.1 Abstract

Over the past two decades, workers of both *Bombus terrestris* and *Bombus pratorum* have been observed foraging during the winter months in the UK. The key driver of this phenomenon remains unknown, though climate change has been shown to affect hibernation period, phenology and voltinism in other insect groups. Data collected by citizen scientists have proved a powerful tool for monitoring species' responses to environmental change. Ths study uses a citizen science dataset to assess the distribution of winter-active bumblebees, analysing records collected by 5,748 volunteers over a four-year period (2007-2011). Spring records suggest that *B. terrestris* and *B. pratorum* are almost ubiquitous throughout Britain. Although winter-active *B. terrestris* were recorded as far north as Scotland, winter records of both species were more common at lower latitudes relative to the number of spring records, suggesting that climatic factors currently limit the distribution of winter-active bumblebees. Possible consequences of the spread of winter active bumblebees are discussed.

3.2 Introduction

In recent decades, climate change has had a notable effect on the distribution, phenology and life history of many invertebrate species (Walther et al. 2002; Robinet and Rocques, 2010; Pöyry et al. 2011). Its effect on butterfly species has been particularly well documented, with Parmesan et al. (1999) providing large-scale

evidence of northerly shifts in the ranges of non-migratory butterfly species. First and peak appearance dates of butterfly species have advanced over the last two decades in response to climate change (Roy and Sparks, 2000) and species show large spatial and temporal differentiation in peak emergence dates due to differences in regional adaptation and plasticity in phenology (Hodgson et al., 2011). Compared with butterflies, there is a paucity of information available on the effect of climate change on UK bumblebees. Dramatic range contractions of some UK species have occurred since the 1960s (Goulson et al., 2008) but the role that climate may have played in these distribution changes remains unclear. Furthermore, little is known of the potential effects of climate change on bumblebee phenology and life history.

The wealth of information available on the effects of climate change on UK butterfly species is largely due to the existence of citizen science surveys involving systematic data collection by volunteers (Pollard and Yates, 1993). Citizen science is becoming increasingly important in species monitoring across many taxa (Silvertown, 2009), with well-designed volunteer surveys facilitating large-scale data collection that would otherwise be impossible (Silvertown, 2009; Couvet et al., 2008; Dickinson et al., 2010). Existing species-specific citizen science surveys may provide a good opportunity to efficiently collect information on a wider range of taxa since standardized protocols and expansive networks of volunteers have already been established. An example of such a survey is the British Trust for Ornithology (BTO)'s Garden BirdWatch survey (GBW), a mass participation citizen science project that has led to numerous publications on the use that birds make of garden habitats and how this relates to population trends at a wider spatial scale (e.g. Cannon et al., 2005, Chamberlain et al., 2007, Ockendon et al.,

2009, Robinson et al., 2010). In addition to recording garden birds, volunteers participating in this existing scheme are invited to collect information on other taxa, including mammals, reptiles, amphibians and various invertebrates. Toms and Newson (2006) showed that data collected on other taxonomic groups through the Garden Birdwatch survey offered new opportunities for the monitoring of species within a built-up environment, a habitat that can be difficult to survey.

Until recently, winter hibernation of bumblebees was thought to be ubiquitous in the UK (Alford, 1975) though populations of *Bombus terrestris* in southern Europe are known to have a second autumn/winter generation (Rasmont et al., 2008). However, in recent years there have been regular sightings of winter-active bumblebees in the UK. This phenomenon was first recorded in southern England in 1990 (Robertson, 1991) where *Bombus terrestris* workers were observed foraging in both December and January. In addition to *B. terrestris*, winter records also include some *B. pratorum*. Stelzer et al. (2010) show that *B. terrestris* can achieve high foraging rates during winter months. While some sightings of winter bumblebees in the south of the UK have been reported and mapped (Stelzer et al., 2010), the distribution of records has not, until now, been formally analysed.

Here we use presence/absence bumblebee data collected by citizen scientists to investigate the distribution of UK winter bumblebees. We analyse record distribution in relation to latitude, temperature, rainfall and level of urbanisation in order to ascertain whether or not winter activity is more pronounced under certain environmental conditions.

3.3 Methods

In 2007, the Bumblebee Conservation Trust and the British Trust for Ornithology (BTO) launched 'Garden BeeWatch', within the existing Garden BirdWatch framework, in order to collect presence/absence data on garden bumblebees across Britain & Ireland. This study concentrated on data from Great Britain because of the smaller number of participants in Ireland. While validation of individual records was not possible, the online system through which these data have been submitted by participants utilises threshold validation to flag-up unusual records, thereby alerting observers to potential errors. Threshold validation involves programming existing species information to allow software to identify anything outside the normal pattern of occurrence for the species in question. In the case of Garden BeeWatch, records outside of each species range and flight season, based on the latest datasets verified by the Bees Wasps and Ants Recording Society (BWARS) experts and made available through the National Biodiversity Network (NBN; National Biodiversity Network, 2017) are flagged up and removed for further investigation by BWARS. Because the survey involved the systematic year-round recording of bumblebees over an extensive network of British garden sites, the resulting dataset provides a suitable opportunity to study the distribution of winter-active bumblebees.

Volunteers were asked to carry out a weekly survey of their garden and to record the maximum number of each species of bumblebee seen together at one point in time during the defined observation period. Volunteers were asked to maintain a consistent level of observation effort from one week to the next and were encouraged to discard data from under- and over-observed weeks. Some variation in observer effort and competence is inevitable; however, it is contended that this does not detract from the

ecological interest of these data when examined at a national scale and over a five-year time period.

14,182 gardens were surveyed as part of the Garden BirdWatch scheme during the period which ran from 1st January 2007 to 31st December 2011, of which 3,497 returned bumblebee records. For the purpose of analysing winter distribution in relation to spring distribution a "winter" (1st December - 31st January) and "spring" (1st March - 30th April) seasonal period was assigned. The rationale for using spring records, rather than records from throughout the spring and summer, is that identification of *B. terrestris* is likely to be far more reliable during the queen flight period than later in the year when worker bumblebees predominate. Workers of *B. terrestris* are difficult to distinguish from similar species.

A binary logistic regression was run in R Statistical Software Version 2.12.2 (R Development Core Team, 2011) in order to test the effect of season (winter/spring), year, latitude, temperature, rainfall and proportion of surrounding urban habitat on record distribution. The presence/absence (1/0) of species observation per 10km square was fitted as the response variable. Data were obtained for a total of 973 10km squares. Mean monthly maximum temperature and rainfall values for each 10km square were interpolated from Met Office weather stations (UK Meteorological Office, 2012) and assigned to each observation. The degree of urbanisation in the 10km square within which each site was located was determined from the Land Cover Map 2007 (Morton et al., 2011) using ArcGIS software, version 10 (ESRI, 2011). This survey produces a land cover map that identifies 23 land cover classes, which combine to map 17 terrestrial 'Broad Habitats', with a minimum mappable unit of 0.5ha. These data were summarised

to derive a measure of the percentage of urbanised land cover within each 10km square that contained one or more GBW sites. The effect of urbanisation could be confounded by geography, since urban areas are concentrated in the southern half of Great Britain, but the inclusion of latitude in the models allows this to be tested. The maximal binary logistic regression model included all explanatory variables along with their two- and three-way interactions. Model selection was performed using a backward stepwise regression with *P*-values at a significance level of 0.05. A likelihood ratio test using chi-squared was performed to assess the contribution of explanatory variables to the final model.

3.4 Results

Spring records of *B. terrestris* were reported in 2,088 gardens, 108 of which also had winter records. *B. pratorum* was recorded in 603 gardens during the spring period and from 11 gardens during the winter. The ratio of the total number of spring to winter bumblebee records was lower for *B. terrestris* (19.3: 1) than for *B. pratorum* (54.8: 1). The number of gardens reporting records in the winter period is far lower than in spring for each species with 95% of total *B. terrestris* records and 98% of total *B. pratorum* records occurring in the spring period (Table 3.1; Fig. 3.1a-b). Both species exhibit a markedly more southern distribution during winter compared with that seen in spring (Fig. 3.1a-b), with binary logistic regression models revealing a highly significant negative effect of the interaction between season and latitude on the distribution of both species (*B. terrestris*: χ^2_{5946}=67.1, *P*< 0.001; *B. pratorum*: χ^2_{2635}= 7.4, *P*< 0.01, Table 3.2).

Table 3.1 Number of gardens reporting spring and winter records of *B. terrestris* and *B. pratorum*.

Year	B. terrestris		B. pratorum	
	Spring	**Winter**	**Spring**	**Winter**
2007/08	714	42	159	3
2008/09	273	27	49	4
2009/10	677	26	195	1
2010/11	786	13	250	3
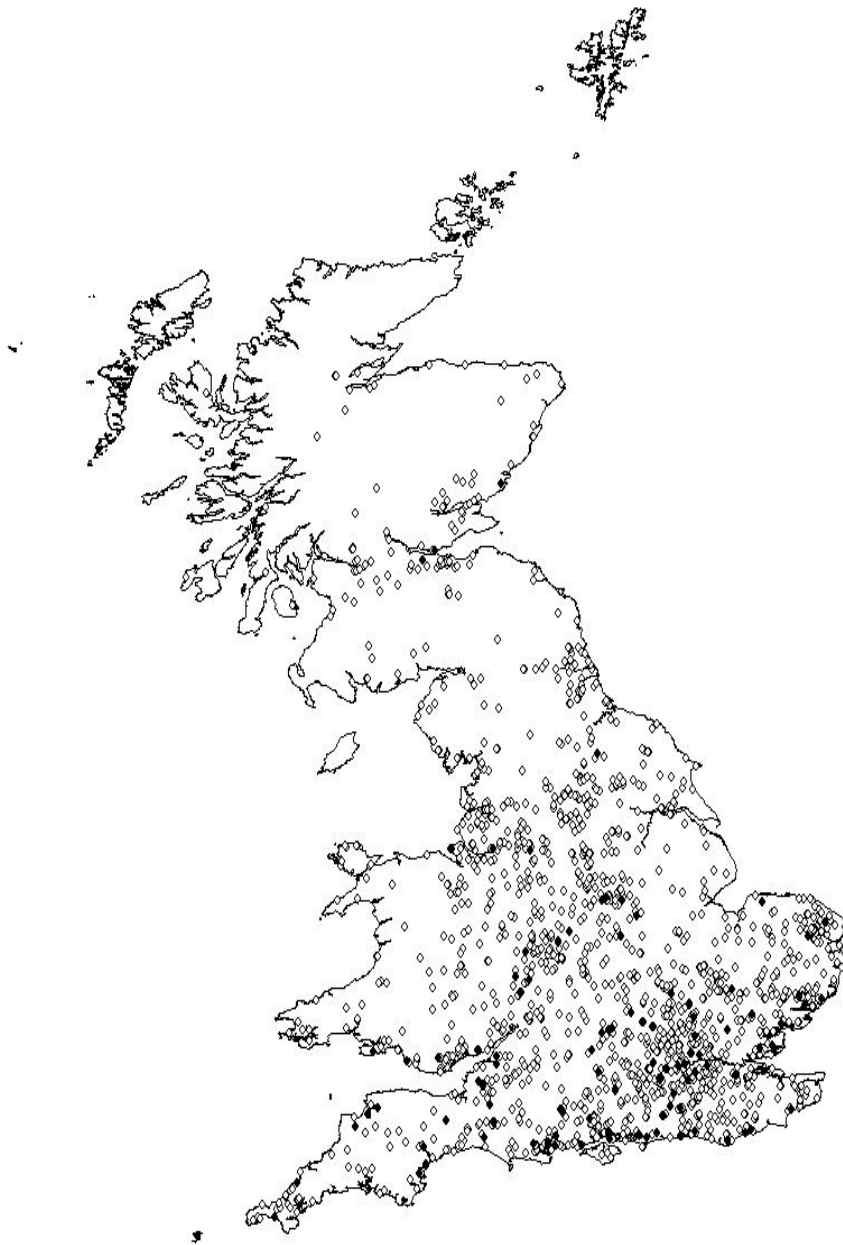
Fig. 3.1a Distribution of *Bombus terrestris* winter records (black) relative to spring records (white).
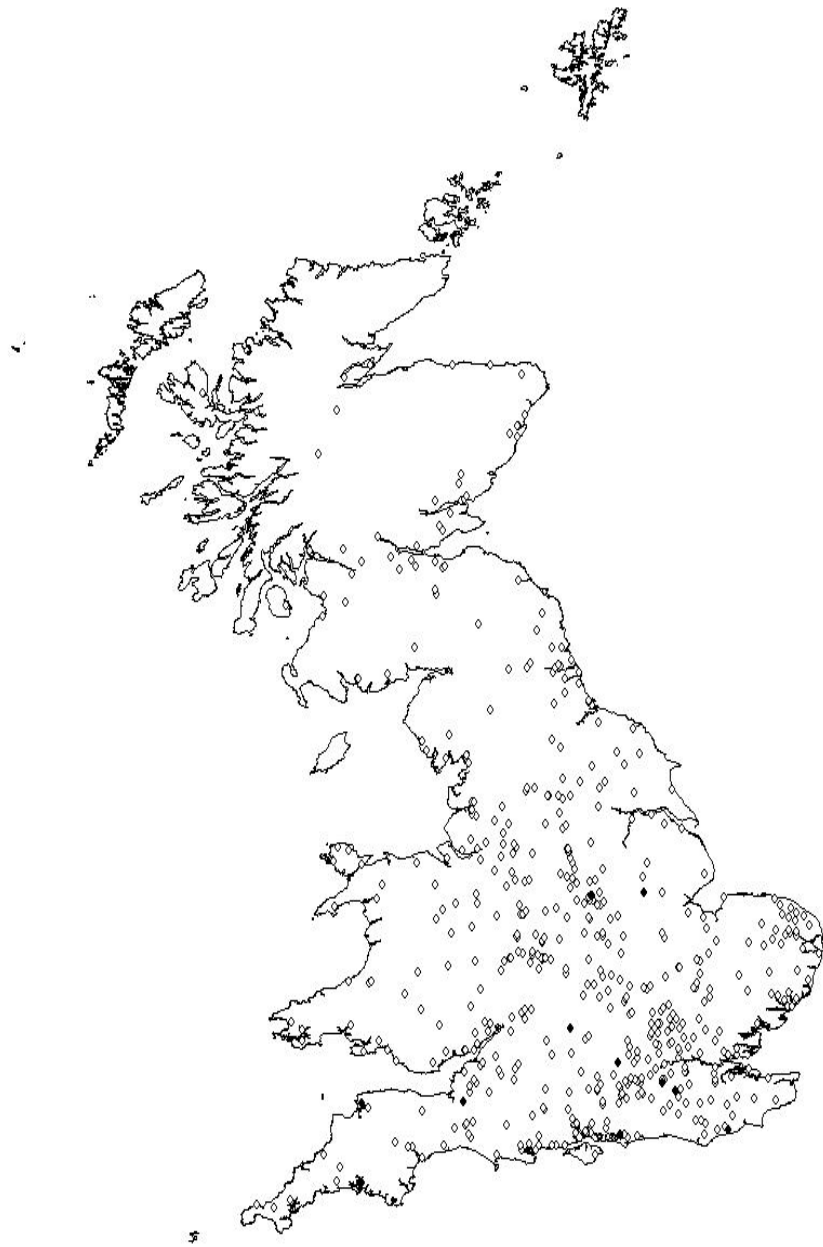
Fig. 3.1b Distribution of *Bombus pratorum* winter records (black) relative to spring record

Table 3.2 Minimal model summary for each species where presence/absence per 10km square is fitted as the response variable in a binary logistic regression. Season, year, proportion of surrounding urban habitat, mean monthly maximum rainfall, mean monthly maximum temperature and latitude along with their 2- and 3-way interactions were fitted as fixed factors.

Species	Variable	Estimate	S.E.	z-value	P	AIC
B. terrestris						
	Winter Season	30.49	4.67	6.523	6.90e-11*	5931.4
	Year2	-1.26	0.13	-9.647	< 2e-16*	
	Year3	-0.10	0.10	-0.981	0.33	
	Year4	0.05	0.15	0.362	0.72	
	Urban Habitat	-9202.00	2799.00	-3.288	1.00e-03*	
	Rainfall	1.39e-03	2.23e-03	0.626	0.53	
	Temperature	0.05	0.02	2.495	0.01*	
	Latitude	-0.10	0.02	-4.121	3.77e-05*	
	Winter Season:Year2	1.01	0.24	4.287	1.81e-05*	
	Winter Season:Year3	-0.18	0.24	-0.743	0.46	
	Winter Season:Year4	-1.62	0.35	-4.651	3.30e-06*	
	Winter Season:Latitude	-0.65	0.09	-7.146	8.94e-13*	
	Urban Habitat:Latitude	177.80	53.55	3.319	1.00e-03*	
B. pratorum	Winter Season	31.20	15.41	2.025	0.04*	2413.7
	Year2	5.40	5.75	0.938	0.35	
	Year3	17.92	4.48	4	6.34e-05*	
	Year4	1.97	4.32	0.457	0.65	
	Urban Habitat	-17.68	120.50	-0.147	0.88	
	Rainfall	-3.25e-03	0.01	-0.637	0.52	
	Temperature	5.64e-04	0.03	0.019	0.99	
	Latitude	0.09	0.06	1.47	0.14	
	Winter Season:Year2	1.80	0.71	2.53	0.01*	

Winter Season:Year3	-1.87	1.14	-1.639	0.10
Winter Season:Year4	-0.61	0.78	-0.778	0.44
Winter Season:Latitude	-0.68	0.30	-2.288	0.02*
Year2:Latitude	-0.14	0.11	-1.237	0.22
Year3:Latitude	-0.34	0.09	-3.977	6.97e-05*
Year4:Latitude	-0.03	0.08	-0.393	0.69

Yearly variation in the number of winter records differed significantly from variation in spring records for both species, with a significant effect of the interaction between season and year on species occurrence (*B. terrestris*: χ^2_{5947}= 67.9, P<0.001; *B. pratorum*: χ^2_{2730}= 11.7, *P*<0.001, Table 3.2). Winter records fluctuated less between years than spring records, in part a consequence of a notable drop in spring records in 2008/09 (Table 3.1). While the interaction between urban habitat and latitude was found to have a significant effect on the occurrence of *B. terrestris* with proportionally more records occurring in southern urban areas, the effect of urban habitat did not differ between seasons (*B. terrestris:* χ^2_{5878}=0.2, *P*> 0.1; *B. pratorum*: χ^2_{2358}= 0.5, *P*>0.1, Table 3.2).

The effect of mean monthly maximum temperature on species occurrence was found to be significant for *B. terrestris* (χ^2_{5883}=3.7, *P* = 0.05, Table 3.2) and non-significant for *B. pratorum* (χ^2_{2632}=0.003, *P*>0.1, Table 3.2).

3.5 Discussion

Results of this study indicate that winter-active bumblebees are widespread across much of Great Britain and occur as far north as Central Scotland, but that they tend to be disproportionately more common in the south. Although recently published maps show records of winter-active bumblebees in the south of the UK (Stelzer et al.*,* 2010), this is the first time their distribution has been assessed using a large-scale dataset that includes records from the north and both presence/absence information derived from systematic weekly observation. It remains unclear whether these bees originated from nests that do not die in autumn, or from newly founded nests established by queens that failed to hibernate or, alternatively, emerged from hibernation very early. Pollen-collecting queen *B. terrestris* have been observed in November/December (D. Goulson

pers. obs.,) and Stelzer et al. (2010) reported a peak in the number of queens observed in October/November, suggesting that the phenomenon may be driven by queens hibernating briefly but then emerging later in autumn. While it would be desirable to have information on caste for records analysed in this study, the use of citizen scientists limits the level of detail at which data can be collected due to lack of expertise and/or the need to keep the recording methods simple when working with multiple taxa. However, the scope of this study would not have been possible without the help of volunteers.

Several theories have previously been suggested to explain the appearance of winter active bumblebees in Great Britain. These include the increased availability of forage material in the form of cultivated, exotic winter-flowering plants in urban parks and gardens; Stelzer et al. (2010) show that *B. terrestris* can achieve high foraging rates in winter by utilising these resources. There is also a possibility of hybridisation of British *B. terrestris audax* with the commercially imported Mediterranean subspecies *B. t. dalmatinus*, which is active during the winter months across its native range (Ings et al., 2006; Gürel et al., 2008). While these factors may play a role in allowing increased winter activity of native bumblebees, the southerly distribution of winter records combined with the lack of a clear influence of surrounding urban habitat on winter bumblebee activity compared with spring activity indicates that regional climate exerts an influence on this phenomenon. Average maximum winter temperature did not exert a significant influence on winter appearance of species in this study but this may be due to the fact that earlier, autumn temperatures, during queen hibernation, are more strongly associated with winter activity. If regional climate does indeed influence winter activity, winter bumblebee populations are likely to be impacted climate change in the future

(IPCC, 2013). Climate change has been cited as a major driver of changes in phenology, range and life history of many other insect species (Menzel et al., 2006; Ayres and Lombardero, 2000; Carroll et al., 2003; Roy and Sparks, 2000). Reduced periods of diapause and changes in voltinism are commonly reported in relation to warming winters (Robinet and Rocques, 2008; Lange et al., 2006).

Yearly fluctuations occurred in the proportion of winter bumblebees recorded. This may reflect natural variation in the density of winter and spring populations. For example, the low numbers of bumblebees recorded during the 2008/09 winter and spring period may reflect the particular severity of that winter, with its low temperatures and associated slow start to spring. It is unknown why these two species in particular have become active during the winter months. It may be that since they are the earliest species to emerge in springtime (Edwards and Jenner, 2001), they are in a better position to adapt to cooler winter temperatures. Also, both of these species already display multivoltine tendancies with *B. pratorum* producing up to two broods in the spring and summer months in the UK and *B. terrestris* populations producing an autumn/winter generation in southern Europe (Rasmont et al., 2008). Long-term monitoring is required in order to further investigate the population dynamics of winter bumblebees, particularly with regard to whether they are becoming more abundant or spreading further northwards. These data will emerge from the Garden BeeWatch records over time.

It is unknown whether the emergence of winter-active bumblebees has significant ecological consequences. The presence of these bees may allow bumblebee-pollinated plants to flower earlier (Stelzer et al., 2010). They may alter the competitive balance

between bumblebee species, because emerging queens of other bumblebee species now face competition from workers from established nests of *B. terrestris* and *B. pratorum*. The presence of active nests throughout the year may favour evolution of more virulent pathogens, since they no longer have to survive the winter via vertical transmission in queens. If the decision to avoid hibernation occurs in relation to warmer temperatures and these are followed by persisting cold extreme events, winter active populations may be negatively affected (Kodra et al., 2011; Owen et al., 2013).

This study highlights the value of citizen science surveys that follow a well-structured, simple protocol in collecting large-scale, extensive datasets, which can be used to investigate ecological phenomena.

Chapter 4

EVIDENCE FOR HABITAT AND CLIMATIC SPECIALISATIONS DRIVING THE LONG TERM
ABUNDANCE TRENDS OF UK AND IRISH BUMBLEBEES

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Relative contribution of authors

L.C., H.R and D.G. conceived the ideas, L.C and H.R collated and analysed the data and
L.C. led the writing.

4.1 Abstract

- There is widespread concern over the current state of global pollinator populations and evidence suggests that bumblebees are declining in many parts of the world. However, there is very little monitoring of pollinator populations, so the extent and patterns of decline are not well characterised.

- The most comprehensive set of bumblebee species records exists for the UK and Ireland and previous analysis of the UK data highlighted severe range contractions for a number of species by the 1980s.

- Here we use the most current dataset to quantify the extent of range change over three time periods (pre1960, 1960-80 and 1981-2012) in order to compare results with earlier studies and ascertain whether species are continuing to decline. We also investigate if species are becoming more marginal i.e. occupying areas with more extreme or specialised climatic conditions within the UK and Ireland.

- For species that have contracted or become more marginal, we predict their climatic specialisation within the UK and Ireland using Maxent models, allowing us to associate records with climatic suitability values for each time period and to investigate whether or not species are contracting towards their climatic optimum.

- We find that populations of most rare bumblebee species appear to have stabilised post-1980, while the more common species appear to have expanded in range. However, rare species tend to have become more marginal in the sites they occupy post-1980, some have contracted towards their predicted climatic optimum, and some of which also retracted towards coastal areas.

- Our results provide a mixed picture of the state of the UK and Ireland's bumblebee fauna, and must be interpreted with caution as changing patterns of recorder effort may distort real trends. They highlight the need for future monitoring of the abundance of pollinators on both a regional and global scale.

4.2 Introduction

Bumblebees (Bombus spp.) are highly valued pollinators of crops (Corbet et al., 1991) and wildflowers (Williams and Osborne, 2009), contributing substantially to the global agricultural economy and providing an ecosystem service that is invaluable to the preservation of global biodiversity (Goulson, 2003). Bumblebees also have an intrinsic value and, due to their popularity, act as a flagship group for pollinator conservation. It is widely accepted that bumblebees, and other key pollinators, have suffered recent declines in many parts of the world. Distributional studies in North America, Europe and Asia reveal severe declines in a high proportion of species (Williams and Osborne, 2009; Goulson et al., 2008; Cameron et al., 2011; Williams et al., 2009b) emphasising the need for research, monitoring and conservation.

Drivers of bumblebee decline are thought to vary to some extent across geographic regions. There is strong evidence for a widespread effect of agricultural intensification on populations through the reduction of forage availability and nesting sites in Europe, N. America and China (Williams and Osborne, 2009; Goulson et al., 2008; Williams et al., 2009). Recent studies suggest that insecticides used in modern agriculture may also be playing a role, particularly the widespread adoption of neonicotinoid insecticides since the early 1990s (Whitehorn et al., 2012; Gill et al., 2012; Goulson, 2013). Pathogen spillover from commercial populations has been suggested to be responsible for recent

dramatic declines of some N. and S. American species (Cameron et al., 2011; Arbetman et al., 2013; Schmid-Hempel et al., 2014). The introduction of the exotic *B. terrestris* to Japan is also thought to have led to declines through competition with native species (Kondo et al., 2009; Inoue and Yokoyama, 2010; Tsuchida et al., 2010). Finally, climate change has been implicated in the range contraction of butterfly species (Thomas et al., 2006) but its role in bumblebee decline remains largely unknown.

Drivers of population change are likely to affect species differently with specialist species being potentially more susceptible to decline than generalists. Specialist species have been declining in recent years in response to global changes in habitat and climate, and numerous studies show that they are being replaced by generalist species that are more readily adaptable to environmental change (Clavel et al., 2011). While some bumblebee species are contracting their ranges, others remain widespread and common and several theories have been proposed to explain inter-species variation in range change patterns. While some studies found evidence of food-plant specialisation in rare species (Goulson and Darvill, 2004; Goulson et al., 2005; Kleijn and Raemaker, 2008), others found no such patterns (Williams, 1988; Williams et al., 2007; Fitzpatrick et al., 2007). Williams (1988) proposes a "marginal mosaic" model describing how habitat fragmentation and resource levels at the edges of a species' climatic range could drive contractions and provides evidence for differences between UK bumblebee species with regard to levels of range contraction, associated habitat types and proximity to species' global climatic ranges. Williams et.al (2007) provides further quantitative evidence to suggest that a combination of habitat and climate specialisations may be associated with decline.

It is clear that there are a number of potentially interacting drivers of bumblebee decline that vary across regions and between species and it is important that we understand primary regional influences and how they affect species populations in order to direct conservation efforts and mitigate against future declines.

Unfortunately, long-term abundance data for bumblebees or other wild pollinators are entirely lacking. However, data on distributions are available for some regions, with the most comprehensive set of records being for the UK and Ireland, based primarily on surveys carried out by the Bumblebee Distribution Maps Scheme (Alford, 1980), the Bumblebee Working Group (Edwards, 2001) and the Bees, Wasps and Ants Recording Society (BWARs). Presence-only species records, particularly those spanning a number of decades, are subject to bias arising from variation in sampling effort (Hortal et al., 2008). While these records are often limited across taxa and regions, they are often the only information available that spans a sufficient time period to answer ecological questions regarding population dynamics in relation to environmental change. Research needs to be directed in such a way that these sampling biases are accounted for. In that context, species distribution models that combine occurrence data with environmental estimates are increasingly being used to this effect (Elith et al., 2006; Hernandez et al., 2006; Elith and Leithwick, 2009; Rebelo and Jones 2010).

Here, we use presence-only species records from the UK and Ireland to quantify patterns of range change over time for all of the extant bumblebee species. We compare our results to Williams (1982), who reported widespread range contractions for UK bumblebees in the period 1960 to 1980, to determine whether these trends have continued. We then use species distribution modelling techniques to predict the climatic

specialisation of each species within the UK and Ireland and compare this to occurrence data in order to test the hypothesis that declining species are contracting towards their climatic optima (climatic conditions most favourable for survival and reproduction; Williams, 2007). We also test the effect of proximity to coastal habitat on species' range change, since some species now appear to have markedly coastal distributions.

4.3 Methods

4.3.1 Species records and environmental data

Our study area covered all of the UK and Ireland. Bumblebee species records were obtained from the Bees, Wasps and Ants Recording Society (UK) and the National Biodiversity Data Centre (Ireland). These data include historical records from the late 1800s onwards and comprise of presence-only data derived from scientific literature, museum specimens and field surveys. Records have been validated by senior members of each society and are made freely available through the National Biodiversity Network (www.nbn.org.uk).

Climatic and topographical variables for current environmental conditions in UK and Ireland were derived from the WORLDCLIM dataset (http://www.worldclim.org, Hijmans et al., 2005) at a 30 arc-seconds (~1 km) resolution. These have been generated by interpolation from climate data spanning fifty years (1950-2000) and are standardly used in species distribution modelling to predict current, past-historic and future distributions (e.g. Fourcade et al., 2013, Cordellier and Pfenninger, 2009). Bioclimatic variables were calculated using monthly data for March-October only, in order to represent the most active period for bumblebees in our study area. This is the flight period of bumblebees in the UK spanning emergence of queens from hibernation, nest

establishment and production of workers, males and new queens after which new queens enter hibernation and the rest of the colony dies off. This approach meant that eight WORLDCLIM variables (Bio8, Bio9, Bio10, Bio11, Bio16, Bio17, Bio18 and Bio19) that were calculated based on quarterly averages were excluded from the analysis. A Pearson-product correlation matrix of all remaining UK and Ireland bioclimatic variables, along with altitude and slope, was produced in R (R Core Team, 2013; see Table S4.1 in Supplementary Material). Where variables were highly correlated (Pearson's r>0.75, Rissler et al., 2006) only the one considered most biologically meaningful was retained. In the case of variables relating to both precipitation and rainfall, average seasonal values (e.g. mean annual temperature) were chosen over seasonal extremes (e.g. maximum temperature of the warmest month) since these were thought to be more likely to affect overall foraging efficiency throughout the season. The final list included: Bio1, annual mean temperature; Bio2, mean diurnal range [Mean of monthly (max temp - min temp)]; Bio4, temperature seasonality (standard deviation of annual mean temperature*100); Bio12, annual precipitation; Bio15, precipitation seasonality (calculated as the coefficient of variation in annual precipitation); altitude; and slope.

4.3.2 Evaluating bumblebee range changes

Bumblebee species records were divided into three time periods (pre1960, 1960-80 and 1981-2012) in order to evaluate range changes since the late nineteenth century. Although the use of time periods that differ in length has been shown to bias results in some analyses, it is not possible to use equal periods in the case of this study due to insufficient data prior to 1960 (Keil et al., 2010). This approach also enables comparison with the most recent study quantifying range contraction and expansion of all UK

bumblebee species (Williams, 1982) along with investigation of post-1980 range dynamics for the first time. Individual species records were mapped separately for each time period in ArcMap (v.10.1, ESRI, 2012) and spatial independence of data was assessed using the Average Nearest Neighbour (Spatial Statistics) tool. Species records falling within clusters were removed at random until a significantly ($p < 0.1$) random distribution was achieved.

In order to account for variation in the sampling effort across space and time, a pre-1960 survey area was assigned (Fig. 4.1) and range changes in subsequent time periods were assessed in relation to this area only. This accounts for the lack of coverage pre-1960, the southerly, urban bias of records in the UK, and the changes in coverage of northerly records as survey effort increased post-1980. It does, however, assume that those pre-1960 areas were resurveyed at some point during each subsequent time period.

To assign a pre-1960 survey area, all pre-1960 species records were mapped in ArcMap and a buffer of 2.5 km was created around each species record. This buffer allows for some variation in coordinates' precision and reliability before the advent of GPS. Overlapping buffers were then dissolved to create a pre-1960 survey area

Rasters of individual species records were created for each time period and these were delimited by the pre-1960 survey, so that only raster cells for which there was at least one bumblebee record in the pre-1960 survey area were considered. This partially controls for increasing intensity of sampling effort over time. The effect of species and time period on the number of occupied raster cells was investigated using a two-way ANOVA (Analysis of Variance) in R.
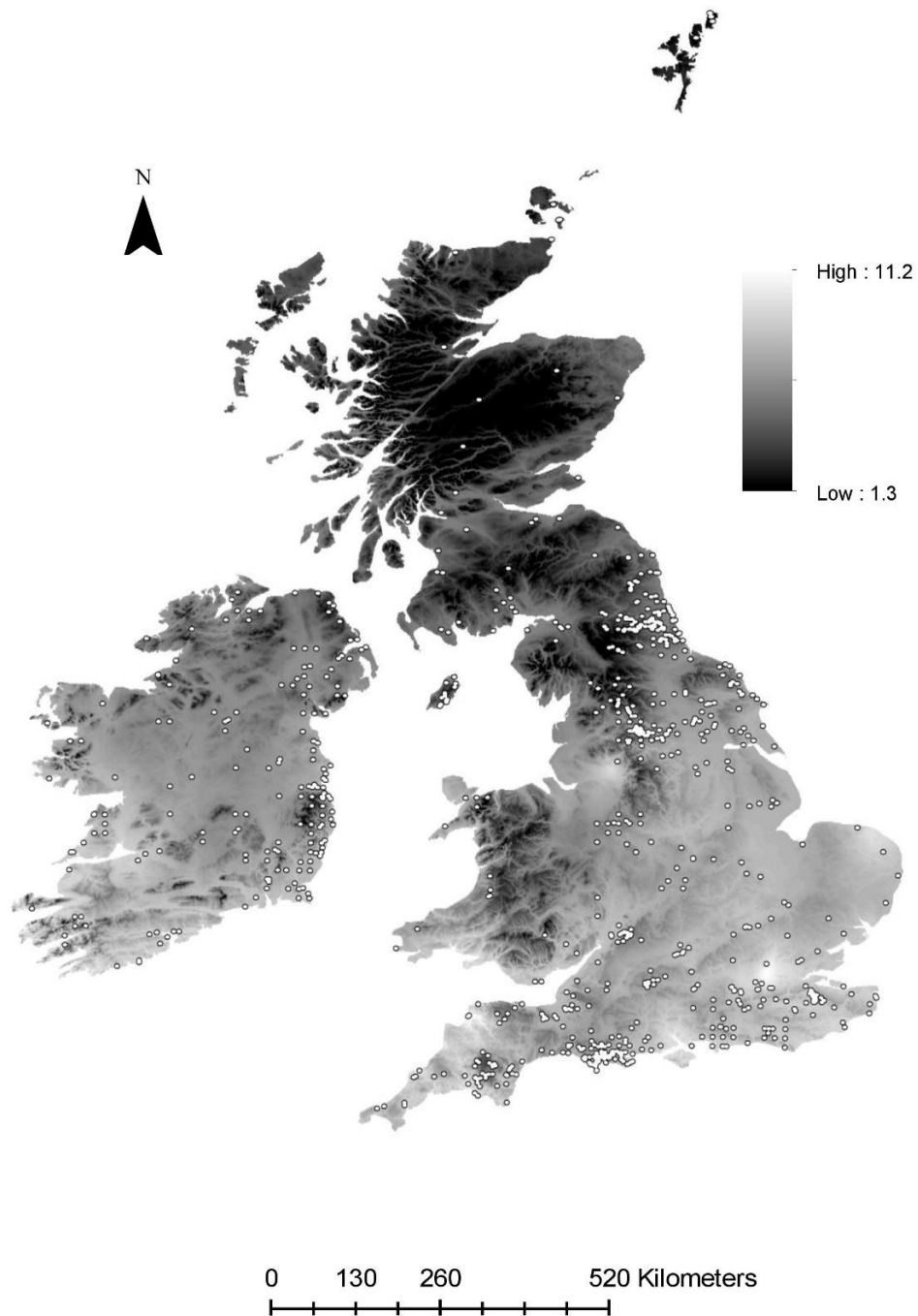
Fig 4.1 Mean annual temperature range (°C) for the UK and Ireland based on WORLDCLIM present temperature data overlaid with the pre-1960 survey area, assigned by compiling all pre-1960 bumblebee records and creating a buffer of 2.5km around each record.

4.3.3 Niche dynamics: are species' environmental niches shifting?

A principal components analysis (PCA), summarising the variation within climatic and topographical variables in the grid cells of our entire study area (all of UK and Ireland) was developed to represent the "environmental space" available for bumblebee species. Climatic and topographical variables were mapped in ArcGIS (v.10.1, ESRI, 2012) in raster format and the values of each grid cell were extracted and used to calculate a PCA in R (v 2.15.3; R Core Team, 2013). Values of the first and second component of the PCA were imported to ArcGIS and associated with individual species presence records for each time period. These per-species component values were then mapped for each time period within the climatic space (potential environmental niche) which was created using two axes (x=component 1; y=component 2).

The niche metric, marginality, was calculated for components 1 and 2 for each species in each time period. Marginality (M) is defined as the absolute difference between the global (study area) mean (m_G) and the species mean (m_s) divided by 1.96 standard deviations of the global distribution (σ_G)

$$M = \frac{\left| m_{G\text{-}} m_s \right|}{1.96 * \sigma_G}$$

Marginality measures whether a species lives in environmental conditions that differ from the average environmental conditions of the study area i.e. are more specialised (Hirzel et al., 2002).

The proportion of variation explained by each component was used to weight marginality calculations and these were combined to produce one metric for each species per time period, for the purpose of analysis. The effect of species and time period on marginality was investigated using a two-way ANOVA (Analysis of Variance) in R.

4.3.4 Are species that have undergone range contractions and/or increases in marginality moving towards areas that are environmentally more suitable?

Species whose range was found to have contracted by >50% and/or whose marginality increased by >50% in 1981-2012 compared with pre-1960 were analysed to test whether they were retreating to areas of higher predicted environmental suitability or were being forced to survive in less suitable conditions.

Maximum entropy modelling (Maxent) was used to predict which areas of the UK are environmentally more suitable for each species. Maxent is a machine-based learning technique that predicts species distributions by determining the distribution of maximum entropy that is closest to the uniform with the added constraint that the expected value of each environmental variable of this distribution must be equivalent to its empirical average (Phillips et al., 2006). This is a common, well-established technique used in species distribution and niche modelling studies that is robust to the use of presence data with potential biases, such as scarcity in the case of rare species and/or variation in sampling effort (Elith et al., 2006; Hernandez et al., 2006; Rebelo and Jones, 2010; Wisz et al., 2008). It is therefore the optimal tool for this analysis since several UK bumblebee species are considered rare (Williams 1988; Goulson et al., 2008)

and citizen science datasets can be prone to bias in recorder effort (Dickinson et al., 2010).

Presence data from all time periods, for all of the UK, were merged for each individual species in order to produce a more complete environmental niche model (see Table S4.2 in Supplementary Material for total number of records per species). Spatial autocorrelation was avoided by employing the same approach used previously (i.e. Average Nearest Neighbour). Species data were imported to Maxent software 3.3.3e (http://www.cs.princeton.edu/~schapire/maxent/), along with environmental variables and run in auto features using a regularization multiplier of 1. Cross validation was selected as the form of replication, using 10 folds (Merow et al., 2013). Model fit was measured using the average Area Under Curve (AUC) of the Receiver Operating Characteristics (ROCs) (Fielding and Bell, 1997) which ranges from 0 to 1, with 0.5 indicating a random prediction and 1 representing perfect discrimination (Phillips et al., 2006). This evaluation method has certain limitations, particularly when sampling intensity is low (Jiménez-Valverde, 2014; Merow et al., 2013). However there is a current lack of alternatives for presence-only models (Merow et al., 2013; see Table S4.2 for number of records per species).

The logistic model output for each species, consisting of environmental suitability maps with probability values of species occurrence (ranging from 0 to 1) assigned to each raster, was imported to ArcMap. Averages of these probability values were then calculated for each 10km square in the UK in order to obtain a measure of environmental suitability at an appropriate resolution, considering bumblebee dispersal distances (e.g. Lepais et al. 2010). The distance from the centre of each 10k square to the UK coastline

was also measured, using the Near (Analysis) tool, since inspection of recent distribution maps suggest that several UK bumblebee species have strongly coastal distributions.

To assess the effect of predicted environmental suitability and distance to coast on the distribution of bumblebee species across time periods, a linear mixed model with binomial distribution was run using the lme4 package (Bates et al.*,* 2014) in R for each species with presence/absence (1/0) per 10km square fitted as the response variable. Fixed factors included average environmental suitability values per 10km square for each species respectively, distance to coast, and time period. The identity of each 10km square was fitted as a random factor to account for repeated measures over time. The number of recorders per 10km square for each time period was also fitted as a random factor to account for possible variation in recorder effort. Maximal models included all explanatory variables along with their two- and three-way interactions. Model selection was performed using AIC (Akaike Information Criterion).

4.4 Results

4.4.1 Evaluating bumblebee range changes

Bumblebee range changes differed significantly between species and time periods (Table 4.1). There was an overall range contraction in the 1960-80 time period compared with pre1960 with some species then expanding their range from 1981-2012, while others remained approximately stable and a small number declined (Fig. 4.2).

There is a clear contrast in the pattern of range change between the six species considered to be endangered (UK Biodiversity Action Plan species; JNCC, 2007) and six perceived as common, widespread species ("Big Six"; Goulson et al., 2005), as previously observed by Williams (1982) (Table 4.1, Fig. 4.2). UKBAP species show a more marked

range contraction in 1960-80 compared to common species. While the more common species' ranges contract by 36-52% of their former distributions, UKBAP species show severe contractions ranging from 74% to 92%. Two other species, *Bombus soroeensis* and *B. rupestris,* also contract severely during this time period (Fig. 4.2).

 In recent years (1981-2012), UKBAP species appear to remain approximately stable in terms of their range pattern while the more common species show marked range expansions, increasing their range size by 25-65% times the area occupied in 1960-80 (Fig. 4.2). *B. vestalis* and *B. jonellus* also show notable range expansions, expanding beyond their pre1960 range along with the common "Big Six" species *B. pratorum*, *B. pascuorum* and *B. hortorum* (Fig. 4.2). Notably, *B. barbutellus* shows a continual decline across both time periods, decreasing its range size by 74% in recent years compared with pre-1960.

Table 4.1 Analysis of Variance table for a two-way ANOVAs investigating the effect of (a) species and (b) species group (Big Six, UKBAP and Other), and time period on range (the number of occupied ~1km raster cells within the pre-1960 survey area) and the degree of marginality.

	df	SS	MS	F value	P value
(a)					
Range					
Species	20	32770	1639	4.466	<0.001
Time period	2	16096	8048	21.936	<0.001
Residuals	40	14675	367		
Marginality					
Species	20	0.14	0.007	4.527	<0.001
Time period	2	0.013	0.007	4.306	<0.01
Residuals	40	0.062	0.002		
(b)					
Range					
Species Group	2	19846	9923	20.85	<0.001
Time period	2	16096	8048	19.91	<0.001
Residuals	58	27600	476		
Marginality					
Species Group	2	0.053	0.026	10.273	<0.001
Time period	2	0.013	0.007	2.591	<0.1
Residuals	58	0.149	0.003		
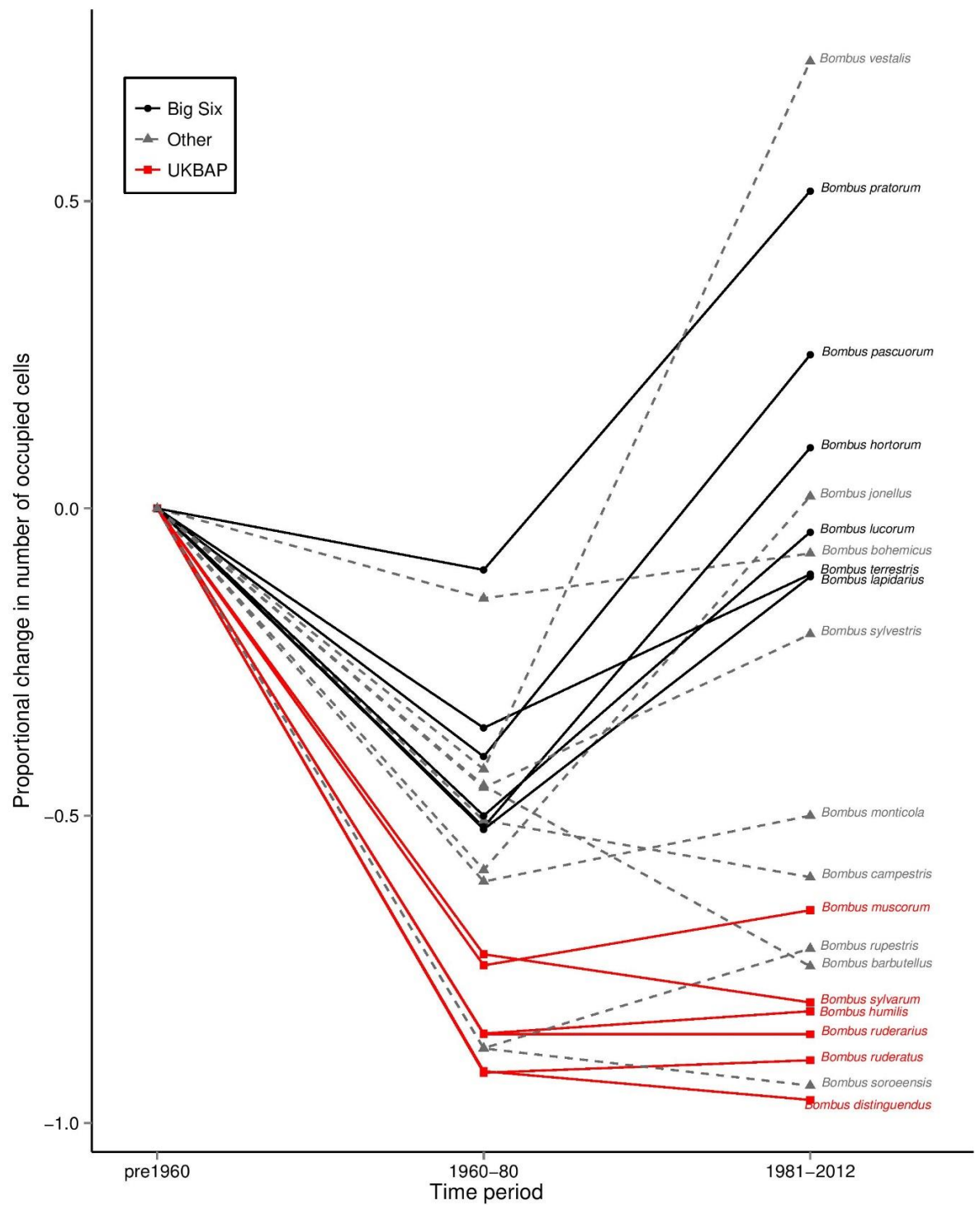
Fig. 4.2 Proportional change in the number of occupied cells within the pre-1960 survey region in the 1960-80 and the 1981-2012 time period for the "Big Six" species (solid black line), UKBAP species (red line) and other species (dotted grey line).

4.4.2 Niche dynamics

The degree of marginality differed significantly between species and time period (Table 4.1). Overall, UKBAP species are increasingly occupying areas that are different in terms of the environmental conditions to the average conditions within the study area. In the 1960-80 time period, unlike the other UKBAP species, *B. sylvarum* and *B. humilis* show a decrease in marginality, occupying conditions closer to the average of what is available in the study area, but by 1981-2012 all six species are increasing in marginality (Fig. 4.3). Other species showing a marked increase in marginality include *B. rupestris*, *B. vestalis*, *B. monticola*, *B. soroeensis* and *B. barbutellus* (Fig. 4.3).

There are contrasting trends of marginality among the more common species between pre1960 and 1960-80. In 1960-80, *B. terrestris* and *B. lapidarius* increase in marginality while *B. pratorum* and *B pascuorum* decrease and *B. hortorum* and *B. lucorum* remain relatively stable. By 1981-2012 *B. pratorum* and *B. pascuorum* are beginning to increase while *B. hortorum*, *B. lucorum* and *B. terrestris* decrease and *B. lapidarius* remains stable (Fig. 4.3). These variations in marginality trends across time periods are, however, less marked than those of UKBAP species.
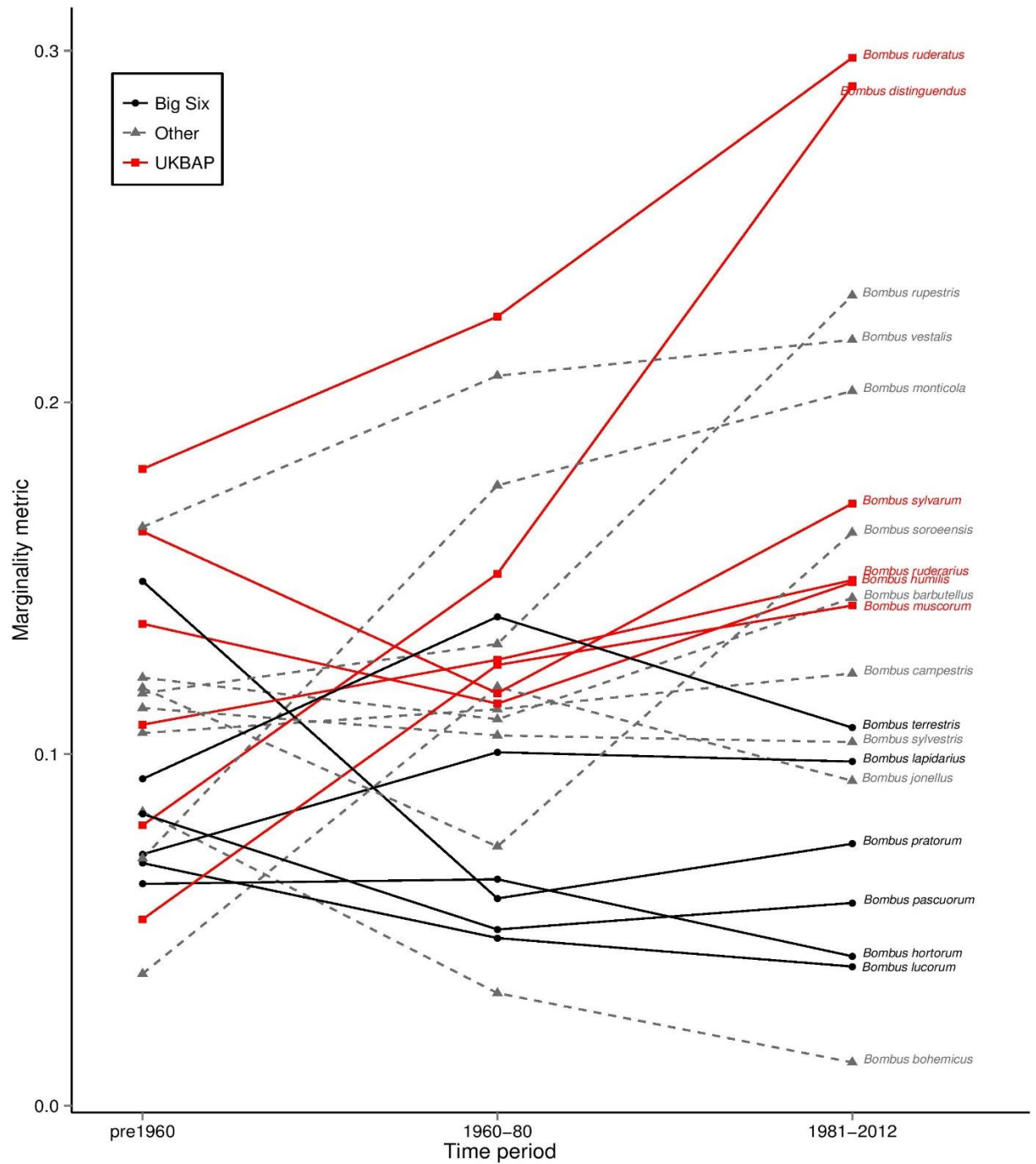
Fig 4.3 Marginality metric for time period 1 (pre1960), 2 (1960-80) and 3 (1981-12) for Big Six",
UKBAP species and other species.

4.4.3 Model results

Maxent species models had a good fit in general with most species producing average AUCs greater than 0.75, which is considered to be indicative of a useful model (Elith et al., 2006). However, two species, *B. muscorum* and *B. distinguendus* fell slightly below the acceptable values (*B. muscorum*: AUC=0.69; *B. distinguendus*: AUC=0.65) and therefore results should be interpreted with some caution.

A significant two-way interaction was found between time period and climatic suitability for seven species, and time period and distance to coast for four species (see Table S4.3 in Supplementary Material, Fig. 4.4). Five of the eleven species that have undergone a range contraction of >50% by 1981-2012 show a significant increase in occupation of areas with a higher predicted climatic suitability index in 1981-2012 compared with pre1960 (Table S4.3; Fig. 4.4). Three of these are UKBAP species (*B. humilis, B. ruderatus, B. sylvarum*) in addition to *B. soroeensis* and *B. rupestris*. *Bombus vestalis* and *B.campestris* occupy more areas of higher climatic suitability in 1960-80 compared with pre1960, but not in 1981-2012 (Table S4.3, Fig. 4.4).

UKBAP species, *B. muscorum,* shows a significant increase in the occupation of areas that are closer to the coast in 1981-2012 compared with pre1960, as does *B. soroeensis*, while *B. rupestris* occupies significantly more inland areas (Table S4.3, Fig. 4.4). *B. campestris* occupies areas significantly further away from to the coast in 1960-80 compared with pre1960 but not in 1981-2012 (Table S4.3, Fig. 4.4).

A significant three-way interaction was found between climatic suitability, distance to coast, and time period for two UKBAP species, *B. distinguendus* and *B. ruderarius*. While it is difficult to interpret these interactions, there are varying trends

over time, which may explain them. *Bombus distinguendus* appears to occupy areas further from the coast in the first two time periods, but strongly retracts to the coast by 1981-2012, while also moving to areas of increased climatic suitability (Fig. 4.4 and 4.5). However, in the final time period it also disappears from inland areas that have high climatic suitability (see S4.4a in Supplementary Material, but note these graphs represent raw data). In contrast, *Bombus ruderarius* appears to be moving inland to areas of high climatic suitability in the first two time periods, but in 1981-2012, while continuing to move inland it no longer shows a trend towards increasing climatic suitability (Figure 4.4 and 4.5), apparently moving to less climatically suitable inland areas and away from climatically suitable coastal areas. (see S4.4a).

(a)

absence
presence

Bombus humilis†
Bombus ruderatus†
Bombus rupestris
Bombus soroeensis
Bombus sylvarum†
Bombus vestalis
Bombus distinguendus†
Bombus ruderarius†

(b)

Bombus humilis†
Bombus muscorum†
Bombus rupestris
Bombus soroeensis
Bombus distinguendus†
Bombus ruderarius†
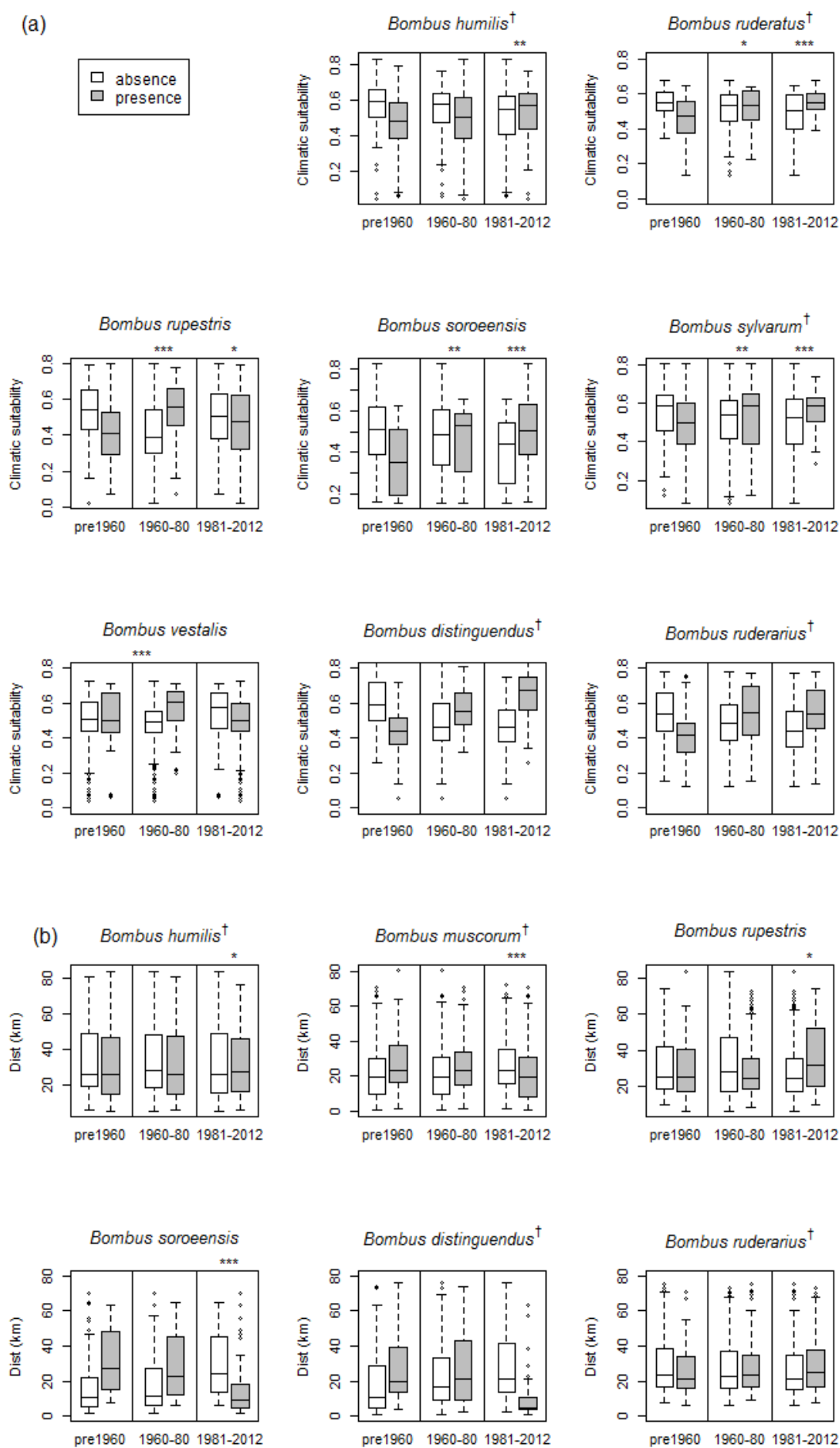
Fig. 4.4 Boxplots illustrating species presence/absence data over the three time periods which was found significant (p<0.05="*", p<0.01="**", p<0.001="***") in a two-way interaction between time period and (a) climatic suitability and (b) distance to coast, for unoccupied (white) and occupied (grey) 10km squares. [†] UK BAP species. *B. distinguendus* and *B. ruderarius* are also included to illustrate the trends for the species which were significant in a three-way interaction.
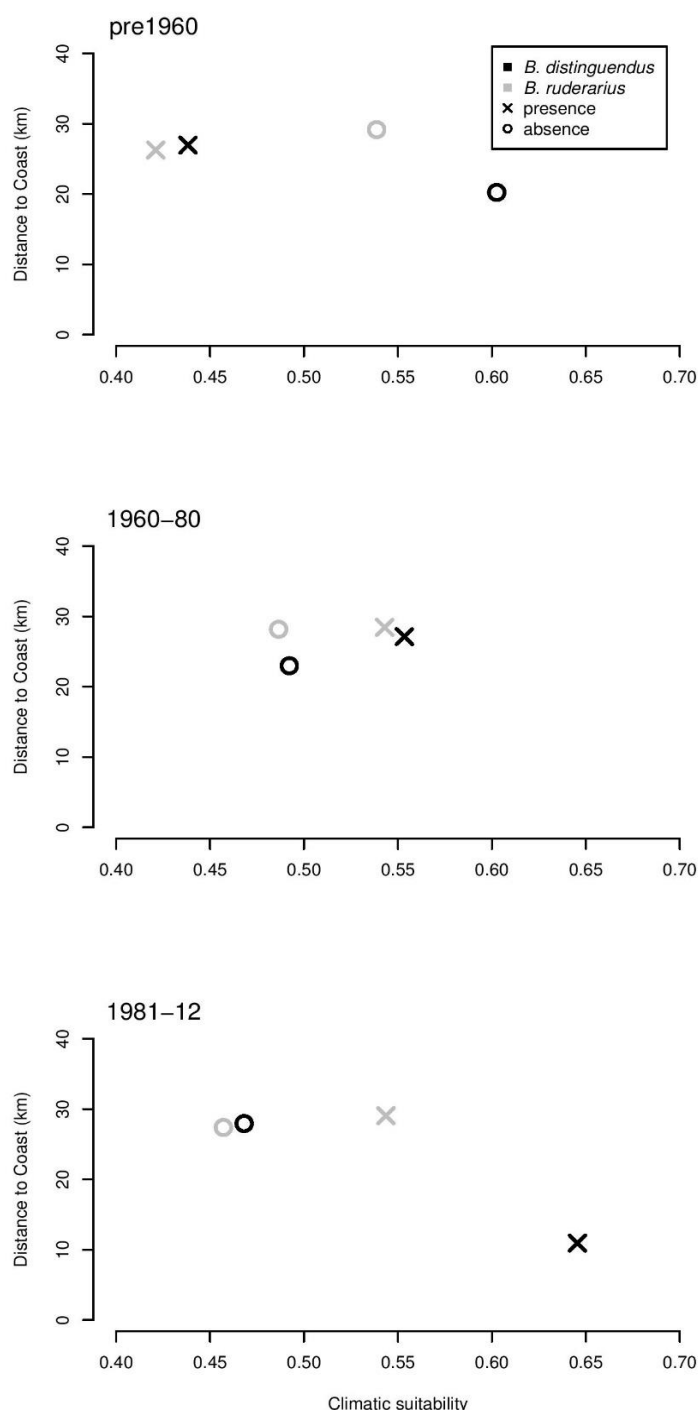
Fig. 4.5 Centroids of the distribution of occupied and unoccupied 10km squares illustrating the 3-way interaction between climatic suitability, distance to coast (km) and time on the distribution of *Bombus distinguendus* and *Bombus ruderarius*.

4.5 Discussion

We have demonstrated that UK and Irish bumblebee species have undergone serious declines, particularly in the period 1960-1980, supporting results from an earlier study in the UK (Williams, 1982). All UK bumblebee species show range contractions between 1960 and 1980, albeit to varying degrees. UKBAP species showed a more pronounced contraction supporting earlier studies by Williams (1982) who highlighted regional declines of social *Bombus* spp. (excluding *Psithyrus* spp.) in the UK within the same time period. He noted a relatively small decrease in the distribution of the "Big Six" species compared to others, with some UKBAP species (*B. ruderatus, B. sylvarum, B. humilis*) showing range contractions of ~50%, and over two thirds in the case of *B. distinguendus,* when compared to their pre-1960 distributions. A notable difference between our study and that of Williams (1982), however, is that we detected a decline of >50% in all UKBAP species and *B. soroeensis* in the 1960-80 time period whereas Williams estimated a decline of only ~26% for *B. soroeensis* and *B. muscorum* with *B. ruderarius* remaining relatively stable. Williams included all of the UK (but not Ireland) in his analysis whereas Scotland was largely excluded from our study area because there were few records from pre-1960 (Fig. 4.1) and so an increase in northern records for *B. muscorum* in 1960-80 was not accounted for with our methods. Williams' study was carried out at a coarser scale, over 113 vice counties, which may explain why *B. ruderarius* appeared to remain relatively stable despite a loss of records from areas in N. England and the south-west UK coastline. Also, in Ireland *B. ruderarius* was lost from much of the east and north of the country in this time period, which contributed to our overall finding of a marked range contraction. It is obvious from species records maps (see S4.4b in Supplementary

Material) that *B. soroeensis* contracted severely towards the west of the UK between 1960 and 1980 compared to pre1960. The magnitude of range contractions in *B. soroeensis* suggest that it should have been conferred BAP status.

Contractions in this time period are thought to be driven mainly by habitat loss due to agricultural intensification which occurred as a result of agricultural policy supporting a drive towards self-sufficiency in Britain that was introduced following WWI (Ollerton et al., 2014) with further intensification following WWII (Williams, 1986; Osborne and Corbet, 1994; Goulson, 2003; Goulson 2005; Goulson et al., 2008; Williams and Osborne, 2009, Ollerton et al., 2014). In Ireland, a change in agricultural practice from hay making to silage also resulted in a loss of hayflower meadows from the 1970s onwards and this is thought to be a major factor in the decline of late emerging species (*B. distinguendus*, *B. ruderarius*, *B. sylvarum* and *B. muscorum*).

Since this time, populations of most species appear to have stabilised or expanded. This recent period of stability and expansion for UK bumblebees conflicts with some other studies of decline in European pollinators, which show further reductions in species diversity and range contractions of a high proportion of species in recent years (Biesmeijer et al., 2006; van Swaay et al., 2006). However, a more recent study by Carvalheiro et al. (2013) indicates that declines in pollinator diversity in North West Europe have slowed down since 1990. When bumblebees of Great Britain were analysed separately, the authors found that, although declines have continued (particularly when measured at finer spatial scales of 10 and 20 km^2) they have become less accentuated. Biesmeijer et al., 2006 noted that bee species expanding their range in the UK after 1980 were disproportionately those species that were already common prior to this. We

report similar findings with the common widespread bumblebee species ("Big Six") showing clear expansions from 1981-2012 while the UKBAP species show little change. One of the other species, *B. barbutellus* appears to decline continually, however inspection of the raw data (see S4.4b) reveals that this is due to the fact that the majority of records of this species from 1960 onwards fall outside of the pre-1960 survey area.

Expansions of common species may be explained in part by increasing occupation of northern sites in species such as *B. terrestris* and *B. lapidarius*, possibly as a result of climate change. Bumblebees are primarily endothermic, generating heat from their flight muscles and regulating their body temperature at ~30-35°C during activity (Heinrich 1979). They are able to maintain a body temperature up to 30°C above the ambient temperature, and are thus able to fly in cold weather and thrive in cool climates, but conversely they are prone to overheating at higher temperatures (Heinrich, 1979). Species are known to differ in their climatic optimum, partly due to variation in fur length and body size and this may explain difference in range shifts between species (Peat and Goulson, 2005). Northwards expansion in response to climate change has been observed for many taxa in recent years (e.g. butterflies, Parmesan et al., 1999).

Expansion of common species and stabilisation of the ranges of the rare species may also be a result of increased conservation effort. Nature reserve protection and management has been more highly prioritised in the UK and Ireland in recent years with the introduction of European legislation under the EU Habitats Directive (Council Directive 92/43/EEC of 21 May 1992). EU member states are also now obliged to operate agri-environmental schemes under the Common Agricultural Policy and these schemes may have had a positive effect on bumblebee populations through the provision of

additional forage material (for example flower strips along field margins) and nesting sites (for example in tussocky grass strips and well-managed hedgerows). It is also possible that urban refuges are increasingly providing a stronghold for bumblebee populations. Urbanisation has increased in recent years and several studies have indicated that urban and suburban parks and gardens are supporting bumblebee populations (Goulson et al., 2002, Goulson et al., 2010, Osborne et al., 2008).

It is important to note, however, that apparent stabilisation and/or expansion of bumblebee species' ranges may be an artefact of more intensive sampling in recent years, despite analysing only areas for which at least one bumblebee had been recorded in the earliest time period. Awareness of bumblebee decline has increased in both the UK and Ireland which is likely to have led to a general increase in survey effort, particularly for rare species. A conservation report highlighting UK BAP priority species was published in 2007 (JNCC, 2007) at which time six Irish species were also considered critically endangered and this increased awareness of and search effort for these species among recorders. In addition, The Bumblebee Conservation Trust (BBCT) and BWARS have launched public surveys with a focus on the rare species, *B. distinguendus*, *B. sylvarum* and *B. monticola*. More intensive sampling in recent years may be masking further decline among the rarer species.

Changes in marginality over time (Fig. 4.3) are more variable than range changes between species and time periods. However, there is an overall trend towards an increase in marginality by UKBAP species, particularly in recent years, while the more common "Big Six" species remain relatively stable. This indicates that, although common species appear to be expanding in range, they continue to occupy similar climatic

conditions to those occupied during their period of decline prior to 1980. This may be due to the fact that environmentally similar areas, previously unoccupied, have recently become more favourable in other ways. For example, an unoccupied area may have suitable environmental conditions, similar to those occupied, but remain unsuitable overall due to intensive agricultural practices so that a change in land-use, such as the introduction of an agri-environment scheme that provides favourable forage and nesting sites, may attract individuals through the additive effect of both suitable environmental and land-use conditions. Occupation of these new environmentally similar areas could lead to a species range expansion without increasing its marginality.

Rare species, on the other hand, appear to be occupying areas that differ on average in terms of their environmental conditions to those occupied previously, with some species increasing in marginality consistently across all time periods and others increasing only in the most recent period. Higher marginality in these species in recent years indicates that, unlike the more common species, their realised environmental niche is shifting. It is unlikely that rare species are now occupying areas where they have not previously existed, and we suspect that this increasing marginality may be an artefact of the recent, targeted survey efforts, which have led to an increase in records of rare species in remote areas in recent years. For example, the Bumblebee Conservation Trust and Highland Biological Recording Group have recently led targeted searches for *B. distinguendus* along the North coast of Scotland and in the Outer Hebrides, areas that are marginal in terms of their climatic conditions in the UK. It is also possible that increased conservation effort in these areas has led to population increase and expansion.

Maxent model results show that all UKBAP species apart from *B. muscorum* have contracted to areas that are predicted to be more suitable in terms of their environmental conditions (Fig. 4.4-4.5). This supports the theory that species retreat to their climatic optimum as they decline and that climate, along with habitat degradation and changes in land use, may be influencing patterns of decline in the bumblebees of Britain and Ireland (Williams et al., 2007). In addition, our analyses support earlier studies by Williams (1988) which suggest that some rare species (*B. muscorum* and *B. distinguendus*) have retreated towards coastal areas. These areas tend to be less affected by agricultural intensification with habitats such as machair, steep sea cliffs, salt marshes and sand dunes providing valuable floral resources and nesting sites (Williams, 1988). Models reveal an interactive effect of proximity to coastal habitat and climate suitability on the pattern of range contraction of *B. distinguendus* and *B. ruderarius*, supporting the idea, proposed by Williams et al. (2007), that the interaction between climate and food-plant preferences and availability is the primary influence on patterns of decline in UK bumblebee species.

Overall, our results show significant differences in patterns of range change between rare and common bumblebee species. Common bumblebee species appear to have expanded in recent years while rare species have generally remained stable. However, caution is necessary in interpreting these results as changes in the intensity and distribution of survey effort over time could obscure patterns of population change. In addition, while it was not addressed in the current study, it is important to consider that climate change may also influence bumblebee range shifts. The evidence that several rare species are contracting to their climatic optimum, occupying more marginal sites,

and moving towards coastal areas demonstrates that their populations are not stable,

and emphasizes the need for continued careful monitoring of their status.

4.6 Supplementary Material

S4.1 Pearson-product correlation matrix of bioclimatic variables* for UK and Ireland, calculated using monthly data for Mar-Oct, along with altitude and slope.

	Bio1	Bio2	Bio3	Bio4	Bio5	Bio6	Bio7	Bio12	Bio13	Bio14	Bio15	altitude	slope
Bio1	1.00	0.34	0.09	0.15	0.89	0.86	0.34	-0.63	-0.68	-0.63	-0.48	-0.73	-0.53
Bio2	0.34	1.00	0.50	0.41	0.66	-0.04	0.80	-0.56	-0.53	-0.56	-0.71	-0.14	-0.28
Bio3	0.09	0.50	1.00	-0.56	0.05	0.21	-0.12	-0.16	-0.10	-0.26	-0.16	-0.28	-0.24
Bio4	0.15	0.41	-0.56	1.00	0.51	-0.33	0.86	-0.30	-0.32	-0.19	-0.46	0.23	0.05
Bio5	0.89	0.66	0.05	0.51	1.00	0.54	0.73	-0.73	-0.77	-0.69	-0.70	-0.55	-0.46
Bio6	0.86	-0.04	0.21	-0.33	0.54	1.00	-0.18	-0.40	-0.45	-0.43	-0.15	-0.83	-0.48
Bio7	0.34	0.80	-0.12	0.86	0.73	-0.18	1.00	-0.53	-0.53	-0.45	-0.70	0.04	-0.15
Bio12	-0.63	-0.56	-0.16	-0.30	-0.73	-0.40	-0.53	1.00	0.97	0.98	0.78	0.56	0.56
Bio13	-0.68	-0.53	-0.10	-0.32	-0.77	-0.45	-0.53	0.97	1.00	0.91	0.74	0.53	0.53
Bio14	-0.63	-0.56	-0.26	-0.19	-0.69	-0.43	-0.45	0.98	0.91	1.00	0.75	0.61	0.60
Bio15	-0.48	-0.71	-0.16	-0.46	-0.70	-0.15	-0.70	0.78	0.74	0.75	1.00	0.19	0.36
altitude	-0.73	-0.14	-0.28	0.23	-0.55	-0.83	0.04	0.56	0.53	0.61	0.19	1.00	0.58
slope	-0.53	-0.28	-0.24	0.05	-0.46	-0.48	-0.15	0.56	0.53	0.60	0.36	0.58	1.00

* Bio1 = Annual Mean Temperature
Bio2 = Mean Diurnal Range (Mean of monthly (max temp - min temp))
Bio3 = Isothermality (BIO2/BIO7) (* 100)
Bio4 = Temperature Seasonality (standard deviation *100)
Bio5 = Max Temperature of Warmest Month
Bio6 = Min Temperature of Coldest Month
Bio7 = Temperature Annual Range (BIO5-BIO6)
Bio12 = Annual Precipitation
Bio13 = Precipitation of Wettest Month
Bio14 = Precipitation of Driest Month
Bio15 = Precipitation Seasonality (Coefficient of Variation)

S4.2 Number of records per species modelled for each time period, following the removal of spatial autocorrelation. The total number of records for each species was used to predict climatic suitability models in Maxent.

Species	Time period			Total
	Pre1960	*1960-80*	*1981-12*	
B. barbutellus	51	114	93	258
B. campestris	65	120	161	346
B. distinguendus	107	50	46	203
B. humilis	224	149	600	973
B. monticola	28	59	135	222
B. muscorum	78	85	212	375
B. ruderarius	90	79	151	320
B. ruderatus	49	19	47	115
B. rupestris	74	43	144	261
B. soroeensis	33	23	85	141
B. sylvarum	99	64	48	211
B. vestalis	33	310	410	753

S4.3 Minimal model summary for each species where presence/absence per 10km square in the UK is fitted as the response variable in a linear mixed effects model. Climatic suitability (C), distance to coast (D) and time period (T1: pre1960, T2: 1960-80 and T3: 1981-12) are fitted as fixed factors and 10km square ID is considered a random factor. The number of recorders per 10km square for each time period was also fitted as a random factor to account for possible variation in recorder effort.

Species	Fixed effects					
	Estimate	S. E	z-value	P	AIC	Log-Liklihood
B. barbutellus						
T2	1.1	0.235	4.723	2.32e-6*	792.3	-391.1
T3	0.391	0.238	1.642	0.1006		
B. campestris						
T2	-9.019	2.154	-4.186	2.84e-5*	664.7	-318.4
T3	2.517	1.629	1.55	0.122		
C	-0.538	2.234	-0.241	0.81		
D	-1.522	3.569	-0.427	0.669		
T2:C	17.369	4.354	3.99	6.62e-5*		
T3:C	-2.634	3.09	-0.853	0.394		
T2:D	19.728	6.909	2.855	0.004		
T3:D	-3.404	4.99	-0.682	0.495		
C:D	2.53	6.41	0.395	0.693		
T2:C:D	-34.477	13.650	-2.526	0.12		
T3:C:D	7.398	9.112	0.812	0.417		
B. distinguendus						
T2	-10.954	1.944	-5.634	1.76e-8*	539.47	-255.73
T3	-15.637	2.370	-6.597	4.19e-11*		
C	-14.227	2.816	-5.052	4.38e-7*		

D	-8.003	4.027	-1.988	0.047*		
T2:C	17.626	3.416	5.160	2.47e-7*		
T3:C	27.857	4.092	6.808	9.93e-12*		
T2:D	8.361	5.443	1.536	0.125		
T3:D	19.322	7.866	2.457	0.014*		
C:D	15.550	7.524	2.067	0.039*		
T2:C:D	-13.453	10.066	-1.336	0.181		
T3:C:D	-47.602	15.375	-3.096	0.002*		
B. humilis						
T2	1.035	1.756	0.589	0.556	703.71	-337.85
T3	-5.493	1.679	-3.271	0.001*		
C	-5.701	2.355	-2.421	0.016*		
D	-2.921	3.013	-0.969	0.332		
T2:C	-2.714	3.301	-0.822	0.411		
T3:C	9.457	3.139	3.013	0.003*		
T2:D	-5.932	4.345	-1.365	0.172		
T3:D	7.810	4.160	1.877	0.061		
C:D	4.890	5.524	0.885	0.376		
T2:C:D	12.010	7.905	1.519	0.129		
T3:C:D	-13.831	7.580	-1.825	0.068		
B. monticola						
T2	0.285	0.486	0.587	0.557	664.74	-323.37
T3	2.815	0.478	5.889	3.89e-9*		
C	0.88	0.706	1.25	0.213		
D	0.193	1.166	0.165	0.869		

T2:D	2.168	1.463	1.482	0.138		
T3:D	-1.617	1.445	-1.119	0.263		
B. muscorum						
T2	-0.17	0.348	-0.487	0.626	1130.75	-557.37
T3	2.044	0.328	6.218	5.02e-10*		
D	1.359	0.73	1.861	0.06274		
T2:D	-0.151	1.031	-0.147	0.883		
T3:D	-2.973	0.980	-3.032	0.002*		
B. ruderarius						
T2	-6.583	1.501	-4.385	1.16e-5*	925.62	-448.81
T3	-9.192	1.437	-6.394	1.61e-10*		
C	-9.252	2.147	-4.310	1.64e-5*		
D	-7.010	2.913	-2.406	0.016*		
T2:C	11.939	2.937	4.065	4.79e-5*		
T3:C	17.640	2.867	6.152	7.64e-10*		
T2:D	9.332	4.26	2.191	0.029		
T3:D	15.515	3.964	3.914	9.06e-5*		
C:D	12.75	5.687	2.242	0.025		
T2:C:D	-16.950	7.999	-2.119	0.034		
T3:C:D	-28.158	7.590	-3.710	<0.001*		
B. ruderatus						
T2	-5.417	1.662	-3.259	0.001*	381.02	-182.51
T3	-7.361	1.635	-4.502	6.74e-6*		
C	-7.195	2.173	-3.311	0.001		
T2:C	7.661	3.185	2.406	0.016		

T3:C	13.939	3.108	4.485	7.29e-6		
B. rupestris						
T2	-2.7	0.746	-3.619	2.96e-4*	780.86	-385.43
T3	-3.121	0.813	-3.841	1.23e-4*		
C	-4.056	0.924	-4.389	1.14e-5*		
D	-0.668	0.834	-0.801	0.423		
T2:C	8.412	1.292	6.514	7.33e-11*		
T3:C	3.21	1.369	2.345	0.019*		
T2:D	-0.238	1.131	-0.210	0.834		
T3:D	2.652	1.208	2.197	0.028*		
B. soroeensis						
T2	-2.658	1.107	-2.401	0.016*	379.32	-178.66
T3	-0.015	0.991	-0.015	0.988		
C	-4.948	1.616	-3.062	0.002*		
D	3.863	1.286	3.004	0.003*		
T2:C	5.518	2.216	2.49	0.013*		
T3:C	8.258	2.117	3.9	9.61e-5*		
T2:D	-1.157	1.768	-0.654	0.513		
T3:D	-9.429	1.754	-5.376	7.62e-8*		
B. sylvarum						
T2	-2.941	0.816	-3.602	3.15e-4*	717.74	-350.87
T3	-4.511	0.931	-4.845	1.26e-6*		
C	-3.144	1.064	-2.955	0.003*		
T2:C	4.085	1.513	2.7	0.007*		
T3:C	6.019	1.677	3.589	3.32e-4*		
B. vestalis						
T2	-1.924	0.989	-1.946	0.05*	977.72	-480.86
T3	4.232	0.977	4.332	1.48e-5*		
C	-0.288	1.501	-0.192	0.847		

T2:C	6.609	1.863	3.547	3.89e-04*
T3:C	-1.257	1.856	-0.677	0.498

S4.4a-b Climatic suitability maps predicted by Maxent models with raw presence data for each bumblebee species that showed a decline in range or increase in marginality of >50% between the pre1960 and 1981-2012 time periods.

(a) UKBAP species

Bombus distinguendus
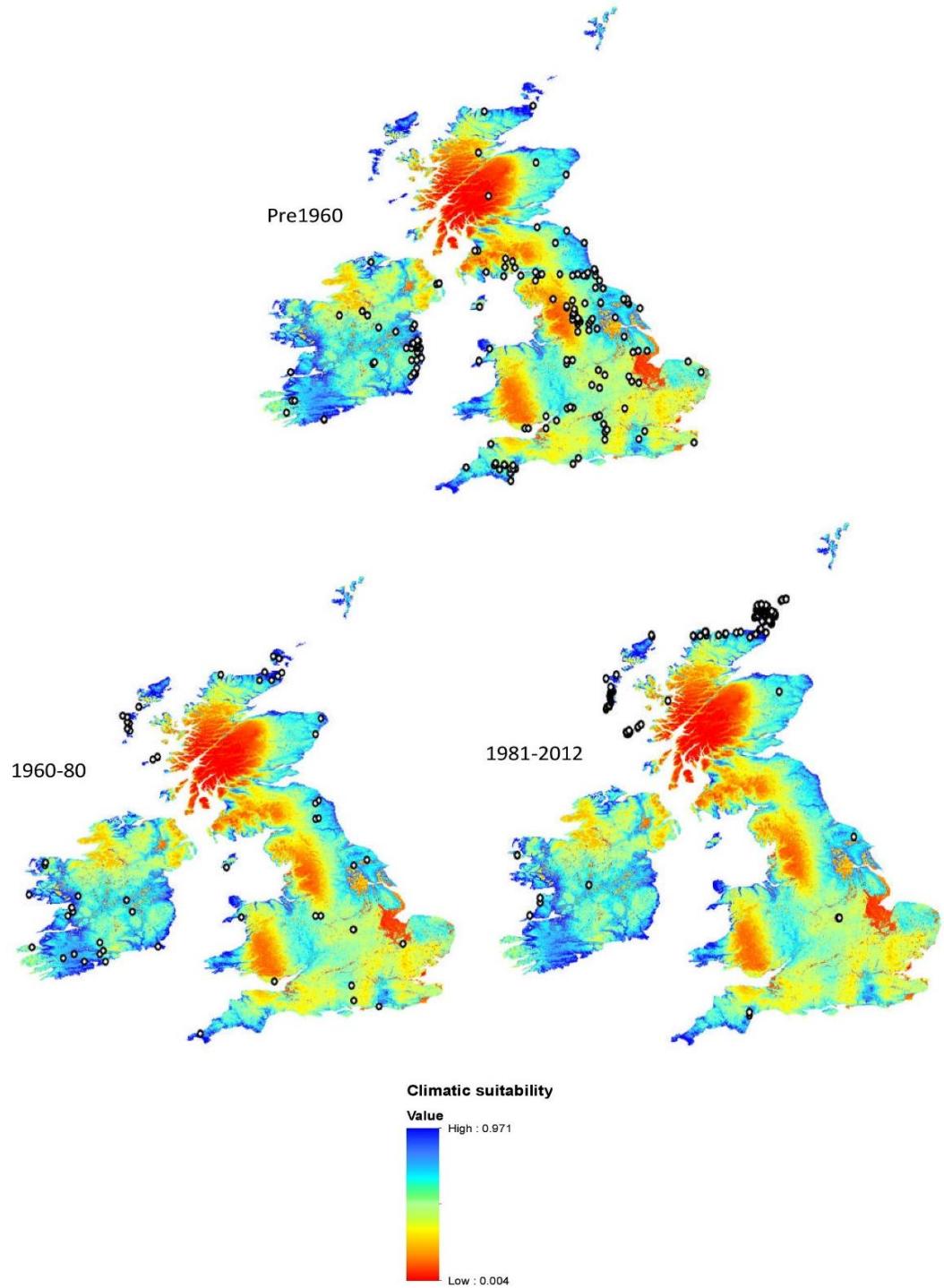
Pre1960

1960-80

1981-2012

Climatic suitability

Value

High : 0.971

Low : 0.004

Bombus humilis

Pre1960

1960-80

1981-2012

Climatic suitability

Value

High : 0.888

Low : 7.6e-006

Bombus muscorum

Pre1960

1960-80

1981-2012

Climatic suitability

Value

High : 0.989

Low : 0.001

Bombus ruderarius

Pre1960

1960-80

1981-2012

Climatic suitability

Value

High : 0.989

Low : 2.09e-005

Bombus ruderatus

Pre1960

1960-80

1981-2012

Climatic suitability

Value

High : 0.851

Low : 3.01e-008

Bombus sylvarum

Pre1960

1960-80

1981-2012

Climatic suitability

Value

High : 0.899

Low : 8.56e-005
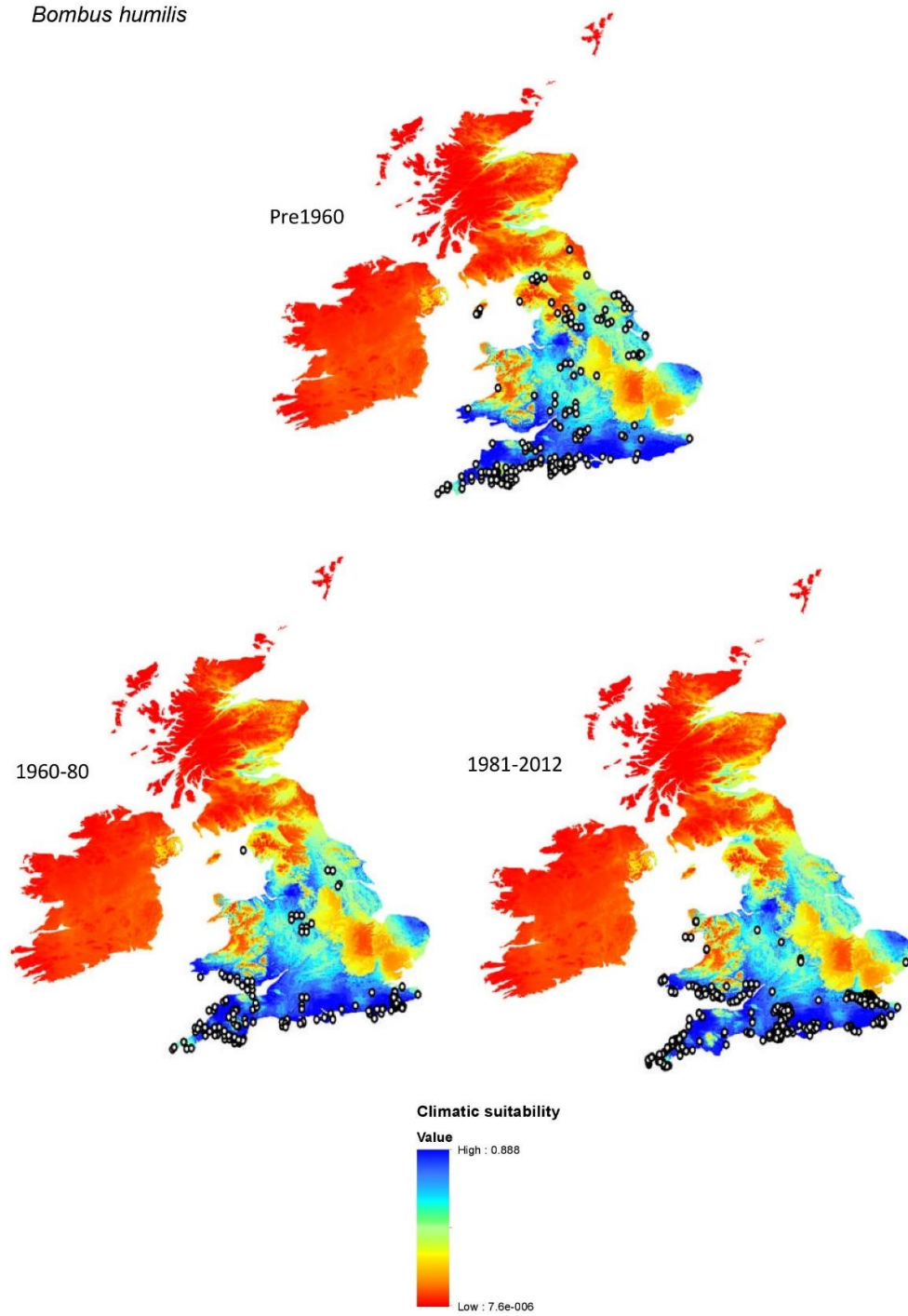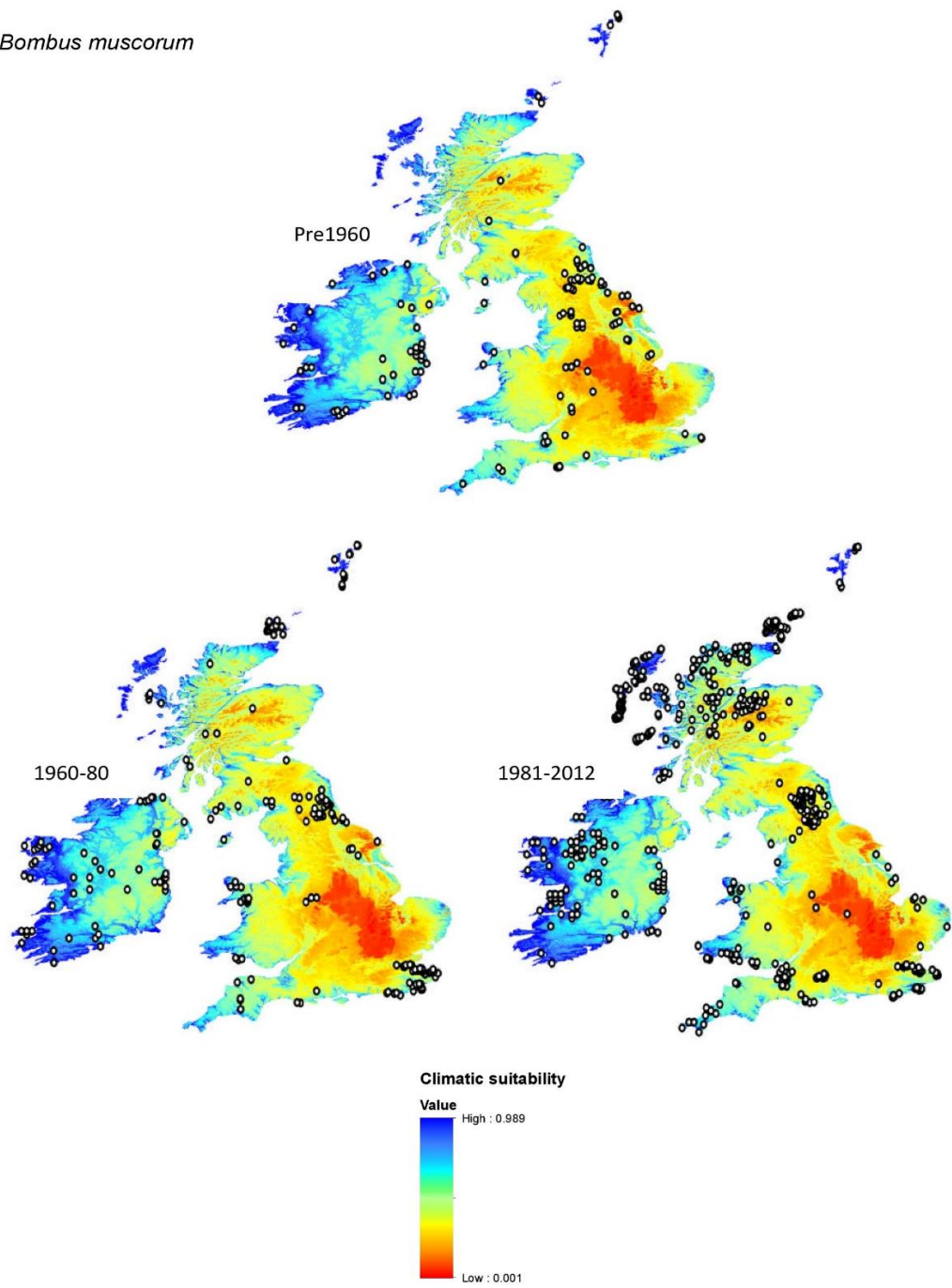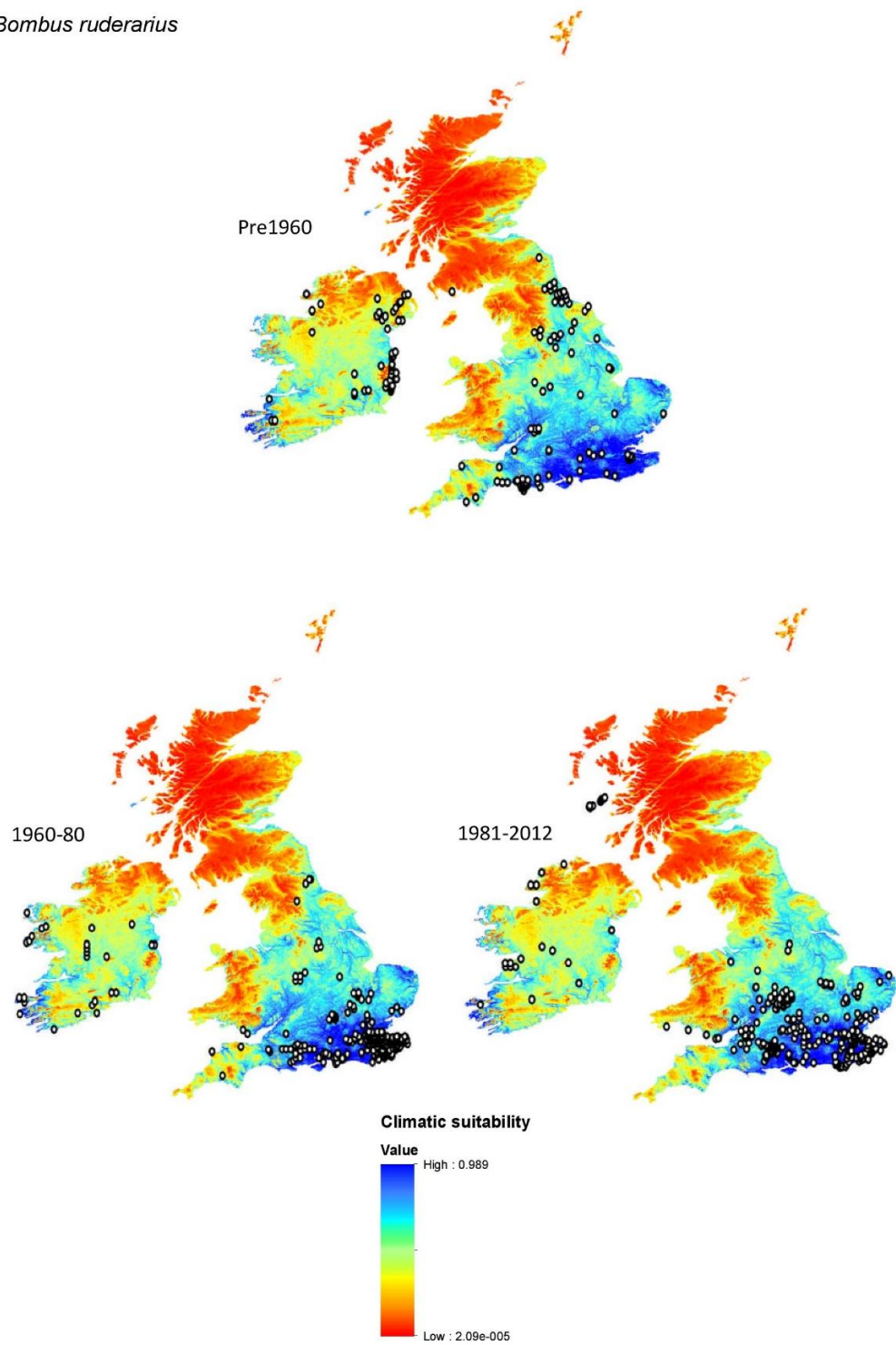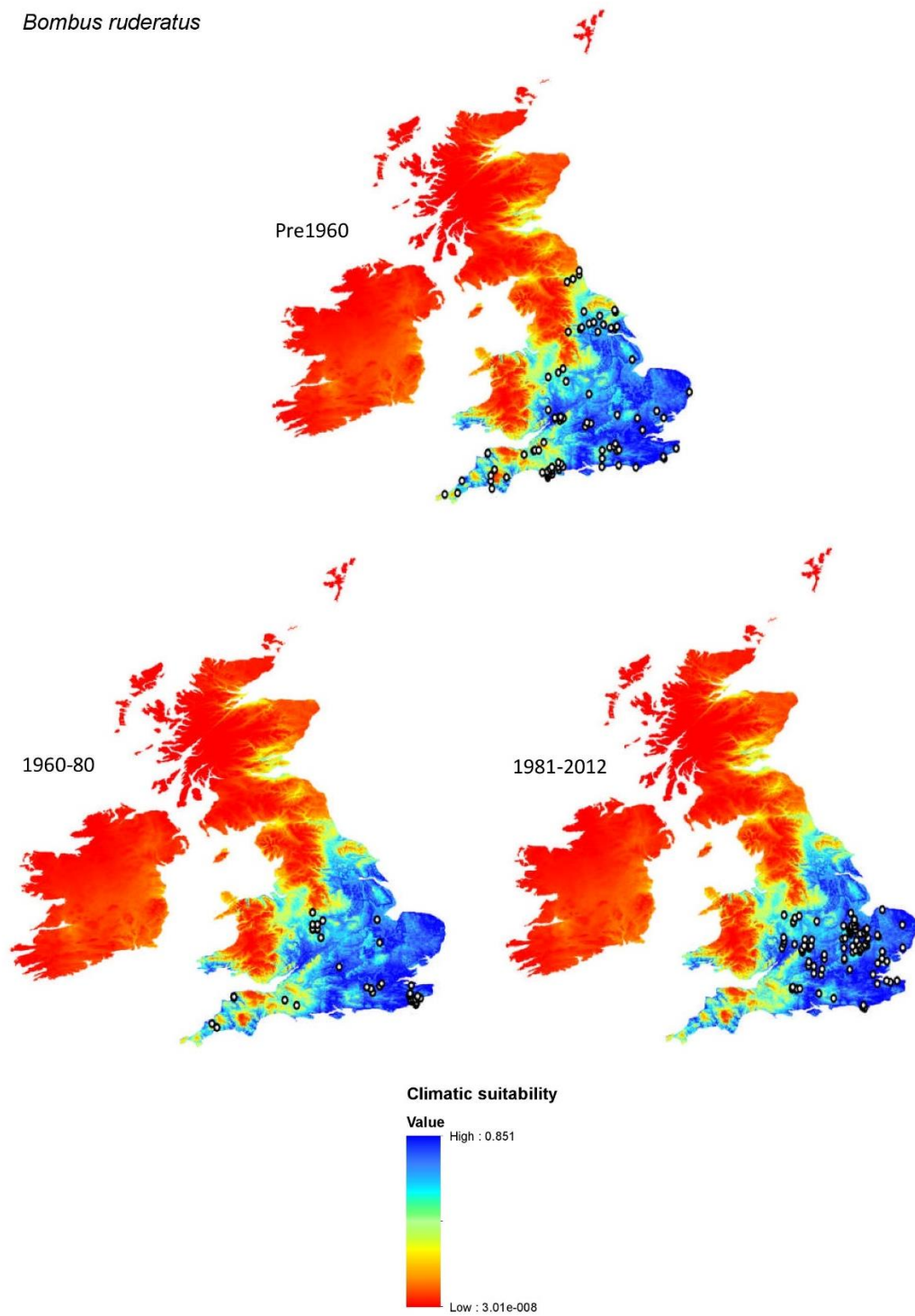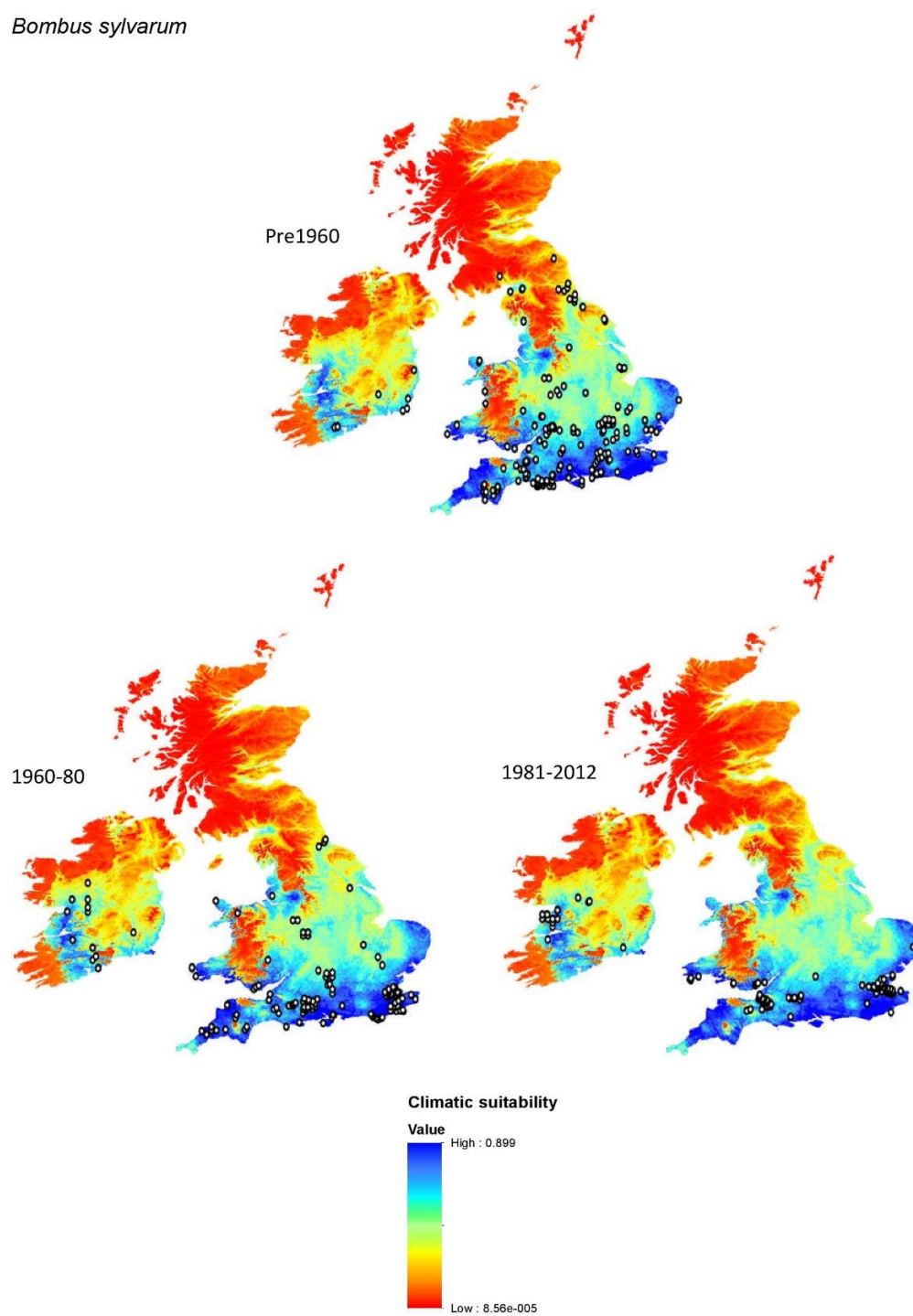
(b) Other species

Bombus barbutellus
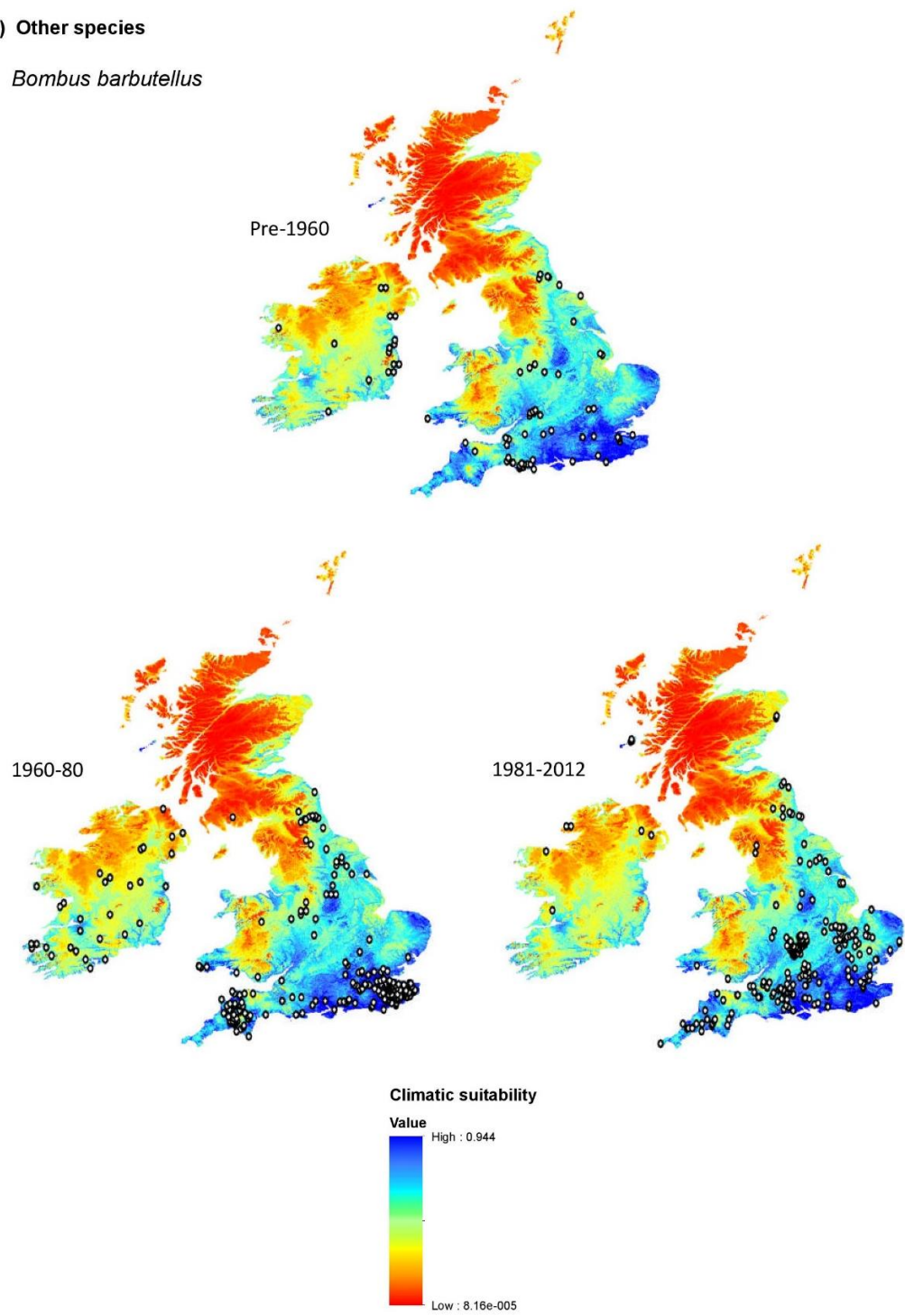
Pre-1960

1960-80

1981-2012

Climatic suitability

Value

High : 0.944

Low : 8.16e-005

Bombus campestris

Pre1960

1960-80

1981-2012

Climatic suitability

Value

High : 0.869

Low : 5.92e-4

Bombus monticola

Pre1960

1960-80

1981-2012

Climatic suitability

Value

High : 0.914

Low : 9.99e-4

Bombus rupestris

Pre1960

1960-80

1981-2012

Climatic suitability

Value

High : 0.947

Low : 4.07e-005

98

Bombus soroeensis

Pre1960

1960-80

1981-2012

Climatic suitability

Value

High : 0.972

Low : 0.002

Bombus vestalis

Pre1960

1960-80

1981-2012

Climatic suitability

Value

High : 0.862

Low : 4.93e-006
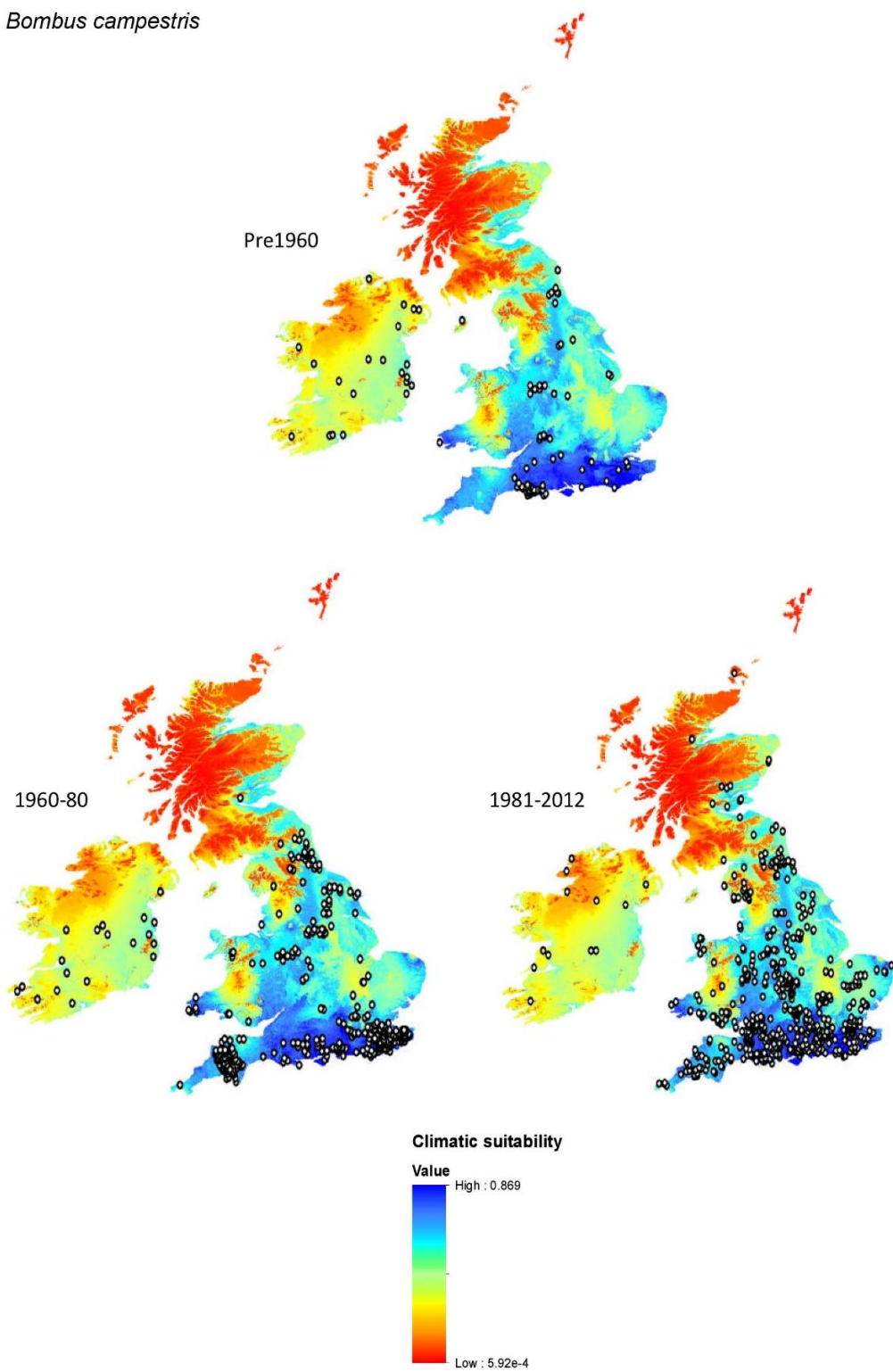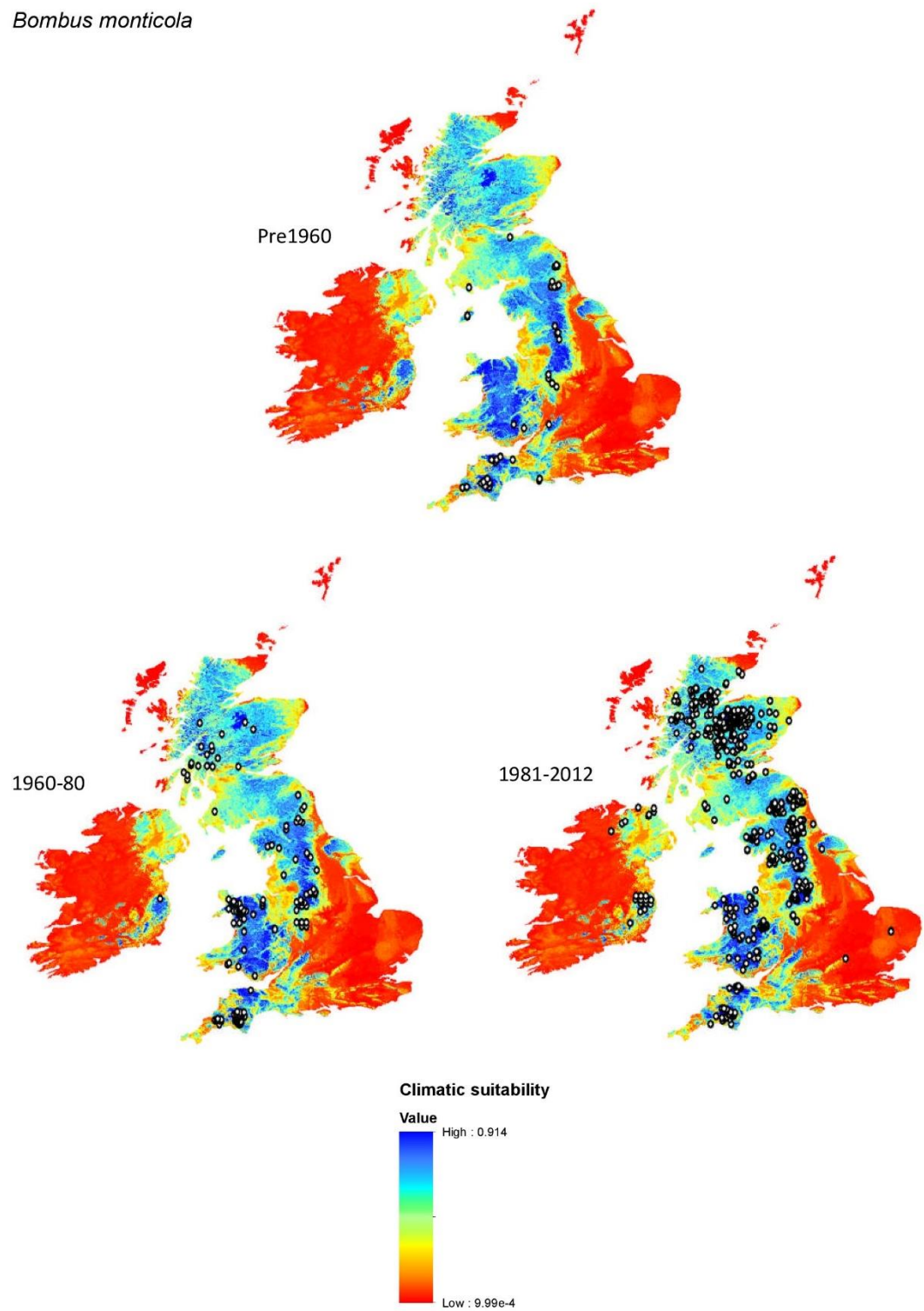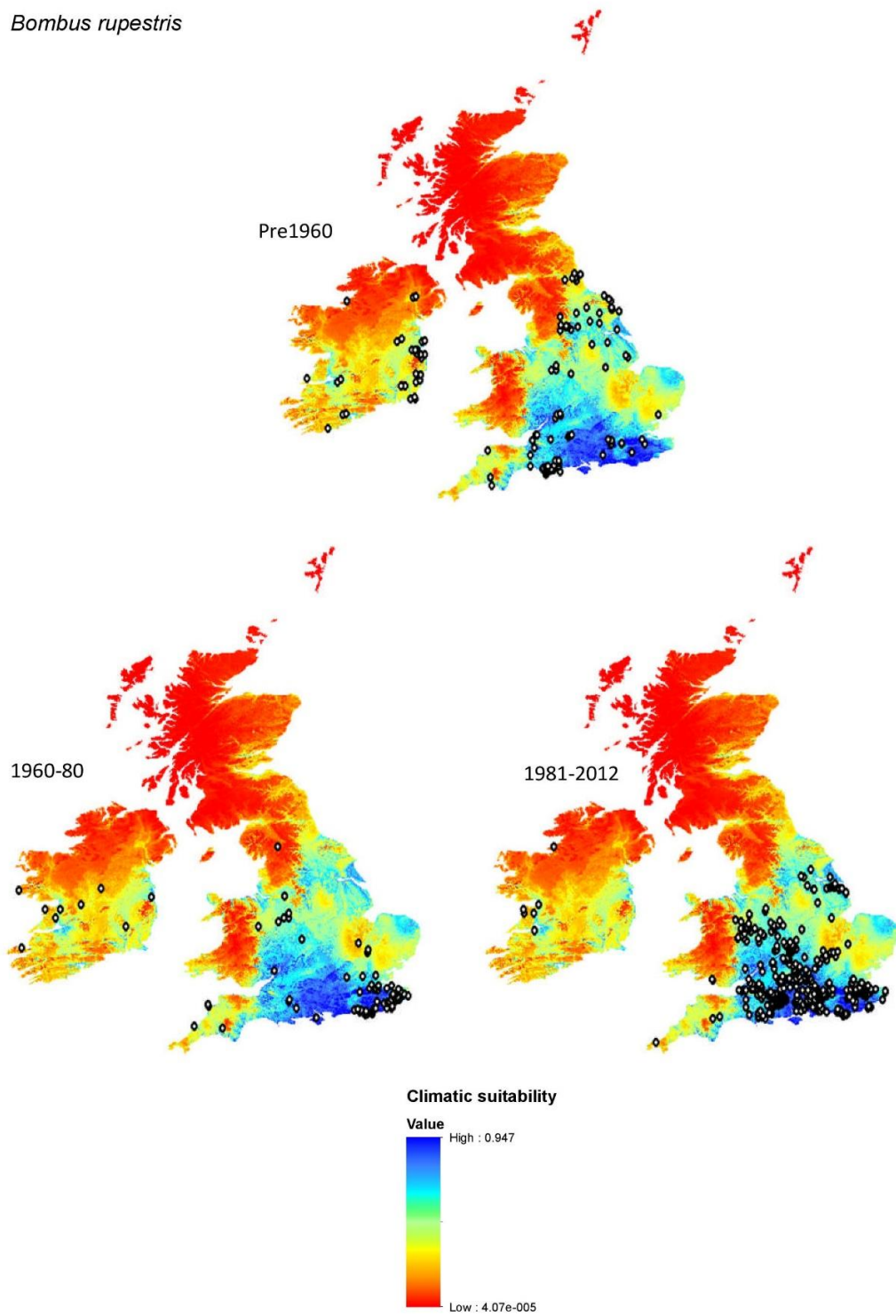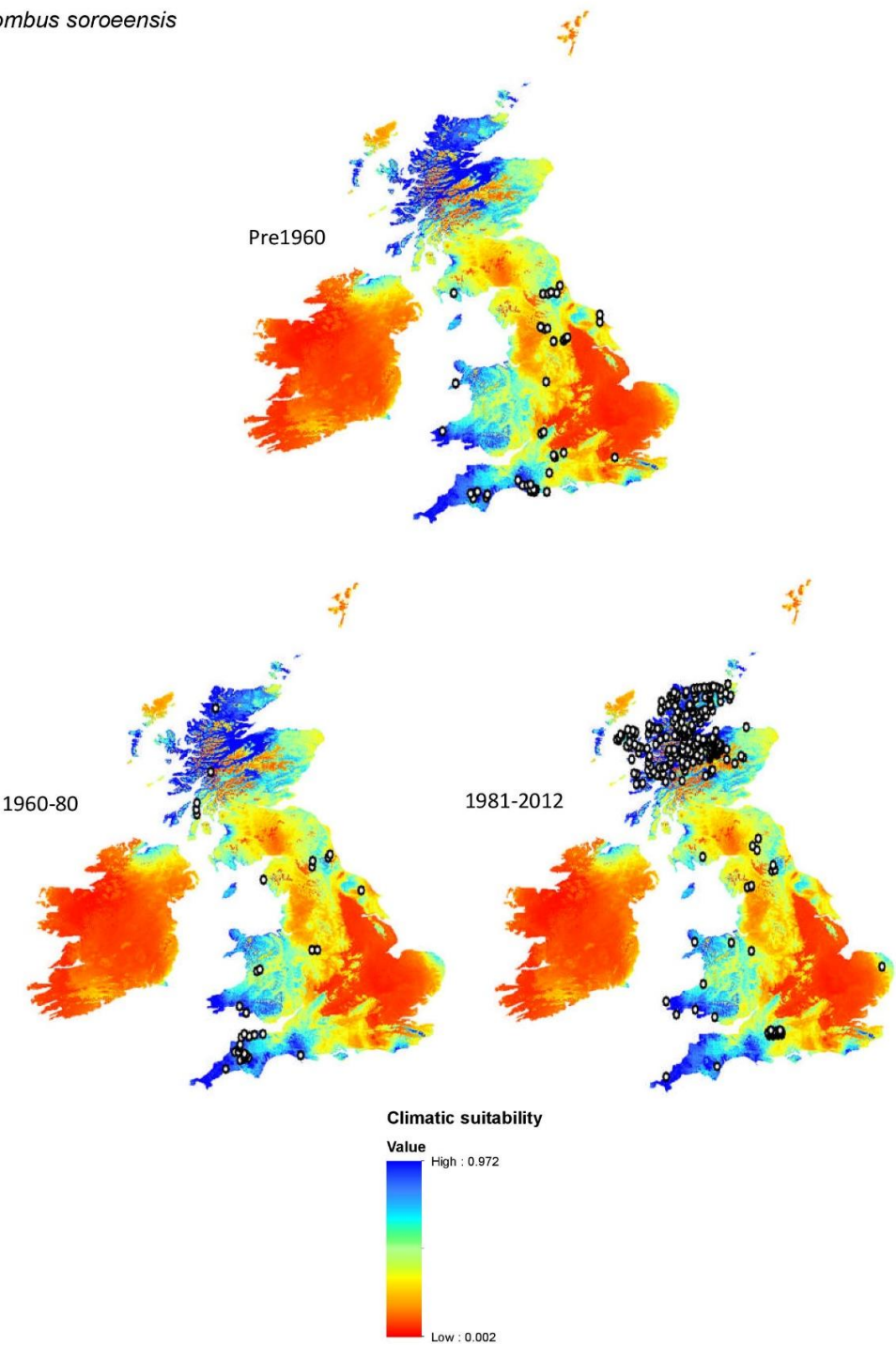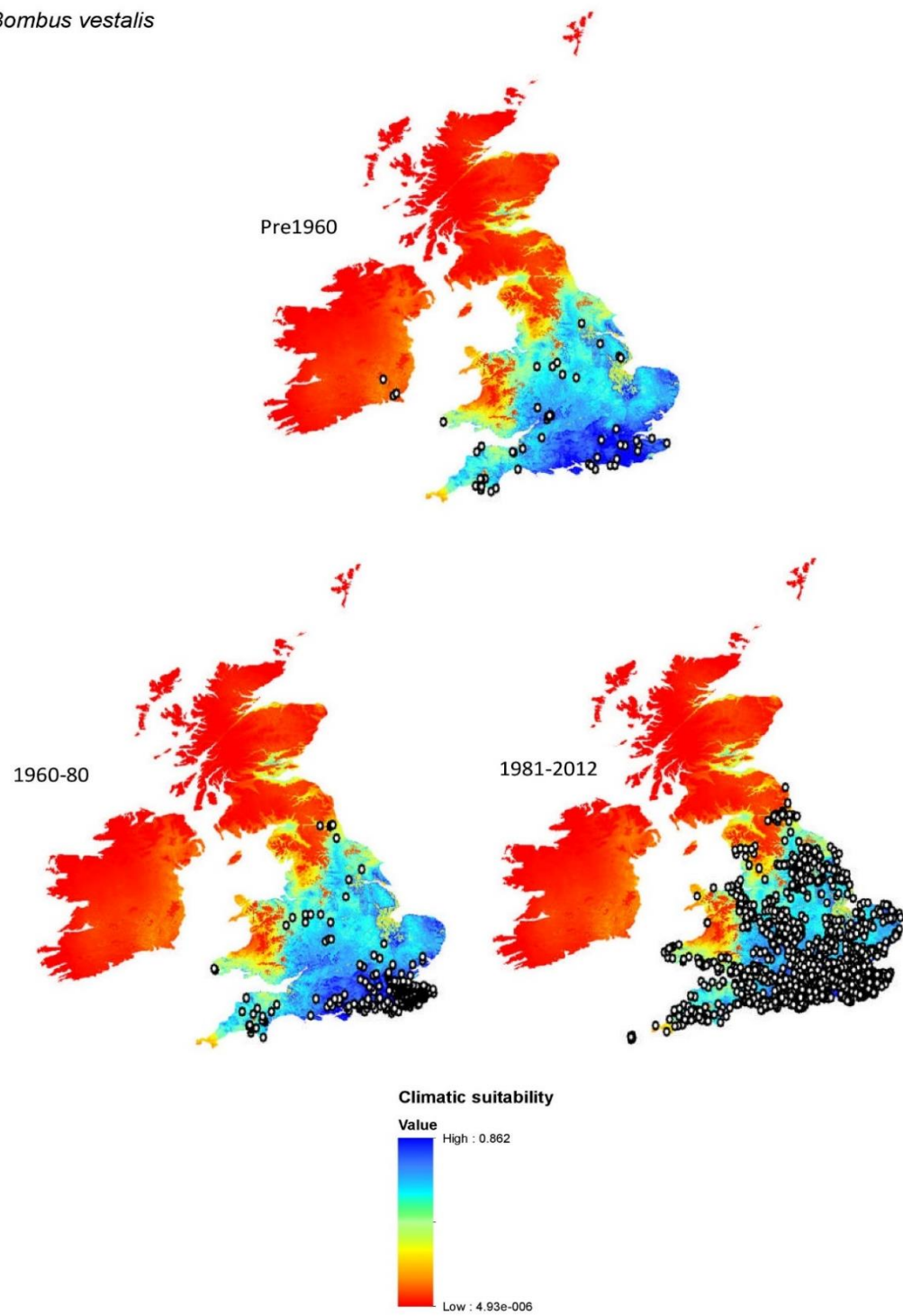
Chapter 5

CITIZEN SCIENTIST RECORDING OF BUMBLEBEES IN GARDENS REVEALS POPULATION CHANGE, RANGE SHIFTS AND LOCAL FACTORS AFFECTING ABUNDANCE.

5.1 Abstract

Rapid urbanisation is leading to dramatic changes in biotic communities. Garden habitats, which comprise a large component of urban green space, are considered an important ecological refuge for many species. Here, volunteer-collected data is used to investigate how garden habitats and the surrounding landscape influence the occurrence and abundance of common UK bumblebee species. Data on the numbers of different bumblebee species present in their gardens were collected by 1,804 volunteers over an 8 year period as part of the British Trust for Ornithology's "Garden Birdwatch" scheme. Findings show that bumblebee species differ in their spatio-temporal trends and vary in response to both garden habitats and features of the surrounding landscape. Populations of three of the common species/groups, *B. lapidarius*, *B. pratorum* and *B. hypnorum,* appear to be increasing over time whereas the others, *B. hortorum*, *B. terrestris/lucorum* and *B. pascuorum,* were found to be declining. Wild habitat, flowerbeds, vegetable plots and berry plants were identified as the most beneficial within-garden habitats, while parkland and marsh habitats in the surrounding landscape positively affected the occurrence and abundance of garden visitors. In addition, nearby coastal habitat was associated with higher numbers of most species. Overall, the majority of species are positively associated with urban and suburban gardens, however, long-tongued bumblebees such as *B. pascuorum* and *B. hortorum* (a group that have declined in abundance over time) are positively associated with rural gardens, giving rise

to concern that as urbanisation spreads, these long-tongued bumblebees may decline further, with potential negative consequences for pollination of deep-flowered plants. These findings have implications for urban ecology management, particularly with regard to pollinator species, and highlight the value of citizen science projects in collecting scientific information.

5.2 Introduction

Insect pollination is critical for maintaining ecosystems, biodiversity and crop production. Wild bees and other pollinators, integral to providing these services, are currently in decline with some species undergoing population crashes and several becoming extinct in recent years (Williams, 1982; Goulson et al., 2008, 2015; Potts et al., 2010; Ollerton et al., 2014). There is widespread concern that we may face a "pollination crisis" with potentially catastrophic knock on effects on ecosystem function and services. Evidence suggests that bee populations are declining in response to habitat degradation, agricultural intensification, pesticide use, parasites and pathogens (Goulson, 2003; Goulson 2015). Monitoring of populations is crucial to understanding the relative significance of these stressors and to enable us to develop strategies to protect against future losses.

Bumblebees are particularly efficient pollinators of some crops and wildflowers and also act as a flagship for insect conservation due to their popularity, visibility and charismatic nature (Goulson et al., 2011). This makes them particularly suited to citizen science monitoring programmes, which combine ecological research with public engagement and environmental education (Dickinson, 2012; Silvertown, 2009). Scientific benefits of these monitoring programs include species and habitat data collection at a scale that

would otherwise be impossible, and hence volunteer-collected data is increasingly being used to answer important ecological questions (Dickinson et al., 2012; Zipkin et al., 2012; Branchini et al., 2015, Osawa, 2015). They also provide a forum for participants to connect with the natural world, which has been shown to have positive effects on human health and wellbeing as well as fostering support for the preservation of biodiversity within communities (Miller, 1995).

More people are living in urban areas following unprecedented urban growth during the latter half of the 20th century. Over half of the world's population now live in urban areas and this proportion is expected to continue to rise steadily, reaching two thirds by 2050 with an additional 2.5 billion urban dwellers (United Nations, 2014). Urbanisation is now considered one of the main drivers of ecological change with rapid land development leading to habitat alterations that affect the composition of biotic communities both within urban areas and in the surrounding landscape (McKinney, 2006; Grimm et al., 2008; Maxwell et al., 2016). Urban ecology studies involving volunteer-collected data are well-placed to quantify the effects of urban expansion on biodiversity (McKinney, 2002; Dickinson et al., 2012). Most studies reveal an overall homogenisation of biotic communities within urban environments as urban adapted species become more widespread and numerous (McKinney, 2006). There is a tendency for generalist species to outcompete specialists as they are better able to adapt to urban environments (Shochat et al., 2006). Degree of mobility, among other species characteristics, is also influential in determining population responses to increasing urbanisation. Concepción et al. (2015) carried out a study on the effects of urbanisation on biotic communities at a variety of spatial scales, showing that urbanisation filters out specialist species that are highly mobile in both bird and butterfly assemblages while encouraging plant

diversification, probably due to the occurrence of a higher proportion of non-native plants in urban areas. The authors concluded that highly mobile specialists were likely to be more impacted by large-scale habitat fragmentation caused by urbanisation than poorly mobile species who operate at a smaller-scale. In a meta-analysis of urban studies, McKinney et al. (2008) also showed that, while in some cases moderate urbanisation in suburban areas increases species richness (~30% of invertebrate studies considered), it is more likely to negatively impact biodiversity. It is therefore particularly important to monitor the effects of urbanisation on taxa such as bumblebees, where mobile specialist species that require patches of suitable foraging habitat within their range, are in decline (Goulson et al., 2008, 2015).

Conservation of pollinators within urban areas is crucial as it improves connectivity for struggling populations in the wider landscape (Goulson et al., 2010). Pollinating species can also enhance urban food production and facilitate the growth of wild and cultivated flower species in parks and gardens, improving the quality of life for people residing in these areas (Savard et al., 2000; Lowenstein et al., 2015). Studies of urban pollinators vary in terms of design, scale and taxa considered with conflicting outcomes. In a country-wide citizen science survey of flower visitors in France, Deguines et al. (2012) noted a variation within and among insect orders with urbanisation negatively affecting Lepidoptera, Diptera and Coleoptera while having little impact on Hymenoptera. Other studies have reported a negative impact on Hymenoptera along with other taxa, for example, Bates et al. (2011) found that the overall diversity and abundance of bees and hoverflies decreased with high levels of urbanisation when comparing rural, urban and suburban London sites. However, the study also highlighted interspecies variation with some species positively associated with urban and suburban habitats. Similarly,

Hernandez et al. (2009) found a negative correlation between bee species richness and urban habitats and also found that species varied in terms of their response with more cavity-nesting solitary bees and fewer floral specialists in urban areas. Ahrne et al. (2009) reported negative effects of urbanisation on bumblebee species in allotment gardens with lower levels of diversity and high levels of urbanisation and a higher variablility in the abundance of long-tongued specialists. Geslin et al. (2013) found that the number of pollinator visits in experimental plant communities of semi-natural, agricultural, suburban and urban habitats was significantly lower in urban habitats and that pollinator communities were more generalist in urban and suburban compared with agricultural environments. While most of these studies suggest that urbanisation lowers pollinator diversity and abundance, driving out specialist species, Baldock et al. (2015) found that bee species richness was higher in urban environments compared to farmland and nature reserves and that urban areas support similar numbers of rare species compared with other habitats. The current literature paints a mixed picture of the effects of urbanisation on pollinator populations and further research is necessary in order to elucidate its true impact on communities.

Green spaces within the larger urban landscape provide an opportunity for both monitoring and conservation management. Private gardens and parks comprise a major component of urban green space and have the potential to act as a network of refuges within the wider landscape. Studies in the U.K. have estimated that gardens comprise 22-36% of the entire urban area (Gaston et al., 2005; Mathieu et al., 2007) and contribute 35-47% of urban green space (Loram et al., 2007). Gardens also act as ecological refuges in a rural landscape where habitat loss due to intensive agricultural practices has led to significant declines in bird (Chamberlain et al., 2000), butterfly

(Warren et al., 2001) and pollinator (Senapathi et al., 2015; Goulson et al., 2010) communities. While Fortel et al. (2014) reported a lower abundance of wild bees at high levels of urbanisation in Grand Lyon, France, they found that species richness peaked in suburban areas containing more parks and gardens. Similarly, McFrederick and LeBuhn (2006) highlighted the importance of parks for bumblebee populations by reporting higher species' abundances in urban parks compared with nearby wild parks and suggested that this may be due to more resources in urban gardens present in the surrounding area. Carper et al. (2014) compared bee communities in suburban and natural forests of South Carolina and found higher species richness and diversity in suburban forests while Fetridge et al. (2008) found that bee fauna in suburban gardens north of New York City resembled the assemblage of a forest research preserve in same region in terms of species richness. Tonietto et al. (2011) carried out a study of the potential ecological value of roof gardens in urban Chicago and found that bee abundance and diversity increased with the proportion of green space in the surrounding landscape. Several studies highlight the importance of gardens as an ecological refuge for bumblebees in particular, as they provide a variety of forage and nesting resources (Fussell and Corbet, 1992a, b; Goulson et al., 2002; Osborne et al., 2008; Lye et al., 2012). Goulson et al. (2010) suggests that gardens may also help to support those bumblebee populations impacted by agricultural intensification in the surrounding landscape with higher numbers of nests represented amongst samples of workers collected up to 1 km from gardens. While these studies highlight the importance of green spaces, the ecological value of gardens is currently under-researched with most studies focusing on either long-term observations of single gardens or short-term studies of multiple gardens (Goddard et al., 2010; Hanley et al., 2014). Citizen science

has previously proven useful in collecting large-scale information on bumblebee populations in garden habitats throughout the bumblebee flight season (Fussell and Corbet, 1992a, b; Lye et al., 2012). This study uses citizen-science data collected at a country wide scale over multiple years to investigate the effect of local garden habitats and the surrounding landscape on the probability of occurrence and relative abundance of common UK bumblebees.

5.3 Methods

5.3.1 Data collection

Bumblebee abundance data were derived from the "Garden BeeWatch" scheme. This was launched in 2007 by the Bumblebee Conservation Trust and the British Trust for Ornithology (BTO), within BTO's existing Garden BirdWatch framework, in order to collect distribution and abundance data on bumblebees that visit gardens across Britain & Ireland. In this study, British records only (2007-2014) are used as they are more consistent over time and are more uniformly distributed in space than Irish records. This is the largest and longest-running bumblebee abundance monitoring program in the world, providing a unique opportunity to study species abundance patterns in a key habitat.

Garden BeeWatch uses the same observation protocol as BTO's Garden Birdwatch, which has previously been described in detail (Morrison et al., 2014). In summary, each week of the year volunteers recorded the maximum number of each bumblebee species seen together in their garden. Volunteers chose a weekly observation period at their own discretion. Observation periods were consistent within sites over time and volunteers were asked to maintain a constant level of observation effort and to

disregard records from any under- or over- observed weeks. The online system through which records are submitted uses threshold validation to highlight unusual records and alert trained experts to potential errors so that they can be removed from the dataset.

In addition to species records, volunteers submitted details of garden habitat characteristics and were asked to update any changes as they occurred. These were submitted as ranked and binomial variables (Table 5.1). Ranked numeric variables were converted to continuous variables for modelling by using the midpoint of each category. Inclusion of garden habitat and landscape variables (Table 5.1) was based on the likelihood of association with bumblebee occurence. Linear surrounding features were included since they are known to guide foraging activity in bumblebees (Cranmer et al., 2012) and in the case of some features, for example buildings and hedges, provide nesting sites (Fussell and Corbett, 1992b; Lye et al., 2012). Flowerbeds, vegetables and wild native plants provide potential forage material while shrubberies are used as nesting sites (Goulson, 2003, Fussell and Corbet, 1992b; Lye et al., 2012). In contrast, a high proportion of barren ground and lawn could negatively affect occurrence due to lack of resources. Altitude was included since higher areas are known to limit the occurrence of certain species to due to the reduced availability of floral resources (Alford, 1980; Williams, 1982). Although volunteers were initially asked to provide information on the occurrence of berry plants in their gardens for the Garden BirdWatch scheme since these are an obvious foraging resource for birds, bees are also known to forage on and pollinate the flowers of berry plants, e.g. common ivy (*Hedera helix*), honeysuckle (*Lonicera periclymenum*), dog rose (*Rosa canina*), hawthorn (*Crataegus monogyna*) (Jacobs et al., 2009, 2010) and use the bases of berry-bearing hedgerow plants for nesting (Fussell and Corbett, 1992b; Lye et al., 2012). Surrounding landscape

variables (Table 5.2c) with linear features including rivers, streams, canals and railways, are used to guide foraging while their edges, when left wild, can be used for nesting and food resources (Williams, 88; Osbourne et al., 2008; Lye et al., 2012). Other variables in the surrounding landscape category consist of known habitats for bumblebees (Williams, 1982, 1988; Goulson, 2003, Osborne et al., 2008).

Table 5.1 Habitat variables recorded by participants in the Garden BirdWatch scheme. The original ranking as recorded by volunteers is given and "*" indicates where this ranking is converted to a continuous variable by using the midpoint of each category (adapted from Chamberlain *et al.,* 2004).

Habitat	Definition	Categories/Ranking
(a) General characteristics		
Type	Urbanisation category	Rural, suburban, urban
Size	Garden area	Large (≥450m²), medium (≥100m²-<450m²), small (<100m²)
Age	Years old	1 (0-4), 2 (5 -10), 3 (11-19), 4 (20-49), 5 (50+)*
(b) Garden Habitat		
Lawn	% of garden covered	1-5 (0% and quartiles)*
Flower beds	% of garden covered	1-5 (0% and quartiles)*
Shrubberies	% of garden covered	1-5 (0% and quartiles)*
Vegetables	% of garden covered	1-5 (0% and quartiles)*
Wild	% of garden covered	1-5 (0% and quartiles)*
Barren	% of garden covered	1-5 (0% and quartiles)*
Orchard	% of garden covered	1-5 (0% and quartiles)*
Fence	% in garden boundary	1-5 (0% and quartiles)*
Wall	% in garden boundary	1-5 (0% and quartiles)*
Buildings	% in garden boundary	1-5 (0% and quartiles)*
High evergreen hedge	% in garden boundary	1-5 (0% and quartiles)*
Low evergreen hedge	% in garden boundary	1-5 (0% and quartiles)*
High deciduous hedge	% in garden boundary	1-5 (0% and quartiles)*
Low deciduous hedge	% in garden boundary	1-5 (0% and quartiles)*
Other boundary	% in garden boundary	1-5 (0% and quartiles)*
Altitude	Height above sea level/m	1 (0-50), 2 (51-100), 3 (101-250), 4(251-499), 5 (500+)*
Berry plants	Berry-bearing plants present	0 or 1
(c)Surrounding landscape		
Canal	Occurrence within 100 m	0 or 1
Gardens	Occurrence within 100 m	0 or 1
Marsh	Occurrence within 100 m	0 or 1
Mixed woodland	Occurrence within 100 m	0 or 1
Nearby orchard	Occurrence within 100 m	0 or 1
Bog	Occurrence within 100 m	0 or 1
Moor	Occurrence within 100 m	0 or 1
Parks	Occurrence within 100 m	0 or 1
Active railway	Occurrence within 100 m	0 or 1
River	Occurrence within 100 m	0 or 1

Scrub	Occurrence within 100 m	0 or 1
Seashore	Occurrence within 100 m	0 or 1
Semi-natural grassland	Occurrence within 100 m	0 or 1
Stream	Occurrence within 100 m	0 or 1

5.3.2 Data analysis

Analysis was restricted to the six bumblebee species/groups most commonly found in UK gardens. These include *Bombus hortorum, B. hypnorum, B. lapidarius*, *B. pascuorum, B. pratorum* and *B. terrestris/lucorum*. *B. terrestris/lucorum* is comprised of four species, *B. terrestris* and the *B. lucorum* complex (*B. lucorum, B. cryptarum and B. magnus*) which are impossible to separate reliably in the field (Scriven et al., 2015). These six groups are ones that have been previously used in citizen-science surveys on bumblebees (Fussell and Corbet, 1992a,b; Osborne et al., 2008; Lye et al*.,* 2012), allowing some comparison with earlier studies. Most rare bumblebee species closely resemble common ones (e.g. *B. muscorum* and *B. humilis* closely resemble *B. pascuorum*), and hence it is likely that a small number of the records obtained for the common species are actually mis-identified rare species. However, the number of such records is likely to be very low as rare bumblebees are not generally found in gardens. To maximise the reliability of records, analysis was restricted to those sites recording all species/groups apart from *B. hypnorum*, which didn't reach Scotland until 2013 (BWARS, 2015), over their entire survey period and those that submitted at least 16 surveys annually.

All statistical analyses were conducted in R version 3.1.3 (R Core Team, 2014). A Pearson-product correlation matrix based on the total number of individuals recorded for each species per garden was produced to investigate interspecific relationships in abundance. Pearson's chi squared tests were used to compare the relative abundance of common

UK species to previous studies in order to assess whether these have changed over time. Abundance data was summed across years (2007-2014) for each species and compared to the number of flower visits reported in national survey on forage use (1987 and 1988; Fussell and Corbet 1992a) and the number of nests recorded in a UK-wide nest survey (1989-91; Fussell and Corbet, 1992b). For the flower visitation survey, which ran April-October, Fussell and Corbett (1992a) analysed records collected by volunteers on a 200-500m transect where they recorded the first visit for each bumble-bee species observed flower-visiting within 1 m of the observer. Transects were selected by volunteers in either garden or wild habitats. For the national nest survey, volunteers sent in species and habitat information about any nests they had found by chance, and the survey was not constrained to particular habitats, or particular times of year. However, the vast majority of nests were found in gardens (Fussell and Corbett 1992b). Both of these previous surveys divided bumblebee species by colour-group with each group designed to include one of the common species, however they did not allow differentiation from rare species if present and males of *B. pratorum* are included in the same colour group as *B. lapidarius*. Garden BeeWatch abundance data for each species was compared to the total number of bee visits and nests reported in its related colour-group (Table 5.3). Pearson product-moment correlation coefficients were computed to investigate the relationship between relative species proportions derived from the Garden BeeWatch abundance dataset and the species proportions in both Fussell and Corbet's nest survey and forage-use survey (Table 5.3; Fig. 5.2). *B. hypnorum* was not included in the analyses since it was not recorded in the UK until 2001 (Goulson and Williams, 2001).

Due to a high proportion of true zeroes in the data set, a hurdle model approach was used for modelling analyses (Cragg, 1971; Potts and Elith, 2006). Firstly, abundance data

(counts of each species per garden visit) were converted to presence/absence binary data. Separate general linear models with binominal distributions were used to investigate the effect of garden size, garden age, garden type (rural, urban, suburban), garden habitat and surrounding landscape variables (Table 5.1), along with latitude, longitude, year, the interaction between latitude and year and the interaction between longitude and year on the occurrence of each species/groups in gardens. Zero records were then removed from the original abundance dataset and separate general linear models were run on abundance data only in order to predict which variables influenced abundance in gardens where individual species were present. Variables were included as fixed factors in both model types. Model selection was performed using Akaike's information criterion (AIC).
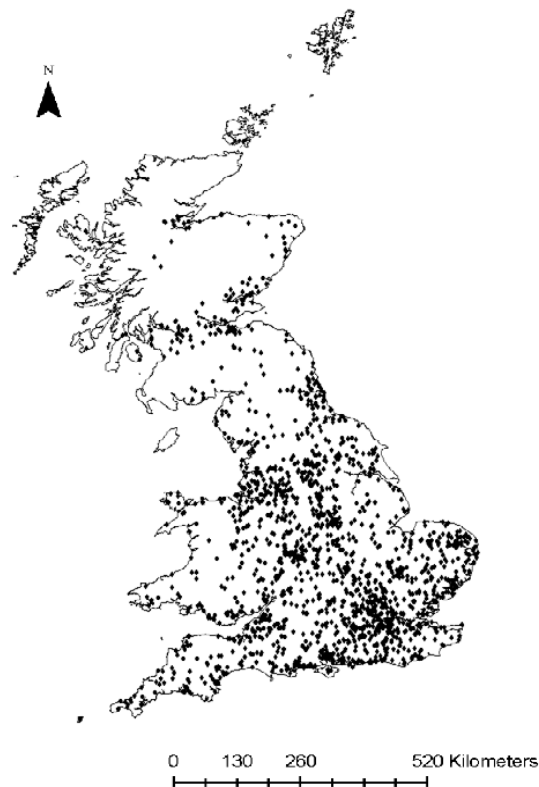
Fig. 5.1 Distribution of UK garden sites included in the analysis.

5.4 Results

Overall, 413,989 bumblebee records were obtained from 1,804 gardens (Fig. 5.1) over the 8 year period (2007-14). *B. terrestris/lucorum* was the most commonly recorded group (215,682 records), followed by *B. pascuorum* (80,033), *B. lapidarius* (48,310), *B. hortorum* (32,588), *B. hypnorum* (20,702) and *B. pratorum* (16, 674). The number of records increased steadily from 19,138 in 2007 to 83,053 in 2013 before dropping to 75,230 in 2014. Recorder effort followed a similar pattern with the number of reported gardens increasing steadily from 295 in 2007 to 1015 in 2013 before dropping to 993 in 2014. The total abundance of each species per garden was positively correlated with all other species (Table 5.2).

Table 5.2 Pearson-product correlation matrix of species abundance calculated using the total number of individuals observed per garden for each species.

	B. hortorum	*B. hypnorum*	*B. lapidarius*	*B. pascuorum*	*B. pratorum*	*B. terrestris/ lucorum*
B. hortorum	0.08	0.27	0.38	0.35	0.27	
B. hypnorum		0.24	0.23	0.28	0.15	
B. lapidarius			0.55	0.38	0.58	
B. pascuorum				0.49	0.55	
B. pratorum					0.34	

5.4.1 Comparison with previous studies

Fussell and Corbet (1992a,b) received 428 records of bumblebee colonies in their nest survey (1989-91) and 16,260 flower visits by individual bees in their forage-use survey (1987-88) (Table 5.3). When Garden BeeWatch abundances (2007-14) were compared to these data a significant difference in species composition was found for both number of colonies (χ^2=34.49, df=4, p<0.001) and number of flower visits (χ^2=11957.84, df=4,

p<0.001). The proportion of *B. pratorum* abundance decreased in 2007-14 in relation to earlier studies while the proportion of *B. terrestris/lucorum* increased (Table 5.3). Overall, however a strong positive correlation was found when species proportions in the Garden BeeWatch dataset were compared with species proportions derived from Fussell and Corbett's nest survey (1989-91) (r=0.991, df=3, p<0.001; Fig. 5.2). A weaker, non-significant positive correlation was found between these data and species proportions in Fussell and Corbett's forage-use survey (r=0.624, df=3, p>0.05; Fig 5.2).

Table 5.3 Total number of individuals recorded for each species in the Garden BeeWatch survey (2007-14) and the total number of nests (1989-91) and flower visits (1987-88) recorded for each colour group in the Fussell and Corbet surveys. Numbers in brackets represent the proportion of the total for each survey.

| Garden BeeWatch		Fussell and Corbet		
Species	No. individuals	Colour pattern category	No. nests	No. bee visits
B. pascuorum	80033 (0.21)	Brown	88 (0.21)	3982 (0.24)
B. lapidarius	48310 (0.13)	Black-bodied, red tails	73 (0.17)	3408 (0.21)
B. pratorum	16674 (0.04)	Banded red tails	39 (0.09)	3337 (0.21)
B. terrestris/lucorum	215682 (0.57)	Two-banded white tails	205 (0.48)	4161 (0.26)
B. hortorum	20702 (0.05)	Three-banded white tails	23 (0.05)	1372 (0.08)

(a)
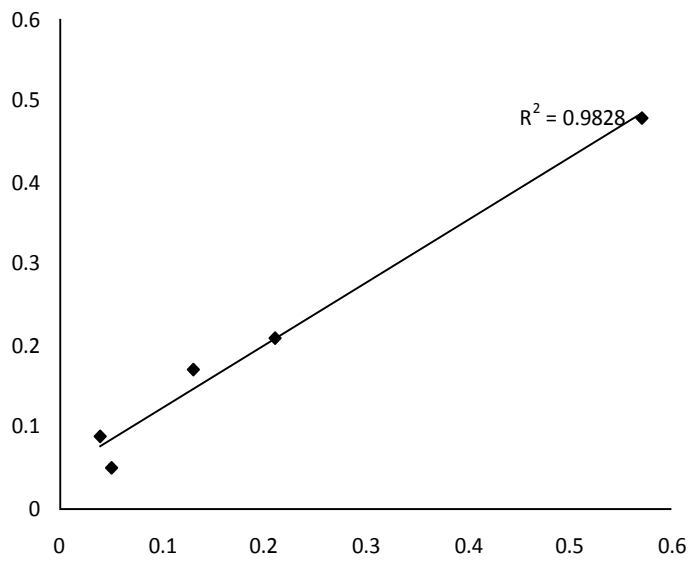
(b)
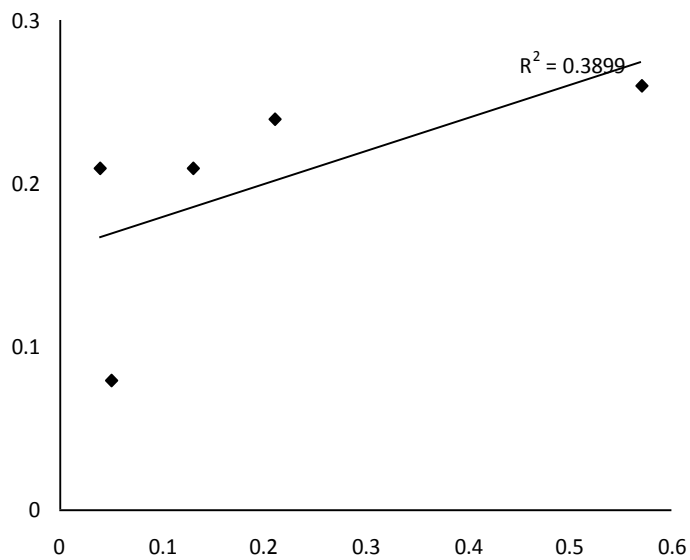
Figure 5.2 Relationship between bumblebee species proportions in the Garden BeeWatch survey (2007-14) and species proportions derived from Fussell and Corbet's (a) nest survey (1989-91) and (b) flower visitation survey (1987-88).

5.4.2 Location

Presence of bumblebees was significantly influenced by location of gardens in the UK. The majority of species were influenced by latitude with three of the six common species/groups (*B. hortorum, B. lapidarius, and B. pascuorum*), significantly more commonly occurring in northern latitudes (Fig. 5.3a, Supplementary Material S5.1a) and two species/groups (*B. hypnorum*, *B. terrestris/lucorum*) significantly associated with southern latitudes (Fig. 5.3a, Supplementary Material S5.1a). Three species/groups were more abundant at higher latitudes within the areas in which they occurred (*B. lapidarius, B. pascuorum,* and *B. terrestris/lucorum*; Fig. 5.4a, Supplementary Material S5.1).

Species also differed in their responses to longitude with two species (*B. hypnorum, B. lapidarius*) more likely to be found at easterly locations and a further two species/groups (*B. pascuorum, B. terrestris/lucorum*) showing a significantly more westerly distribution. Four species/groups (*B. lapidarius, B. pascuorum, B. pratorum, B. terrestris/lucorum*) were more likely to occur in lower numbers at locations further east (Fig. 5.4a; Supplementary Material S5.1). All species, apart from *B. hypnorum,* are more likely to occur in gardens at lower altitudes (Fig. 5.3c; Supplementary Material S5.1).

5.4.3 Year

Several species/groups showed inter-annual variation in their presence and abundance in gardens. Overall, *B. lapidarius* and *B. hypnorum* populations appear to be increasing, becoming significantly more abundant and more likely to occur in recent years, whereas *B. hortorum*, *B. terrestris/lucorum* and *B. pascuorum* appear to be declining (Fig. 5.3a, 5.4a; Supplementary Material S5.1).

B. terrestris/lucorum, *B. pascuorum* and *B. hypnorum* are more likely to occur in northern latitudes in recent years, with an interaction between year and latitude positively affecting species occurrence (Supplementary Material S5.1a). Over the entire time period, *B. pascuorum* is also likely to be more abundant at higher latitudes, as is *B. hortorum* (Supplementary Material S5.1a). *B. lapidarius* and *B. pratorum* results reveal an opposite trend, with occurrence becoming more associated with southern latitudes over time (Supplementary Material S5.1a).

B. lapidarius is becoming significantly more abundant in easterly locations in recent years, with a two-way interaction between longitude and year positively affecting abundance, whereas *B. terrestris/lucorum* is increasing in westerly locations (Supplementary Material S5.1a).

5.4.4 Garden type and size

Four species were more commonly present in urban gardens compared to rural. Compared to rural gardens, *B. hypnorum* was significantly more likely to occur in both suburban and urban gardens (Fig. 5.3b, Supplementary Material 5.1) and was more abundant in urban ones, as were *B. lapidarius*, *B. pratorum* and *B. terrestris/lucorum* (Fig. 5.4b; Supplementary Material S5.1). In contrast, the occurrence of *B. hortorum* and *B. pascuorum* is significantly more associated with rural gardens (Fig. 5.4b; Supplementary Material S5.1). Garden size also appears to influence populations, with all species showing significant positive trends in occurrence and/or abundance in larger gardens (Fig 5.3b, 5.4b; Supplementary Material S5.1).

5.4.5 Garden Habitat and Boundaries

Several garden habitats are positively associated with bumblebee occurrence. The percentage coverage of flower beds is significantly positively associated with the occurrence of all species (Fig. 5.3c, Supplementary Material S5.1). More wild areas within a garden positively predicts the occurrence of all species apart from *B. lapidarius*, and is also associated with a higher abundance of four species/groups (*B. lapidarius, B. pascuorum, B. pratorum,* and *B. terrestris/lucorum*). In addition, four of the six species/groups (*B. hypnorum, B. lapidarius, B. pascuorum,* and *B. pratorum*) are more likely to be present in gardens where a higher proportion of land is used for vegetable growing (Fig. 5.3c; Supplementary Material S5.1). All species/groups, apart from *B. terrestris/lucorum*, are more likely to occur in gardens where berry plants are present (Fig. 5.3c; Supplementary Material S5.1).

Regarding garden boundaries, the proportion of low evergreen hedge is positively associated with the occurrence of all bumblebee species (Supplementary Material S5.1). The proportion of high deciduous hedge is positively associated with abundance of all species apart from *B. pascuorum,* though numbers of all species drop off when the percentage of garden boundary consisting of high deciduous hedge is over 75% (perhaps indicating high levels of shade). Low deciduous hedge is positively associated with abundance in the case of four species/groups (*B. hortorum*, *B. hypnorum*, *B. pascuorum* and *B. terrestris/lucorum*; Supplementary Material S5.1, Fig. 5.4c).

5.4.6 Surrounding Landscape

Marshes and parks located near gardens have an overall positive effect on garden bumblebees. Nearby marsh habitat is positively associated with both the occurrence and abundance of all species apart from *B. hypnorum* (Fig., 5.3d, 5.4d; Supplementary

Material S5.1). The presence of parks nearby predicts the occurrence of all species and is positively associated with higher abundance of all species apart from *B. lapidarius*.

Gardens located near the coast are more likely to have higher numbers of most species (*B. lapidarius, B. pascuorum, B. pratorum* and *B. terrestris/lucorum*; Fig. 5.4d).

(a)

B. hortorum

B. hypnorum

B. lapidarius

B. pascuorum

B. pratorum

B. terrestis/lucorum

Latitude/decimal degrees

Longitude/decimal degrees

Year

(b)

B. hortorum

B. hypnorum

B. lapidarius

B. pascuorum

B. pratorum

B. terrestis/lucorum

Garden type

Garden size

(c)

B. hortorum

B. hypnorum

B. lapidarius

B. pascuorum

B. pratorum

B. terrestis/lucorum

Flower beds/%

Proportion of presence (light gray) and absence (dark gray) records

Proportion of presence (light gray) and absence (dark gray) records

B. hortorum

B. lapidarius

B. pascuorum

B. pratorum

B. terrestis/lucorum

(d) *B. hortorum*

B. hypnorum

B. lapidarius

B. pascuorum

B. pratorum

B. terrestis/lucorum

0	1-25	26-50 51-75

Vegetables/ %

0	1-25	26-50 51-75 76-100

Wild/%

0-50	51-100	101-250 251-499 500+

Altitude/m

absent	present

Berry plants

absent	present

Semi-natural grassland

| absent	present

Marsh

Fig. 5.3 Spine plots illustrating the proportion of presence (light gray) and absence (dark gray) records of species in relation to (a) Latitude, Longitude and Year (b) general garden characteristics (c) garden habitat characteristics and (d) surrounding landscape characteristics (See Table 5.1). "*" indicates significance of $p < .05$

(a)

Legend: □ B. hortorum, ■ B. hypnorum, ⊞ B. lapidarius, □ B. pascuorum, ▨ B. pratorum, ▥ B. terrestris/lucorum

B. hortorum B. hypnorum B. lapidarius
B. pascuorum B. pratorum B. terrestris/lucorum

(b)

Garden type

Garden size

(c)

Low deciduous hedge

High deciduous hedge

Percentage coverage

Percentage coverage

(d) Marsh

Parks

Percentage coverage

Percentage coverage

Average abundance per transect/number of gardens per category

125

Fig. 5.4 Bar charts illustrating the relative abundance of species in relation to (a) Latitude, Longitude and Year (b) general garden characteristics (c) garden habitat characteristics and (d) surrounding landscape characteristics (See Table 1). "*" indicates significance of $p<.05$ (in a least one category for categorical variables). Figures above bars represent number of garden sites per category.

5.5 Discussion

The findings of this study have demonstrated that the occurrence and abundance of common bumblebees in UK gardens is strongly influenced by certain garden habitats and characteristics as well as features of the surrounding landscape. Since gardens play an important ecological role in the conservation of biodiversity, acting as green space refuges in both rural and urban landscapes (Osborne et al., 2008; Goulson et al., 2010; Goddard et al., 2010), understanding the species' population responses to these characteristics is of increasing importance (Chamberlain et al., 2004; Cannon, 1999), particularly in the context of recent agricultural intensification and rapid urbanisation. In the UK, gardens comprise a substantial area of green space and if we can understand how to manage them to protect declining species, then they have a great potential to help minimise the impact of human activity on wildlife populations (Davies et al., 2009; Goddard et al., 2010).

5.5.1 Assuring record reliability

Citizen science schemes have the potential to provide valuable ecological information, however some biases are inherent in the resulting data due to differences in individuals' expertise, effort and experience. These issues must be addressed at each stage of the scientific process; data collection, data analysis through to the interpretation of results, in order to draw any dependable conclusions relating to ecological trends (Dickinson et al., 2010, Hochachka et al., 2012). In order to address this, volunteers were provided with clear instructions of a simple, standardised protocol that has proven successful as part of BTO's Garden BirdWatch scheme and submissions were validated through their online threshold system that flags up unusual species records allowing them to be

assessed by experts. Only recorders that had a consistent level of effort, submitting a certain number of records annually and recording all bumblebees common to UK gardens (apart from *B. hypnorum* which only recently reached Scotland, BWARS 2015) were included in the analysis and modelling techniques that account for spatial and temporal biases were applied. Results are discussed below, focusing on broad-scale trends of common bumblebee garden visitors. The frequency of occurrence of rare species in garden habitats is likely to be very low and the inclusion of the odd, misidentified rare individual is unlikely to affect overall trends.

5.5.2 Interspecific variation in spatio-temporal trends and response to level of urbanisation

Relative abundances of common species have changed over the last two decades. Compared with earlier studies by Fussell and Corbet (1992a,b), *B. terrestris/lucorum* appear to have increased in abundance while *B. pratorum* and *B. lapidarius* populations have declined. Similarly, higher abundances of *B. terrestris/lucorum* were found by Osborne et al. (2008) and Lye et al. (2012) when they compared nest densities to those reported by Fussell and Corbet (1992b). This may be explained the fact that *B. terrestris* is a particularly robust species that has proven successful in invading areas outside of its native range making it more resistant to recent climate and landscape changes, such as urbanisation, than other species.

Bumblebee species showed differing spatio-temporal trends in both their probability of occurrence and abundance in gardens, with three of the six common species/groups (*B. pascuorum*, *B. hortorum, B. terrestris/lucorum*) displaying patterns of recent decline. The relative abundance of *B. terrestris/lucorum* has increased compared to earlier

studies by Fussell and Corbet (1992a,b) but analysis of the Garden BeeWatch records (2007-14) suggest a recent decline. It is important to note that, when comparing results between surveys, differences in methodology may influence trends. One important example of this is that, in Fussell and Corbett's flower visitation study (Fussell and Corbett 1992a), the proportion of habitats surveyed comprised of 49% gardens, 37% wild sites and 14% included both. This may explain why species proportions derived from the Garden Beewatch results were more highly correlated with Fussell and Corbett's nest study which was mainly based in garden habitats (Fussell and Corbett, 1992b) than with their flower visitation study (Fussell and Corbett, 1992a, Fig. 5.2). When inferring long-term population trends it is also important to remember that these surveys, particularly the earlier ones, which were shorter lasting just two seasons, represent a temporal snapshot and the data may be influenced by variation in environmental conditions and other short-term factors such as resource availability and natural enemy populations.

Analysis of garden BeeWatch records reveals that *B. pascuorum* and *B. hortorum* are more associated with northerly latitudes and *B. terrestris/lucorum* is more likely to be found in the south but in higher numbers in the northern areas where it occurs. It is difficult, however, to interpret trends for *B. terrestris/lucorum* since *B. lucorum* is a species complex comprised of three cryptic species that differ in terms of their geographic range and ecology (Scriven *et. al*, 2015). Interestingly, the two species that are associated with northerly latitudes and appear to be declining over time, *B. hortorum* and *B. pascuorum,* are also more associated with rural than urban (*B. hortorum*) and suburban (*B. pascuorum*) gardens, which are more likely to be found in the north (UK National Ecosystem Assessment, 2011). Studies have shown that

bumblebees differ in their foraging specialisation in accordance with tongue length with long-tongued species being more specialised and prone to decline than short-tongued species (Goulson et al., 2005; Goulson and Darvill, 2004; Goulson et al., 2008). Both *B. pascuorum* and *B. hortorum* are relatively long-tongued and this may explain their decline, in contrast to the remaining three short-tongued species whose generalism may confer an advantage in adapting more readily to rapidly changing environments. Both species emerge later than most other common species and timing of emergence has been suggested as a factor contributing to bumblebee declines due to reduced time for colony growth. Later emerging species also tend to have a stronger association with unimproved grassland, which has undergone a remarkable decline over the last few decades (Goulson et al., 2005). Carvell et al. (2006) also described a national decline in bumblebee forage plants, including those of particular value to long-tongued species. It is likely that there are a number of potentially interacting drivers of decline with other studies suggesting a combination of habitat and climatic factors influencing distribution and abundance of UK species (Williams et al., 2007; Chapter 4). Previous studies that used volunteer-collected data to investigate bumblebee nest density found similar patterns of decline for *B. pascuorum* (Osborne et al., 2008; Lye et al., 2012), however this is the first evidence of decline in *B. hortorum*. It is of particular concern that the last remaining long-tongued species, previously thought to be common, are now showing signs of threat. This is likely to impact on the survival of plants with deep corollas specialized for pollination by long-tongued bumblebees, many of which are already in decline (e.g. *Trifolium pratense*, *Rhinanthus minor*; Carvell et al., 2006) and could lead to knock on ecosystem effects.

Bombus hypnorum, a recent arrival from the continent (Goulson and Williams, 2001), has been steadily moving northwards and increasing in abundance over time. It is also associated with easterly gardens and urban habitats. This pattern is unsurprising since the rapid expansion of *B. hypnorum* has been well documented since its arrival (Prys-Jones, 2014) and it is known to be an urban species, now common in cities such as London (Crowther et al., 2014; Bates et al., 2011). Very little is known of the ecological impact of its colonisation and rapid expansion in the UK. Further studies are required to determine whether or not this species competes with others and is a contributing factor in their decline.

Altitude was negatively associated with all bumblebee species apart from *B. hypnorum.* This may be due to a lack of suitable floral resources at higher altitudes limiting other species, some of which are towards the northern edge of their ranges in the UK (Alford, 1980) while *B. hypnorum* is found in a wide range of biotopes, including montane regions of Europe and Asia (Goulson and Williams, 2001).

This study reveals an association of most common species with urban environments, with urban gardens and park habitat located near gardens having a positive effect on species occurrence and abundance. Where more gardens were located within 100m of the garden sites surveyed, occurrence and abundance of most species was higher (S5.1), further indicating that residential suburban and urban areas benefit populations of some species. This is in line with previous studies which have shown that gardens and parks are important refuges for bumblebees within the wider landscape (Osborne et al., 2008; Chapman et al., 2003; McFrederick and LeBuhn, 2006; Goulson et al., 2010). This may be due to urban gardens and parks comprising regional areas of green space with a

high diversity of floral resources that tend to be managed throughout the bumblebee flight season (March-October), offering continuity of forage material. Gunnarsson and Federsel (2014) found that a high flowering frequency was positively associated with bumblebee abundance in urban gardens and ornamental flowerbeds within urban park sites. Parks and gardens also tend to be dominated by ornamental, non-native species whose showy floral displays and prolific nectar content are often attractive to bees (Stout et al., 2006; Stout and Casey, 2014; Lopezaraiza-Mikel et al., 2007), particularly generalists. Interestingly, in a study carried out on flower visitation by bumblebees in English urban gardens, Hanley et al. (2014) revealed a significant preference for native plants by the long-tongued *B. hortorum* and *B. pascuorum* compared to other, short-tongued species, which were more generalist in their preferences. This supports the hypothesis that the recent decline of these species shown here is due to common generalist species outcompeting specialists as they adapt to expanding urban areas.

5.5.3 Species patterns of occurrence and abundance in relation to the surrounding landscape

Higher abundances of four bumblebee species (*B. lapidarius, B. pascuorum, B. pratorum, B. terrestris/lucorum*) were associated with gardens located near the coast. This is not unexpected since coastal habitats such as sand dunes, shingle and saltmarsh are known to be key UK habitats for bumblebees (Williams 1988); they support high levels of bumblebee species richness, with many rare species contracting towards the coast as populations decline (Goulson et al., 2006; Chapter 3). Gardens near marshes were more likely to record bumblebee species and have a higher abundance of most species. These habitats are less affected by agricultural intensification due to their relative unsuitability for farming and so tend to be richer in floral diversity and abundance than many inland

areas, as well as having a longer growing season (Williams, 1988). *B. hypnorum* was the only species that was found to be negatively associated with both nearby seashore and marsh habitat, most likely due to its preference for urban areas and for nesting in trees, bird boxes and roof spaces.

Surprisingly, the occurrences of most bumblebee species were negatively associated with gardens near semi-natural grassland. This may be due to nectar rich grassland flowers attracting bumblebees away from gardens since they tend to favour foraging strategies that are optimal in terms of resource acquisition (Goulson, 2003). Also, semi-natural grassland tends to occur in more rural areas where gardens are likely to be comparatively more spread out with patchily distributed foraging habitat.

5.5.4 Species patterns of occurrence and abundance in relation to within- garden habitats

Wild habitat within gardens positively affected occurrence and abundance of species. Similar findings were reported by McFrederick and LeBuhn (2006) in their study of urban parks, with a higher proportion of wild areas increasing bumblebee abundance. Additionally, Tommasi et al. (2004) also found a higher diversity of bees in wild areas within Canadian urban environments compared to botanical gardens, backyards and managed flower-beds. This result is unsurprising since areas left unchanged by human activity are more likely to offer floral resources and suitable nesting sites. Flowerbeds, vegetables and berry plants were also positively associated with the occurrence of bumblebee species in gardens, most likely due to their high foraging rewards. Hedgerows were found to be the most beneficial linear features surrounding garden sites with low evergreen hedges predicting occurrence and both high and low deciduous

hedges positively associated with a higher abundance of most species. Bumblebees use linear features to guide foraging activity (Cranmer, 2004; Cranmer et al., 2012; Öckinger and Smith, 2007) and the base of hedges additionally provide good nesting sites and shelter (Osborne et al., 2008). Deciduous hedges may also provide floral resources.

This study supports the growing body of evidence that gardens are increasingly important habitats for bumblebees, providing a much needed network of nesting and foraging resources in rural and urban landscapes strongly impacted by human activity. While urban gardens support most of the common species of bumblebee, it is of great concern that declining long-tongued specialists appear to be struggling to adapt to the rapidly spreading urban matrix. These findings stress the need for managing parks and gardens sympathetically for declining specialist pollinators such as long-tongued species by including suitable deep flowers along with the conservation of key coastal habitats and marshland in the surrounding landscape.

5.6 Supplementary Material

S5.1 Minimal model summary for each species where (a) presence/absence and (b) abundance per garden visit is fitted as the response variable in a general linear model. Latitude and Longitude of each garden site, year of record and all bumblebee habitat variables (Table 5.1) were fitted as fixed factors. "*" denotes P-value at a significance level of <0.05.

Species Fixed Effects	Estimate	S.E.	z-value	P	AIC
B. hortorum					
(a) Latitude	0.070	0.032	2.218	0.027*	58917
Longitude	0.222	0.033	6.679	2.41e-11*	
Year (2008)	-0.265	2.105	-0.126	0.900	
Year (2009)	2.445	1.928	1.268	0.205	
Year (2010)	1.690	1.950	0.867	0.386	
Year (2011)	0.886	1.899	0.467	0.641	
Year (2012)	-1.984	1.951	-1.017	0.309	
Year (2013)	-1.754	1.861	-0.942	0.346	
Year (2014)	1.462	1.860	0.786	0.432	
Garden size (medium)	-0.249	0.029	-8.528	1.49e-17*	

Garden size (small)	-0.001	0.037	-0.039	0.969	
Garden age	-0.004	4.83e-04	-9.302	1.37e-20*	
Garden type (suburban)	-0.183	0.027	-6.695	2.15e-11*	
Garden type (urban)	-0.229	0.063	-3.609	3.08e-04*	
Lawn	-0.002	0.001	-4.023	5.75e-05*	
Flower beds	0.009	0.001	8.950	3.54e-19*	
Vegetables	-0.011	0.001	-8.348	6.94e-17*	
Wild	0.020	0.001	20.497	2.31e-93*	
Barren	-0.011	0.001	-10.169	2.73e-24*	
Orchard	-0.003	0.002	-1.937	0.053	
Buildings	-0.012	0.001	-9.246	2.34e-20*	
Coniferous hedge (low)	0.004	0.001	4.950	7.43e-07*	
Coniferous hedge (high)	0.003	0.001	4.163	3.14e-05*	
Other boundary	-0.015	0.001	-13.728	6.86e-43*	
Altitude	-0.003	0.001	-5.123	3.01e-07*	
Berry plants (present)	0.746	0.074	10.115	4.74e-24*	
Scrub (present)	-0.221	0.027	-8.074	6.81e-16*	
Semi-natural grassland (present)	0.481	0.028	16.895	4.91e-64*	
Marsh (present)	0.132	0.050	2.609	0.009*	
Moor (present)	0.333	0.061	5.490	4.02e-08*	
Bog (present)	-0.263	0.102	-2.576	0.010*	
Nearby orchard (present)	-0.151	0.044	-3.434	0.001*	
Garden (present)	-0.245	0.036	-6.849	7.46e-12*	
Parks (present)	0.079	0.026	3.040	0.002*	
Active railway (present)	-0.390	0.051	-7.612	2.71e-14*	
Stream (present)	0.071	0.028	2.513	0.012*	
River (present)	0.154	0.046	3.358	0.001*	
Canal (present)	-1.038	0.159	-6.530	6.56e-11*	
Latitude:Year (2008)	0.003	0.040	0.066	0.947	
Latitude:Year (2009)	-0.049	0.037	-1.327	0.184	
Latitude:Year (2010)	-0.039	0.037	-1.054	0.292	
Latitude:Year (2011)	-0.026	0.036	-0.707	0.480	
Latitude:Year (2012)	0.028	0.037	0.755	0.450	
Latitude:Year (2013)	0.027	0.036	0.750	0.453	
Latitude:Year (2014)	-0.039	0.036	-1.104	0.270	
Longitude:Year (2008)	-0.023	0.042	-0.551	0.582	
Longitude:Year (2009)	-0.037	0.038	-0.963	0.336	
Longitude:Year (2010)	-0.028	0.039	-0.719	0.472	
Longitude:Year (2011)	-0.110	0.038	-2.924	0.003	
Longitude:Year (2012)	-0.004	0.039	-0.099	0.921	
Longitude:Year (2013)	-0.124	0.037	-3.345	0.001*	
Longitude:Year (2014)	-0.145	0.037	-3.950	7.83e-05*	
(b) Latitude	-0.038	0.022	-1.722	0.085	38291
Longitude	-0.028	0.019	-1.534	0.125	
Year (2008)	2.990	1.403	2.131	0.033*	
Year (2009)	-6.329	1.318	-4.801	1.58e-06*	

Year (2010)	-4.511	1.348	-3.347	0.001*
Year (2011)	-2.788	1.290	-2.161	0.031*
Year (2012)	-3.547	1.357	-2.614	0.009*
Year (2013)	-3.611	1.250	-2.889	0.004*
Year (2014)	-4.035	1.253	-3.220	0.001*
Garden size (medium)	-0.172	0.019	-8.837	9.8e-19*
Garden size (small)	0.003	0.024	0.133	0.894
Garden age	-0.003	3.34e-04	-8.958	3.3e-19*
Lawn	-0.004	3.87e-04	-10.949	6.73e-28*
Flower beds	-0.007	0.001	-10.309	6.41e-25*
Shrubberies	0.003	0.001	5.758	8.49e-09*
Vegetables	-0.007	0.001	-8.126	4.44e-16*
Wild	-0.002	0.001	-2.463	0.014*
Barren	-0.008	0.001	-10.581	3.66e-26*
Orchard	0.003	0.001	2.515	0.012*
Fence	0.002	3.17e-04	6.550	5.76e-11*
Wall	-0.003	4.82e-04	-6.289	3.2e-10*
Buildings	0.003	0.001	3.097	0.002*
Deciduous hedge (low)	0.006	0.001	10.049	9.26e-24*
Deciduous hedge (high)	0.006	4.89e-04	11.992	3.89e-33*
Other boundary	0.004	0.001	5.144	2.69e-07*
Berry plants (present)	0.193	0.059	3.296	0.001*
Mixed woodland (present)	0.067	0.017	4.088	4.36e-05*
Scrub (present)	-0.094	0.019	-4.914	8.92e-07*
Semi-natural grassland (present)	-0.149	0.020	-7.462	8.52e-14*
Marsh (present)	0.235	0.031	7.565	3.89e-14*
Moor (present)	0.128	0.040	3.211	0.001*
Bog (present)	0.379	0.057	6.695	2.15e-11*
Nearby orchard (present)	-0.095	0.034	-2.838	0.005*
Garden (present)	-0.207	0.023	-9.138	6.38e-2*
Parks (present)	0.039	0.018	2.214	0.027*
Active railway (present)	-0.182	0.040	-4.573	4.8e-06*
Stream (present)	-0.080	0.019	-4.294	1.76e-05*
Canal (present)	-0.537	0.140	-3.832	1.27e-04*
Seashore (present)	-0.310	0.087	-3.563	3.67e-04*
Latitude:Year (2008)	-0.057	0.027	-2.125	0.034*
Latitude:Year (2009)	0.117	0.025	4.638	3.51e-06*
Latitude:Year (2010)	0.086	0.026	3.329	0.001*
Latitude:Year (2011)	0.048	0.025	1.969	0.049*
Latitude:Year (2012)	0.064	0.026	2.467	0.014*
Latitude:Year (2013)	0.067	0.024	2.803	0.005*
Latitude:Year (2014)	0.072	0.024	3.011	0.003*
Longitude:Year (2008)	-0.026	0.024	-1.088	0.276
Longitude:Year (2009)	0.004	0.022	0.198	0.843
Longitude:Year (2010)	0.076	0.023	3.384	0.001*
Longitude:Year (2011)	-0.026	0.022	-1.173	0.241

Longitude:Year (2012)	0.015	0.023	0.666	0.505	
Longitude:Year (2013)	-0.002	0.021	-0.112	0.911	
Longitude:Year (2014)	-0.052	0.021	-2.474	0.013*	
B. hypnorum					
(a) Latitude	-0.455	0.173	-2.629	0.009*	40185
Longitude	0.103	0.127	0.813	0.416	
Year (2008)	5.028	12.304	0.409	0.683	
Year (2009)	-4.703	9.613	-0.489	0.625	
Year (2010)	0.293	9.428	0.031	0.975	
Year (2011)	-8.717	9.115	-0.956	0.339	
Year (2012)	-13.509	9.083	-1.487	0.137	
Year (2013)	-15.916	9.040	-1.761	0.078	
Year (2014)	-18.432	9.016	-2.044	0.041*	
Garden size (medium)	-0.183	0.035	-5.293	1.2e-07*	
Garden size (small)	-0.521	0.047	-10.995	4.04e-28*	
Garden type (suburban)	0.532	0.035	15.211	2.98e-52*	
Garden type (urban)	0.889	0.073	12.168	4.63e-34*	
Lawn	0.002	0.001	3.597	3.22e-04*	
Flower beds	0.008	0.001	6.434	1.24e-10*	
Shrubberies	0.011	0.001	10.236	1.36e-24*	
Vegetables	0.009	0.002	6.078	1.22e-09*	
Wild	0.009	0.001	6.591	4.36e-11*	
Orchard	-0.024	0.003	-8.792	1.46e-18*	
Wall	-0.001	0.001	-1.626	0.104	
Buildings	-0.010	0.001	-6.734	1.65e-11*	
Coniferous hedge (low)	0.006	0.001	6.517	7.18e-11*	
Deciduous hedge (low)	-0.002	0.001	-1.776	0.076	
Deciduous hedge (high)	-0.005	0.001	-5.366	8.06e-08*	
Other boundary	-0.010	0.001	-6.724	1.77e-11*	
Berry plants (present)	0.684	0.101	6.803	1.02e-11*	
Mixed woodland (present)	-0.178	0.031	-5.712	1.12e-08*	
Scrub (present)	-0.092	0.035	-2.651	0.008*	
Semi-natural grassland (present)	-0.686	0.048	-14.199	9.23e-46*	
Bog (present)	-1.245	0.285	-4.373	1.22e-05*	
Garden (present)	0.233	0.058	4.049	5.15e-05*	
Parks (present)	0.265	0.029	9.045	1.5e-19*	
Active railway (present)	-0.356	0.062	-5.717	1.09e-08*	
Stream (present)	0.370	0.035	10.545	5.34e-26*	
Canal (present)	0.246	0.134	1.828	0.067	
Seashore (present)	-0.561	0.221	-2.538	0.011*	
Latitude:Year (2008)	-0.093	0.237	-0.393	0.695	
Latitude:Year (2009)	0.111	0.185	0.600	0.549	
Latitude:Year (2010)	0.026	0.182	0.145	0.885	
Latitude:Year (2011)	0.211	0.176	1.201	0.230	
Latitude:Year (2012)	0.312	0.175	1.782	0.075	
Latitude:Year (2013)	0.367	0.174	2.107	0.035*	

Latitude:Year (2014)	0.420	0.174	2.420	0.016*
Longitude:Year (2008)	0.193	0.162	1.194	0.232
Longitude:Year (2009)	0.103	0.135	0.760	0.447
Longitude:Year (2010)	0.208	0.132	1.577	0.115
Longitude:Year (2011)	0.052	0.129	0.401	0.688
Longitude:Year (2012)	0.177	0.128	1.378	0.168
Longitude:Year (2013)	0.160	0.128	1.249	0.212
Longitude:Year (2014)	0.108	0.127	0.844	0.399
(b) Latitude	0.084	0.169	0.494	0.621	31194
Longitude	-0.024	0.123	-0.196	0.845
Year (2008)	11.235	11.777	0.954	0.340
Year (2009)	11.540	9.240	1.249	0.212
Year (2010)	8.565	9.113	0.940	0.347
Year (2011)	3.335	8.879	0.376	0.707
Year (2012)	6.797	8.869	0.766	0.443
Year (2013)	-6.972	8.821	-0.790	0.429
Year (2014)	6.628	8.809	0.752	0.452
Garden size (medium)	-0.049	0.024	-2.086	0.037*
Garden size (small)	-0.105	0.033	-3.148	0.002*
Garden age	0.001	4.38e-04	1.416	0.157
Garden type (suburban)	-0.159	0.025	-6.453	1.1e-10*
Garden type (urban)	0.162	0.046	3.558	3.73e-04*
Lawn	-0.001	4.76e-04	-1.869	0.062
Flower beds	-0.009	0.001	-10.861	1.76e-27*
Shrubberies	0.004	0.001	5.706	1.16e-08*
Vegetables	0.003	0.001	2.449	0.014*
Wall	0.005	0.001	9.137	6.45e-20*
Buildings	0.010	0.001	8.422	3.69e-17*
Coniferous hedge (low)	-0.006	0.001	-7.953	1.82e-15*
Coniferous hedge (high)	-0.001	0.001	-2.206	0.027*
Deciduous hedge (low)	0.014	0.001	17.992	2.24e-72*
Deciduous hedge (high)	0.003	0.001	4.738	2.15e-06*
Other boundary	-0.008	0.001	-7.268	3.64e-13*
Berry plants (present)	-0.179	0.069	-2.579	0.01*
Mixed woodland (present)	-0.165	0.023	-7.212	5.5e-13*
Scrub (present)	-0.253	0.025	-9.950	2.53e-23*
Semi-natural grassland (present)	0.163	0.035	4.683	2.83e-06*
Marsh (present)	-0.630	0.061	-10.337	4.78e-25*
Moor (present)	-0.296	0.100	-2.953	0.003*
Nearby orchard (present)	-0.263	0.039	-6.829	8.57e-12*
Garden (present)	0.067	0.044	1.533	0.125
Parks (present)	0.177	0.021	8.593	8.44e-18*
Active railway (present)	0.202	0.043	4.670	3.02e-06*
Stream (present)	0.198	0.024	8.219	2.05e-16*
River (present)	-0.134	0.051	-2.642	0.008*
Canal (present)	1.216	0.057	21.432	6.72e-106*

Latitude:Year (2008)	-0.212	0.227	-0.933	0.351	
Latitude:Year (2009)	-0.211	0.178	-1.188	0.235	
Latitude:Year (2010)	-0.158	0.175	-0.902	0.367	
Latitude:Year (2011)	-0.055	0.171	-0.320	0.749	
Latitude:Year (2012)	-0.125	0.171	-0.733	0.464	
Latitude:Year (2013)	0.146	0.170	0.861	0.389	
Latitude:Year (2014)	-0.116	0.170	-0.685	0.493	
Longitude:Year (2008)	0.030	0.157	0.193	0.847	
Longitude:Year (2009)	0.113	0.130	0.870	0.385	
Longitude:Year (2010)	0.024	0.129	0.190	0.849	
Longitude:Year (2011)	0.012	0.124	0.097	0.922	
Longitude:Year (2012)	0.072	0.124	0.580	0.562	
Longitude:Year (2013)	0.145	0.123	1.177	0.239	
Longitude:Year (2014)	0.001	0.123	0.005	0.996	
B. lapidarius					
(a) Latitude	0.171	0.025	6.788	1.14e-11*	88200
Longitude	0.114	0.027	4.229	2.35e-05*	
Year (2008)	3.424	1.760	1.945	0.052	
Year (2009)	7.266	1.566	4.641	3.47e-06*	
Year (2010)	11.645	1.514	7.690	1.47e-14*	
Year (2011)	12.788	1.482	8.630	6.13e-18*	
Year (2012)	6.976	1.507	4.630	3.65e-06*	
Year (2013)	11.673	1.521	7.674	1.66e-14*	
Year (2014)	9.186	1.488	6.174	6.67e-10*	
Garden size (medium)	-0.091	0.022	-4.195	2.73e-05*	
Garden size (small)	-0.420	0.030	-14.117	2.99e-45*	
Garden age	-0.003	3.74e-04	-8.940	3.9e-19*	
Lawn	-0.001	4.19e-04	-1.875	0.061	
Flower beds	0.007	0.001	8.287	1.16e-16*	
Shrubberies	-0.002	0.001	-2.992	0.003*	
Vegetables	0.005	0.001	4.996	5.84e-07*	
Barren	-0.003	0.001	-4.506	6.6e-06*	
Orchard	0.006	0.001	4.461	8.16e-06	
Fence	-0.001	4.04e-04	-3.378	0.001*	
Wall	0.001	0.001	1.613	0.107	
Buildings	-0.007	0.001	-7.451	9.24e-14*	
Coniferous hedge (low)	0.008	0.001	10.434	1.74e-25*	
Coniferous hedge (high)	-0.004	0.001	-5.653	1.58e-08*	
Deciduous hedge (low)	-0.004	0.001	-5.177	2.25e-07*	
Deciduous hedge (high)	-0.002	0.001	-3.205	0.001*	
Other boundary	-0.011	0.001	-12.189	3.58e-34*	
Altitude	-0.004	0.001	-7.665	1.79e-14*	
Berry plants (present)	0.180	0.050	3.634	2.79e-04*	
Mixed woodland (present)	-0.083	0.019	-4.358	1.31e-05*	
Scrub (present)	0.216	0.021	10.422	1.97e-25*	
Semi-natural grassland (present)	-0.445	0.026	-17.217	1.97e-66*	

Marsh (present)	0.339	0.042	8.083	6.33e-16*	
Moor (present)	-0.172	0.064	-2.701	0.007*	
Garden (present)	0.291	0.032	9.083	1.06e-19*	
Parks (present)	0.142	0.019	7.620	2.53e-14*	
Active railway (present)	-0.106	0.035	-3.027	0.002*	
Stream (present)	-0.078	0.022	-3.514	4.41e-04*	
River (present)	-0.580	0.041	-14.033	9.77e-45*	
Canal (present)	-0.237	0.089	-2.677	0.007*	
Latitude:Year (2008)	-0.072	0.034	-2.153	0.031*	
Latitude:Year (2009)	-0.141	0.030	-4.709	2.49e-06*	
Latitude:Year (2010)	-0.217	0.029	-7.500	6.4e-14*	
Latitude:Year (2011)	-0.235	0.028	-8.297	1.07e-16*	
Latitude:Year (2012)	-0.134	0.029	-4.654	3.25e-06*	
Latitude:Year (2013)	-0.222	0.029	-7.632	2.31e-14*	
Latitude:Year (2014)	-0.174	0.028	-6.131	8.76e-10*	
Longitude:Year (2008)	0.001	0.036	0.023	0.981	
Longitude:Year (2009)	0.008	0.031	0.252	0.801	
Longitude:Year (2010)	-0.017	0.031	-0.543	0.587	
Longitude:Year (2011)	-0.002	0.030	-0.053	0.958	
Longitude:Year (2012)	-0.026	0.030	-0.853	0.394	
Longitude:Year (2013)	0.044	0.030	1.448	0.148	
Longitude:Year (2014)	0.060	0.030	2.011	0.044	
(b) Latitude	0.125	0.016	7.867	3.62e-15*	63191
Longitude	-0.078	0.018	-4.234	2.3e-05*	
Year (2008)	7.129	1.288	5.534	3.14e-08*	
Year (2009)	6.630	1.081	6.135	8.51e-10*	
Year (2010)	7.486	0.998	7.503	6.24e-14*	
Year (2011)	7.030	0.959	7.330	2.3e-13*	
Year (2012)	6.085	1.003	6.069	1.28e-09*	
Year (2013)	6.524	1.002	6.511	7.47e-11*	
Year (2014)	2.791	0.969	2.880	0.004*	
Garden size (medium)	-0.204	0.015	-13.891	7.13e-44*	
Garden size (small)	-0.181	0.020	-8.976	2.8e-19*	
Garden age	-0.001	2.48e-04*	-4.465	8.01e-06*	
Garden type (suburban)	0.027	0.015	1.832	0.067	
Garden type (urban)	0.145	0.034	4.280	1.87e-05*	
Lawn	0.001	2.86e-04	4.476	7.61e-06*	
Flower beds	-0.005	0.001	-7.838	4.57e-15*	
Shrubberies	0.002	0.001	3.397	0.001*	
Wild	0.005	0.001	8.183	2.78e-16*	
Barren	-0.005	0.001	-8.914	4.92e-19*	
Fence	0.001	2.44e-04	4.851	1.23e-06*	
Buildings	-0.002	0.001	-2.633	0.008*	
Coniferous hedge (low)	-0.003	0.001	-6.133	8.62e-10*	
Deciduous hedge (low)	-0.001	0.001	-2.654	0.008*	
Deciduous hedge (high)	0.009	3.69e-04*	23.104	4.2e-118*	

Altitude	0.001	3.67e-04*	1.467	0.142	
Scrub (present)	-0.082	0.014	-5.845	5.06e-09*	
Semi-natural grassland (present)	-0.102	0.019	-5.337	9.47e-08*	
Marsh (present)	0.077	0.028	2.728	0.006*	
Bog (present)	-0.099	0.066	-1.504	0.133	
Nearby orchard (present)	-0.171	0.025	-6.791	1.11e-11*	
Garden (present)	0.099	0.023	4.358	1.32e-05*	
River (present)	-0.252	0.033	-7.665	1.79e-14*	
Canal (present)	-0.196	0.069	-2.840	0.005*	
Seashore (present)	0.409	0.055	7.450	9.31e-14*	
Latitude:Year (2008)	-0.133	0.025	-5.438	5.4e-08*	
Latitude:Year (2009)	-0.121	0.021	-5.869	4.38e-09*	
Latitude:Year (2010)	-0.139	0.019	-7.324	2.4e-13*	
Latitude:Year (2011)	-0.132	0.018	-7.242	4.41e-13*	
Latitude:Year (2012)	-0.116	0.019	-6.098	1.08e-09*	
Latitude:Year (2013)	-0.118	0.019	-6.197	5.75e-10*	
Latitude:Year (2014)	-0.053	0.018	-2.865	0.004*	
Longitude:Year (2008)	0.121	0.025	4.921	8.59e-07*	
Longitude:Year (2009)	0.198	0.022	9.131	6.79e-20*	
Longitude:Year (2010)	0.110	0.021	5.309	1.1e-07*	
Longitude:Year (2011)	0.080	0.020	3.980	6.89e-05*	
Longitude:Year (2012)	0.087	0.021	4.114	3.89e-05*	
Longitude:Year (2013)	0.197	0.020	9.650	4.93e-22*	
Longitude:Year (2014)	0.091	0.020	4.477	7.58e-06*	
B. pascuorum					
(a) Latitude	0.099	0.023	4.365	1.27e-05*	101659
Longitude	-0.090	0.024	-3.710	2.07e-04*	
Year (2008)	-5.319	1.505	-3.534	4.09e-04*	
Year (2009)	-6.994	1.377	-5.079	3.79e-07*	
Year (2010)	-4.286	1.360	-3.152	0.002*	
Year (2011)	-3.486	1.339	-2.604	0.009*	
Year (2012)	-3.613	1.339	-2.698	0.007*	
Year (2013)	-0.729	1.326	-0.550	0.582	
Year (2014)	-2.676	1.310	-2.043	0.041*	
Garden size (medium)	-0.017	0.021	-0.829	0.407	
Garden size (small)	-0.177	0.027	-6.446	1.15e-10*	
Garden age	0.003	3.53e-04	9.717	2.56e-22*	
Garden type (suburban)	-0.067	0.019	-3.482	4.97e-04*	
Garden type (urban)	-0.066	0.045	-1.459	0.145	
Lawn	0.001	3.9e-04	2.789	0.005*	
Flower beds	0.002	0.001	2.642	0.008*	
Shrubberies	0.002	0.001	2.135	0.033*	
Vegetables	0.015	0.001	16.782	3.31e-63*	
Wild	0.006	0.001	7.739	1e-14*	
Barren	0.006	0.001	8.751	2.11e-18*	
Orchard	-0.011	0.001	-8.367	5.92e-17*	

Fence	-0.002	3.70e-04	-5.615	1.96e-08*
Wall	-0.003	4.75e-04	-5.360	8.32e-08*
Buildings	-0.003	0.001	-4.218	2.47e-05*
Coniferous hedge (low)	0.004	0.001	6.111	9.92e-10*
Coniferous hedge (high)	-0.001	0.001	-2.487	0.013*
Deciduous hedge (low)	0.002	0.001	2.891	0.004*
Deciduous hedge (high)	-0.003	0.001	-5.177	2.26e-07*
Other boundary	-0.005	0.001	-6.081	1.19e-09*
Altitude	-0.001	4.5e-04	-1.549	0.121
Berry plants (present)	0.174	0.043	4.085	4.4e-05*
Mixed woodland (present)	-0.145	0.017	-8.356	6.49e-17*
Scrub (present)	0.224	0.019	11.884	1.44e-32*
Semi-natural grassland (present)	-0.293	0.023	-12.986	1.47e-38*
Marsh (present)	0.092	0.038	2.397	0.017*
Bog (present)	-0.208	0.074	-2.821	0.005*
Nearby orchard (present)	-0.118	0.030	-3.890	1e-04*
Garden (present)	0.071	0.027	2.571	0.010*
Parks (present)	0.100	0.018	5.610	2.03e-08*
Active railway (present)	-0.424	0.033	-12.748	3.19e-37*
River (present)	-0.054	0.033	-1.627	0.104
Canal (present)	-0.170	0.078	-2.187	0.029*
Seashore (present)	0.320	0.080	4.025	5.7e-05*
Latitude:Year (2008)	0.102	0.029	3.535	4.08e-04*
Latitude:Year (2009)	0.134	0.026	5.086	3.66e-07*
Latitude:Year (2010)	0.079	0.026	3.041	0.002*
Latitude:Year (2011)	0.067	0.026	2.631	0.009*
Latitude:Year (2012)	0.068	0.026	2.668	0.008*
Latitude:Year (2013)	0.021	0.025	0.814	0.416
Latitude:Year (2014)	0.048	0.025	1.910	0.056
Longitude:Year (2008)	0.070	0.031	2.270	0.023*
Longitude:Year (2009)	0.053	0.028	1.880	0.060
Longitude:Year (2010)	-0.012	0.028	-0.436	0.663
Longitude:Year (2011)	0.060	0.027	2.187	0.029*
Longitude:Year (2012)	0.026	0.027	0.954	0.340
Longitude:Year (2013)	0.008	0.027	0.287	0.774
Longitude:Year (2014)	-0.037	0.027	-1.400	0.162
(b) Latitude	0.057	0.017	3.358	0.001*	115405
Longitude	-0.054	0.019	-2.810	0.005*
Year (2008)	-3.269	1.130	-2.895	0.004*
Year (2009)	-3.915	1.027	-3.813	1.37e-04*
Year (2010)	-2.541	1.023	-2.484	0.013*
Year (2011)	-2.151	1.010	-2.131	0.033*
Year (2012)	-2.201	1.009	-2.181	0.029*
Year (2013)	0.026	0.985	0.027	0.979
Year (2014)	-1.646	0.987	-1.668	0.095
Garden size (medium)	-0.004	0.016	-0.249	0.803

Garden size (small)	-0.111	0.022	-5.132	2.87e-07*
Garden age	0.002	2.79e-04	7.583	3.38e-14*
Garden type (suburban)	-0.037	0.015	-2.482	0.013*
Garden type (urban)	-0.037	0.035	-1.034	0.301
Lawn	0.001	3.06e-04	2.072	0.038
Flower beds	0.001	0.001	1.995	0.046*
Shrubberies	0.001	0.001	1.471	0.141
Vegetables	0.009	0.001	13.187	1.05e-39*
Wild	0.003	0.001	5.748	9.02e-09*
Barren	0.004	0.001	6.786	1.15e-11*
Orchard	-0.007	0.001	-6.499	8.11e-11*
Fence	-0.001	2.91e-04	-4.956	7.21e-07*
Wall	-0.002	3.67e-04	-4.413	1.02e-05*
Buildings	-0.002	0.001	-3.129	0.002*
Coniferous hedge (low)	0.003	0.001	4.974	6.57e-07*
Coniferous hedge (high)	-0.001	4.63e-04	-2.019	0.044*
Deciduous hedge (low)	0.001	0.001	2.332	0.020*
Deciduous hedge (high)	-0.002	4.41e-04	-4.339	1.43e-05*
Other boundary	-0.003	0.001	-5.275	1.33e-07*
Berry plants (present)	0.109	0.035	3.165	0.002*
Mixed woodland (present)	-0.088	0.014	-6.502	7.94e-11*
Scrub (present)	0.133	0.014	9.272	1.83e-20*
Semi-natural grassland (present)	-0.179	0.018	-10.046	9.56e-24*
Marsh (present)	0.055	0.029	1.869	0.062
Bog (present)	-0.135	0.055	-2.448	0.014*
Nearby orchard (present)	-0.072	0.024	-2.996	0.003*
Garden (present)	0.031	0.021	1.466	0.143
Parks (present)	0.065	0.014	4.663	3.11e-06*
Active railway (present)	-0.282	0.028	-10.206	1.86e-24*
River (present)	-0.038	0.025	-1.520	0.129
Canal (present)	-0.104	0.063	-1.660	0.097
Seashore (present)	0.166	0.055	2.984	0.003*
Latitude:Year (2008)	0.063	0.022	2.895	0.004*
Latitude:Year (2009)	0.075	0.020	3.816	1.35e-04*
Latitude:Year (2010)	0.047	0.020	2.384	0.017*
Latitude:Year (2011)	0.042	0.019	2.153	0.031*
Latitude:Year (2012)	0.042	0.019	2.154	0.031*
Latitude:Year (2013)	0.004	0.019	0.194	0.846
Latitude:Year (2014)	0.029	0.019	1.550	0.121
Longitude:Year (2008)	0.047	0.025	1.893	0.058
Longitude:Year (2009)	0.036	0.022	1.623	0.105
Longitude:Year (2010)	-0.008	0.022	-0.354	0.723
Longitude:Year (2011)	0.039	0.022	1.793	0.073
Longitude:Year (2012)	0.017	0.022	0.766	0.444
Longitude:Year (2013)	0.010	0.021	0.468	0.640
Longitude:Year (2014)	-0.025	0.021	-1.167	0.243

B. pratorum

(a) Latitude	0.055	0.045	1.226	0.220	41869
Longitude	0.007	0.050	0.149	0.882	
Year (2008)	-5.855	3.137	-1.867	0.062	
Year (2009)	-0.491	2.657	-0.185	0.853	
Year (2010)	-0.083	2.664	-0.031	0.975	
Year (2011)	5.093	2.574	1.979	0.048*	
Year (2012)	-2.756	2.636	-1.045	0.296	
Year (2013)	2.348	2.578	0.911	0.362	
Year (2014)	3.375	2.494	1.353	0.176	
Garden size (medium)	-0.090	0.035	-2.579	0.01*	
Garden size (small)	-0.097	0.047	-2.087	0.037*	
Garden age	0.002	0.001	3.058	0.002*	
Garden type (suburban)	0.025	0.035	0.721	0.471	
Garden type (urban)	-0.576	0.098	-5.903	3.56e-09*	
Lawn	0.007	0.001	10.507	8.02e-26*	
Flower beds	0.013	0.001	9.870	5.61e-23*	
Shrubberies	0.010	0.001	8.413	4e-17*	
Vegetables	0.007	0.002	4.295	1.75e-05*	
Wild	0.025	0.001	20.741	1.47e-95*	
Barren	0.006	0.001	4.446	8.73e-06*	
Fence	-0.005	0.001	-8.966	3.07e-19*	
Wall	-0.006	0.001	-6.921	4.47e-12*	
Coniferous hedge (low)	0.002	0.001	2.042	0.041*	
Deciduous hedge (low)	-0.005	0.001	-4.052	5.08e-05*	
Deciduous hedge (high)	-0.007	0.001	-6.823	8.94e-12*	
Other boundary	-0.008	0.001	-6.128	8.91e-10*	
Altitude	-0.009	0.001	-10.065	7.92e-24*	
Berry plants (present)	0.669	0.097	6.897	5.3e-12*	
Mixed woodland (present)	0.138	0.030	4.581	4.62e-06*	
Scrub (present)	-0.226	0.035	-6.450	1.12e-10*	
Semi-natural grassland (present)	-0.272	0.042	-6.509	7.58e-11*	
Marsh (present)	0.726	0.060	12.156	5.3e-34*	
Moor (present)	0.738	0.075	9.797	1.16e-22*	
Bog (present)	-2.207	0.307	-7.198	6.11e-13*	
Nearby orchard (present)	0.181	0.050	3.622	2.92e-04*	
Parks (present)	0.230	0.032	7.279	3.35e-13*	
Active railway (present)	-0.558	0.069	-8.072	6.92e-16*	
River (present)	-0.136	0.058	-2.337	0.019*	
Canal (present)	-1.435	0.233	-6.170	6.83e-10*	
Latitude:Year (2008)	0.114	0.060	1.892	0.059	
Latitude:Year (2009)	0.016	0.051	0.309	0.757	
Latitude:Year (2010)	0.011	0.051	0.220	0.826	
Latitude:Year (2011)	-0.090	0.049	-1.824	0.068	
Latitude:Year (2012)	0.058	0.051	1.149	0.251	
Latitude:Year (2013)	-0.037	0.049	-0.755	0.450	

Latitude:Year (2014)	-0.053	0.048	-1.119	0.263	
Longitude:Year (2008)	0.198	0.066	3.002	0.003*	
Longitude:Year (2009)	0.045	0.056	0.805	0.421	
Longitude:Year (2010)	0.155	0.056	2.761	0.006*	
Longitude:Year (2011)	-0.034	0.054	-0.637	0.524	
Longitude:Year (2012)	0.099	0.056	1.789	0.074	
Longitude:Year (2013)	0.025	0.054	0.455	0.649	
Longitude:Year (2014)	-0.009	0.053	-0.178	0.859	
(b) Latitude	0.034	0.022	1.602	0.109	21362
Longitude	-0.097	0.007	-14.350	1.07e-46*	
Year (2008)	7.243	1.764	4.105	4.04e-05*	
Year (2009)	9.099	1.456	6.251	4.08e-10*	
Year (2010)	4.163	1.415	2.943	0.003*	
Year (2011)	4.030	1.345	2.997	0.003*	
Year (2012)	1.988	1.356	1.466	0.143	
Year (2013)	2.271	1.317	1.725	0.085	
Year (2014)	-2.427	1.241	-1.955	0.051	
Garden size (medium)	0.092	0.026	3.483	4.96e-04*	
Garden size (small)	0.049	0.037	1.308	0.191	
Garden age	-0.002	4.8e-04	-4.578	4.7e-06*	
Garden type (suburban)	0.072	0.028	2.620	0.009*	
Garden type (urban)	0.242	0.071	3.411	0.001*	
Lawn	0.003	0.001	6.025	1.69e-09*	
Shrubberies	0.008	0.001	9.305	1.34e-20*	
Vegetables	-0.006	0.001	-5.412	6.24e-08*	
Wild	0.011	0.001	12.884	5.53e-38*	
Fence	0.002	4.52e-04	4.818	1.45e-06*	
Buildings	-0.003	0.001	-2.052	0.04*	
Coniferous hedge (high)	0.002	0.001	2.064	0.039*	
Deciduous hedge (high)	0.011	0.001	17.355	1.82e-67*	
Other boundary	0.008	0.001	9.677	3.78e-22*	
Berry plants (present)	-0.156	0.070	-2.229	0.026*	
Mixed woodland (present)	-0.067	0.023	-2.930	0.003*	
Scrub (present)	0.150	0.025	6.078	1.22e-09*	
Semi-natural grassland (present)	-0.048	0.032	-1.488	0.137	
Marsh (present)	0.242	0.043	5.596	2.19e-08*	
Moor (present)	0.187	0.052	3.627	2.87e-04*	
Nearby orchard (present)	-0.514	0.044	-11.781	4.87e-32*	
Parks (present)	0.149	0.024	6.158	7.39e-10*	
Active railway (present)	-0.165	0.057	-2.917	0.004*	
Stream (present)	-0.096	0.027	-3.524	4.25e-04*	
River (present)	-0.205	0.046	-4.488	7.2e-06*	
Seashore (present)	0.276	0.088	3.127	0.002*	
Latitude:Year (2008)	-0.142	0.033	-4.286	1.82e-05*	
Latitude:Year (2009)	-0.175	0.027	-6.374	1.84e-10*	
Latitude:Year (2010)	-0.081	0.027	-3.056	0.002*	

Latitude:Year (2011)	-0.079	0.025	-3.123	0.002*
Latitude:Year (2012)	-0.042	0.025	-1.660	0.097
Latitude:Year (2013)	-0.045	0.025	-1.810	0.070
Latitude:Year (2014)	0.044	0.023	1.909	0.056
B. terrestris/lucorum				
(a) Latitude	-0.242	0.025	-9.717	2.55e-22*
Longitude	-0.064	0.027	-2.341	0.019*
Year (2008)	-3.737	1.628	-2.296	0.022*
Year (2009)	-13.393	1.487	-9.004	2.17e-19*
Year (2010)	-12.243	1.475	-8.302	1.02e-16*
Year (2011)	-10.376	1.454	-7.134	9.75e-13*
Year (2012)	-9.778	1.463	-6.683	2.34e-11*
Year (2013)	-8.600	1.451	-5.927	3.09e-09*
Year (2014)	-8.377	1.427	-5.871	4.33e-09*
Garden size (medium)	-0.094	0.021	-4.524	6.07e-06*
Garden size (small)	-0.266	0.027	-9.881	5.03e-23*
Garden age	0.002	3.5e-04	4.837	1.32e-06*
Lawn	-0.003	3.95e-04	-7.538	4.76e-14*
Flower beds	0.004	0.001	5.234	1.65e-07*
Shrubberies	-0.002	0.001	-2.771	0.006*
Vegetables	0.009	0.001	9.502	2.06e-21*
Wild	0.008	0.001	9.396	5.66e-21*
Barren	-0.002	0.001	-3.304	0.001*
Orchard	0.004	0.001	3.215	0.001*
Fence	-0.005	3.24e-04	-14.818	1.12e-49*
Coniferous hedge (low)	0.002	0.001	3.170	0.002*
Coniferous hedge (high)	-0.005	0.001	-9.423	4.39e-21*
Deciduous hedge (low)	-0.009	0.001	-13.281	2.99e-40*
Deciduous hedge (high)	-0.001	0.001	-1.825	0.068
Other boundary	-0.006	0.001	-7.231	4.78e-13*
Altitude	-0.001	4.57e-04	-1.837	0.066
Berry plants (present)	-0.323	0.043	-7.549	4.37e-14*
Mixed woodland (present)	0.096	0.018	5.438	5.4e-08*
Scrub (present)	0.180	0.020	9.169	4.79e-20*
Semi-natural grassland (present)	-0.239	0.022	-10.759	5.38e-27*
Marsh (present)	0.375	0.042	8.889	6.18e-19*
Bog (present)	0.567	0.087	6.496	8.24e-11*
Nearby orchard (present)	-0.049	0.030	-1.629	0.103
Garden (present)	0.107	0.028	3.808	1.40e-04*
Parks (present)	0.131	0.018	7.432	1.07e-13*
Active railway (present)	-0.295	0.031	-9.516	1.80e-21*
River (present)	0.101	0.035	2.853	0.004*
Canal (present)	-0.333	0.075	-4.450	8.57e-06*
Seashore (present)	0.435	0.093	4.667	3.06e-06*
Latitude:Year (2008)	0.069	0.031	2.211	0.027*
Latitude:Year (2009)	0.250	0.028	8.798	1.40e-18*

Latitude:Year (2010)	0.227	0.028	8.043	8.74e-16*
Latitude:Year (2011)	0.193	0.028	6.943	3.84e-12*
Latitude:Year (2012)	0.182	0.028	6.505	7.76e-11*
Latitude:Year (2013)	0.160	0.028	5.780	7.45e-09*
Latitude:Year (2014)	0.156	0.027	5.704	1.17e-08*
Longitude:Year (2008)	0.017	0.034	0.491	0.623
Longitude:Year (2009)	0.070	0.031	2.283	0.022*
Longitude:Year (2010)	0.027	0.031	0.875	0.382
Longitude:Year (2011)	0.062	0.030	2.070	0.038
Longitude:Year (2012)	0.010	0.030	0.313	0.754
Longitude:Year (2013)	0.048	0.030	1.598	0.110
Longitude:Year (2014)	0.046	0.030	1.552	0.121
(b) Latitude	0.055	0.008	6.861	6.85e-12*
Longitude	-0.023	0.009	-2.563	0.010*
Year (2008)	0.139	0.536	0.259	0.796
Year (2009)	-2.100	0.487	-4.316	1.59e-05*
Year (2010)	-1.070	0.493	-2.170	0.030*
Year (2011)	-0.251	0.480	-0.522	0.602
Year (2012)	0.197	0.475	0.414	0.679
Year (2013)	3.174	0.466	6.813	9.55e-12*
Year (2014)	0.348	0.465	0.748	0.455
Garden size (medium)	-0.046	0.007	-6.208	5.37e-10*
Garden size (small)	-0.085	0.010	-8.278	1.25e-16*
Garden age	0.001	1.3e-04	3.881	1.04e-04*
Garden type (suburban)	0.001	0.007	0.103	0.918
Garden type (urban)	0.047	0.017	2.687	0.007*
Lawn	0.001	1.43e-04	8.186	2.7e-16*
Flower beds	-0.001	2.88e-04	-2.714	0.007*
Shrubberies	0.003	2.57e-04	12.596	2.22e-36*
Wild	0.012	2.51e-04	47.156	2.59e-05*
Barren	-0.003	2.81e-04	-11.501	1.3e-30*
Fence	0.001	1.24e-04	6.281	3.37e-10*
Buildings	-0.003	3.3e-04	-10.012	1.35e-23*
Coniferous hedge (low)	-0.002	2.58e-04	-7.594	3.1e-14*
Coniferous hedge (high)	-0.001	2.21e-04	-4.210	2.56e-05*
Deciduous hedge (low)	0.003	2.46e-04	13.872	9.41e-44*
Deciduous hedge (high)	0.004	1.88e-04	23.695	4.08e-12*
Other boundary	-0.001	2.62e-04	-3.330	0.001*
Altitude	0.001	1.7e-04	3.033	0.002*
Berry plants (present)	-0.079	0.016	-4.899	9.64e-07*
Mixed woodland (present)	-0.091	0.006	-14.051	7.61e-45*
Semi-natural grassland (present)	-0.124	0.008	-14.765	2.48e-49*
Marsh (present)	0.058	0.013	4.464	8.05e-06*
Moor (present)	-0.057	0.017	-3.317	0.001*
Bog (present)	-0.171	0.025	-6.939	3.96e-12*
Nearby orchard (present)	-0.239	0.013	-18.857	2.55e-79*

Garden (present)	0.050	0.010	4.912	9.02e-07*
Parks (present)	0.032	0.007	4.602	4.19e-06*
Active railway (present)	0.109	0.012	8.871	7.23e-19*
Stream (present)	0.058	0.007	7.832	4.79e-15*
River (present)	-0.077	0.012	-6.239	4.4e-10*
Canal (present)	-0.163	0.031	-5.285	1.26e-07*
Seashore (present)	0.607	0.023	26.830	1.44e-16*
Latitude:Year (2008)	-0.003	0.010	-0.265	0.791
Latitude:Year (2009)	0.040	0.009	4.323	1.54e-05*
Latitude:Year (2010)	0.020	0.009	2.139	0.032*
Latitude:Year (2011)	0.004	0.009	0.440	0.660
Latitude:Year (2012)	-0.005	0.009	-0.506	0.613
Latitude:Year (2013)	-0.056	0.009	-6.232	4.61e-10*
Latitude:Year (2014)	-0.009	0.009	-0.966	0.334
Longitude:Year (2008)	0.031	0.011	2.774	0.006*
Longitude:Year (2009)	0.047	0.011	4.473	7.72e-06*
Longitude:Year (2010)	0.074	0.010	7.060	1.67e-12*
Longitude:Year (2011)	0.043	0.010	4.215	2.5e-05*
Longitude:Year (2012)	0.010	0.010	0.966	0.334
Longitude:Year (2013)	0.033	0.010	3.362	0.001*
Longitude:Year (2014)	-0.018	0.010	-1.784	0.074

Chapter 6

BROAD-SCALE CITIZEN SCIENCE SURVEY SUGGESTS THAT URBAN ENVIRONMENTS IN THE UK ARE AN IMPORTANT REFUGE FOR BUMBLEBEES

6.1 Abstract

Bumblebees are currently in global decline and honeybees are declining in Europe and North America, threatening pollination services essential to our health, economy and the functioning of natural ecosystems. In order to effectively protect these pollinators and the services they provide, we first need to understand their population dynamics in relation to changing environments. However, there is currently a paucity of information on species population dynamics making it difficult to assess drivers of decline and target management and conservation measures. Citizen science is increasingly being used to address this knowledge gap as it enables the collection of ecological monitoring data at a scale broad enough to measure population trends. This study assesses the first national bumblebee and honeybee transect monitoring scheme, BeeWalk, a citizen science project launched to gather much needed information on bee abundance trends and identify key habitats that have the potential to support populations. Data is analysed from the first four years (2009-12) of this scheme, investigating the spatial distribution of species abundances and how they relate to local habitat and land-use variables. Findings show that bee abundance varied between species in relation to location within the UK, habitat type and land-use type, affirming the need to look at species-specific conservation requirements. All species were, however, significantly more abundant in parks and gardens compared with other habitats. In addition, generalist bumblebee species were more abundant in the more urbanised southeast regions suggesting that

they may be adapting more readily to rapid urban sprawl compared with long-tongued specialists. These initial results highlight the need for continued species monitoring in order to assess whether encroaching urban habitats will support bee populations in the long-term, and if so in what way should we enhance these habitats to support and increase bee abundance and diversity.

6.2 Introduction

Ecosystem services are the direct and indirect benefits to humankind of ecosystems (Costanza et al., 1997). Human activity has led to wide scale disruptions of ecosystems, eroding their capacity to provide services that are critical to our survival (Daily 1997; Margaret et al., 2004). Animal pollination is considered an important ecosystem service that is critical for the maintenance of biodiversity, human health and the global economy (Millennium Ecosystem Assessment, 2005). Pollination is necessary for the reproduction of many crops (Nabhan and Buchmann, 1997) and the majority of wild plant species (Kearns et al., 1998). Ollerton et al. (2011) estimated that 87.5% of flowering plants depend on animal pollinators with plant-pollinator interactions sustaining the biodiversity and functioning of most terrestrial ecosystems. The global economic value of insect pollination services is estimated at US$215 billion and insect pollinators are responsible for 9.5% of global food production (Gallai et al., 2009). Williams (1994) assessed the pollination requirements of 264 crop species within the European Union and estimated that 84% depended on pollination by insects, particularly bees. Klein et al. (2007) found that of the 124 main crops consumed by humans, ~70%, fruit and vegetables in particular, depend on insect pollinators to reproduce, highlighting the importance of pollinators for human health. Given the scope and importance of

pollination services, it is of great concern that insect pollinators are in decline (Goulson et al., 2008, 2015; Potts et al., 2010; Ollerton, J. et al., 2014). In response to this decline and the associated threat to a crucial ecosystem service, the Fifth Conference of the Parties to the Convention on Biological Diversity established an International Initiative for the Conservation and Sustainable Use of Pollinators in 2000 and subsequent reports stress an urgent need to monitor pollinators in order to prevent further losses (Convention on Biological Diversity, 2016). Vanbergen et al. (2013) emphasised the need for monitoring insect pollinator populations at both a local and landscape scale and over a range of habitats in order to understand anthropogenic impacts on their decline and prevent the erosion of pollination services.

Citizen science engages non-professional volunteers in scientific research and its use in ecology has burgeoned in recent decades (Silvertown, 2009; Dickinson et al., 2010). Benefits of citizen science include educating the public in scientific methods while fostering a positive attitude towards the environment, which has the potential to influence policy change (Dickinson et al., 2010; Trumbull et al., 2000; Bonney et al., 2009; Stepenuck and Green 2015). Studies have shown that it also provides direct benefits to volunteers with individuals reporting a better connectedness with nature and improvements in physical and mental wellbeing (Koss, 2010; Stepenuck and Green 2015; Gooch, 2005; Pillemer et al., 2010). From an ecological perspective, citizen science projects are particularly useful for collecting long-term monitoring data over a broad geographical scale that can be used to investigate the effects of global change on biodiversity (Devictor et al., 2010). There are many examples of these projects across a wide range of taxonomic groups that have revealed species declines and range shifts, changes in community ecology along with the influences of environmental factors such

as climate, habitat and land use change on species populations (see Devictor et al., 2010 for review). This information is integral to nature conservation as it informs future research and influences natural resource planning and policy decisions (Dickinson et al., 2010).

In the UK, bird and butterfly populations are particularly well monitored by national citizen science schemes (Pollard and Yates, 1993; Bibby, 2003; Silvertown, 2009). These schemes have been highly successful in revealing species population changes on a temporal and spatial scale and in elucidating environmental drivers of species population trends (Silvertown, 2009) and this information has been used to set conservation priorities and influence national policies (Eaton et al., 2009). In the case of butterfly populations, volunteer-collected data has revealed climate-induced range shifts (Pateman et al. 2012), increases in population variability towards climatic range boundaries (Oliver et al., 2012) and a stabilising effect of habitat heterogeneity on populations (Oliver et al., 2010). Warren et al. (2001) analysed 24 years' worth of citizen science monitoring data for 46 UK butterfly species and found the dual forces of climate and land-use change were likely to have more of a negative impact on habitat specialists compared with widespread generalists, though half of the generalist species that were analysed still showed signs of decline. Similar environmental drivers of population change have been revealed for birds by analysing large datasets derived from long-term citizen science projects. Pearce-Higgins et al. (2015) analysed trends for 59 breeding bird species in a dataset that was compiled over 45 years, highlighting that habitat specialists and cold-associated species were most at risk from climate change. In a study of the distribution of 88 bird species, Evans et al. (2011) found that habitat specialists had lower urban densities and ratios of urban to rural densities than generalists.

While there is a lot of focus on birds and butterflies in citizen science programmes, other taxonomic groups are often neglected in monitoring and conservation policies despite their importance for biodiversity and humankind (Cardoso et al., 2011). Invertebrates make up 80% of all described species (Cardoso et al., 2011) and provide ecosystem services essential to our economy, well-being and survival (Prather et al., 2012). Worryingly, of the invertebrates that are relatively well recorded such as butterflies, making some analysis of population trends possible, large scale declines in range and abundance have been reported (Gaston and Fuller, 2007; Thomas et al., 2004; van Swaay et al., 2006). Similar declines in other, less surveyed groups may be going undetected. Bee populations are thought to have undergone global decline with range contractions evident for a number of species and some becoming locally or globally extinct in recent years (Williams, 1982; Goulson et al., 2008, 2015; Potts et al., 2010). However, due to a lack of monitoring, changes in population abundance trends are relatively unknown. A recent report on the status of European bees (Nieto et al., 2014), published as part of the International Union for Conservation of Nature (IUCN) European Red List of Bees and the Status and Trends of European Pollinators (STEP) project, found that nearly one in ten wild bee species (for which sufficient data is available) are threatened with extinction due to habitat degradation from intensive farming, pesticide use, urban development and climate change. However, over half of 1,965 European species were classed as data deficient and their population trends remain unknown. Given the importance of wild and domesticated bees as pollinators (Williams 1994; Goulson et al., 2008; Potts et. al., 2010; Goulson et al., 2015), experts have called for more widespread monitoring of their populations to guide effective conservation action

and reverse their decline (Steffan-Dewenter et al., 2005; Holden, 2006; Potts et al., 2010; Nieto et al., 2014; Goulson et al., 2015).

Bumblebees and honeybees are popular, visible and charismatic insects, traits that make them particularly suited to citizen science monitoring programmes that combine ecological research with public engagement and reconnecting people with nature (Dickinson et al., 2012; Silvertown, 2009). In response to the need for gathering widespread monitoring data on bee populations, the Bumblebee Conservation Trust set up a national bee-monitoring scheme called BeeWalk in 2009. This scheme is broadly based on the very successful Butterfly Monitoring Scheme (Pollard and Yates, 1993) with volunteers identifying and counting honeybees and bumblebees along a regular, monthly transect. The resulting dataset is analysed to provide an initial investigation of the spatial distribution of species densities and assess how they relate to surrounding habitat and land use variables.

6.3 Methods

6.3.1 Data collection

Abundance data were derived from BeeWalk, a honeybee and bumblebee transect monitoring scheme launched in 2009 by the Bumblebee Conservation Trust (BBCT). The aim of the survey is to collect abundance data over time in relation to habitat and climatic variables in order to better monitor UK populations. There are currently over 250 transects established throughout the UK that contribute monthly records. Although honeybee and bumblebee distributions have been historically well documented in the UK with presence records reaching as far back as the 1800s (National Biodiversity Network, 2015), there is a paucity of information on species abundance trends. Garden

BeeWatch, a scheme launched in 2007 by the British Trust for Ornithology, collects information on the abundance of bumblebees in gardens (Chapter 5). BeeWalk is the first survey to use a transect method covering a wide variety of habitat and land-use types (Appendix S6.1). It therefore provides a unique opportunity to analyse widespread species abundance trends and identify key honeybee and bumblebee habitats.

BeeWalk uses a similar survey protocol to the UK Butterfly Monitoring Scheme (UKBMS), a long-term citizen science survey launched in 1976 that has provided key information on butterfly population trends in relation to habitat and climate (Pollard and Yates, 1993; Devictor et al., 2012; Pateman et al., 2012; Oliver et al., 2010 and Oliver et al., 2012). Methods for the UKBMS are described in detail elsewhere (Pollard and Yates, 1993). In summary, volunteers walk a fixed route weekly transect which is divided into sections based on habitat and land use types. The most dominant habitat and land use type in each section is recorded. Participants are asked to walk transects under standardised weather conditions, keeping a steady pace and recording species within a fixed distance either side of them. In the case of BeeWalk, volunteers monitor transects once a month (March-October) rather than weekly since honeybee and bumblebee flight seasons are longer and varies less between species compared with butterflies. Surveys take place between 11am and 5pm in sunny weather conditions with volunteers observing 2m either side of them. (See Appendix S6.1 for full instructions to volunteers). Most volunteers were not experienced in honeybee and bumblebee recording and they were advised to focus on the six common species/groups only in their first year of recording to minimise confusion and misidentification (see Chapter 2). An identification guide for these species and support via email and telephone were provided and

volunteers were encouraged to submit photographs of individual species for identification by an expert when in doubt.

6.3.2 Data analysis

For our analysis, data for the six most common bee species/groups was extracted, which included the bumblebees, *B. hortorum*, *B. hypnorum*, *B. pascuorum*, *B. pratorum*, *B. terrestris/lucorum* and the honey bee, *Apis mellifera*. *B. terrestris* and *B. lucorum* agg. (a species complex comprised of three separate species, *B. lucorum, B. cryptarum* and *B. magnus*) were grouped together as the workers of these species are impossible to separate in the field (Wolf et al*.,* 2010; Scriven et al., 2015). Similar groupings have been used for previous citizen science bumblebee surveys relating to nest density, allowing some comparison with earlier studies (Fussell and Corbet, 1992b; Osborne et al., 2008; Lye et al., 2012). Although it is possible that some rare bumblebee species were mistaken for common ones and included in the final dataset, it is unlikely that this will affect overall trends due to the relatively low frequency of rare species compared to these six common groups within the UK.
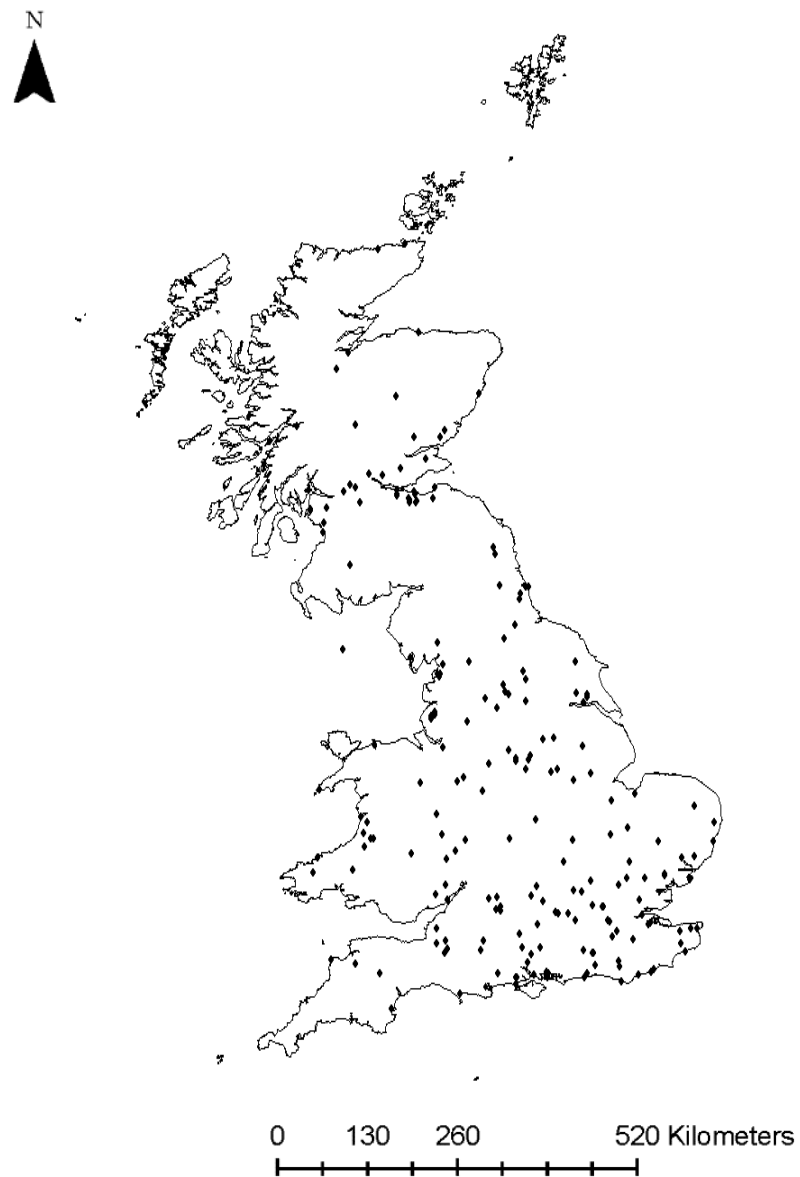
Fig. 6.1 Distribution of BeeWalk transects (2009-12) included in the analysis

All statistical analyses were conducted in R version 3.1.3 (R Core Team, 2014). Under-represented habitat and land-use variables (covering < 10km overall) were excluded from the analysis after which eight categories of each variable were selected based on those containing the highest number of bees. All other categories were grouped together under "Other" (see Table 6.1). A 2-way ANOVA, with species density (the number of individuals recorded per metre per survey) as the dependant variable and species, habitat and land-use categories fitted as factors, was used to investigate interspecies variation in abundance and whether species differed in response in terms of their density to habitat and land-use types. A frequency-comparison analysis was applied to BeeWalk results (see Chapter 5). BeeWalk bumblebee abundance data was summed across years (2009-2012) for each species and compared to the number of flower visits reported in Fussell and Corbet's national survey on forage use (1987 and 1988; Fussell and Corbet 1992a) and the number of nests recorded in their UK-wide nest survey (1989-91; Fussell and Corbet, 1992b). Both of these surveys divide bumblebee species by colour-group with each group designed to include one of the common species, however they do not allow differentiation from rare species if present and males of *B. pratorum* are included in the same colour group as *B. lapidarius*. BeeWalk bumblebee abundance data for each species was compared to the total number of bee visits and nests reported in its related colour-group (Table 5.3). Relationships between relative species proportions derived from the BeeWalk bumblebee abundance dataset and the species proportions in both Fussell and Corbet's nest survey and forage-use survey and the Garden BeeWatch survey (Chapter 5) were investigated using Pearson product-moment correlation coefficients (Table 5.3; Fig. 6.2). *B. hypnorum* was not

included in these analyses since it had not yet been recorded in the UK at the time of the Fussell and Corbet studies (Goulson and Williams, 2001).

Separate negative binomial, zero-inflated, general linear mixed models were run for each species/group using the glmmADMB package in R (Fournier et al., 2012) with number of bees fitted as the response and habitat, land-use, latitude and longitude as fixed factors. Year and transect length were included as random factors to account for inter-annual variation and the likelihood that more bees would be observed on longer transects. This also accounted for repeated measures per transect since transect lengths were unique to each individual transect. Model selection was performed using Akaike's information criterion (AIC).

Table 6.1 Description of variables, with the highest overall bee density, included in the analysis.

	Code	Description
(a) Habitat Variables		
	H10	Fen/swamp/marsh vegetation of inland freshwater edges
	H17	Dry semi/unimproved (flower-rich) neutral grassland
	H21	Stands of tall herbs (e.g. nettle and willow-herb beds)
	H24	Wet willow scrub of fen, river and lake-side
	H30	Small man-made woodlands
	H36	Horticultural crops
	H38	Bare ground/weeds of arable field margins or fallow/recently abandoned arable crops (set-aside so that the land can regenerate naturally)
	H39	Ornamental shrubs/trees/lawns of churches/parks/domestic gardens
	Other	All other habitat types (Appendix S6.2a)
(b) Land Use Variables		
	L1	Agriculture
	L3	Managed forest
	L4	Un-managed forest
	L6	Outdoor amenity and open spaces
	L12	Transport tracks and ways
	L17	Waterways
	L23	Residential
	L41	Unused Land
	Other	All other land use types (Appendix S6.2b)

6.4 Results

Overall, 38,987 individual bees were recorded along a total distance of 371.99 km on 234 transects between 2009 and 2012 (see Fig. 6.1 for spatial distribution of transects). Species/groups differed significantly in overall density (Table 2). *Bombus terrestris/lucorum* had the highest density overall (mean 0.008±0.0005 per metre per survey) followed by *B. pascuorum* (0.006±0.0005), *B. lapidarius* (0.004±0.0003), *A. mellifera* (0.002±0.0003), *B. hortorum* (0.0011±0.0003), *B. pratorum* (0.001±0.0001) and *B. hypnorum* (0.0004±4.68e^{-5})*.* Species density varied in relation to habitat type with parks and gardens associated with the highest density of *B. terrestris/lucorum, B. hypnorum and B. pratorum*, man-made woodland associated with the highest density of *B. lapidarius and B. pascuorum*, herbs associated with the highest density of *B. hortorum* and arable field margins and brownfield sites associated with the highest density of *A. mellifera* (Table 6.2; Fig. 6.3b). The effect of land-use on density also varied according to species (Table 6.2). Gardens were associated with the highest density of four species: *B. terrestris/lucorum, B. hortorum, B. pascuorum* and *B. pratorum* while outdoor amenity/open spaces was associated with the highest density of *B. terrestris/lucorum* and waterways were associated with the highest density of *B. hypnorum* (Fig. 6.3b).

Table 6.2 Analysis of Variance table for a two-way ANOVAs investigating the effect of species along with, (a) habitat and (b) land use on density (the number of individuals recorded per metre per survey)

	df	SS	MS	F value	P value
(a)					
Species	6	0.0853	0.1422	88.81	<0.001
Habitat	8	0.0073	0.0026	16.43	<0.001
Species:Habitat	48	0.238	0.0004	3.1	<0.001
Residuals	11886	1.903	0.0001		
(b)					
Species	6	0.0853	0.1422	87.66	<0.001
Land use	8	0.0073	0.0009	5.61	<0.001
Species: Land use	48	0.0128	0.0002	1.638	<0.01
Residuals	11886	1.928	0.001		

6.4.1 Comparison with earlier studies

Fussell and Corbet received 428 records of bumblebee colonies in their nest survey (1989-91; Fussell and Corbet, 1992b) and 16,260 flower visits by individual bees in their forage-use survey (1987-88; Fussell and Corbet, 1992a). For the same species groups (by excluding *Apis mellifera* and *B. hypnorum*), 33,830 individual bumblebees were recorded by the BeeWalk survey (2009-12). When BeeWalk abundances were compared to Fussell and Corbet's studies, a significant difference in species composition was found for both number of colonies (χ^2=22.89, df=4, p<0.001) and number of flower visits (χ^2=3806.4, df=4, p<0.001). The proportion of *B. pratorum* abundance decreased in 2009-12 in relation to earlier studies while the proportion of *B. pascuorum* increased. The proportion of *B. terrestris/lucorum* is higher in 2009-12 when compared to the number of bee visits in Fussell and Corbet's 1987-88 study but similar to the proportion of nests observed in their 1989-91 survey (Table 6.3; Fussell and Corbet 1992a,b). Similarly to results found for Garden BeeWatch species proportions in Chapter 5, a strong positive correlation (r=0.962, df=3, p<0.01; Fig. 6.2) was found when BeeWalk species proportions were compared with those derived from Fussell and Corbett's nest survey (1989-91) and a weaker, non-significant positive correlation (r=0.724, df=3, p>0.05; Fig 6.2) was found between these data and species proportions in Fussell and Corbett's forage-use survey. A strong positive correlation (r=0.947, df=3, p<0.05) was found between relative species proportions in the Garden BeeWatch survey (2007-14) and those in the BeeWalk survey (2009-12).

Table 6.3 Total number of individuals recorded for each species in the BeeWalk survey (2009-12) and the total number of nests (1989-91) and flower visits (1987-88) recorded for each colour group in the Fussell and Corbet surveys. Numbers in brackets represent the proportion of the total for each survey.

BeeWalk		**Fussell and Corbet**		
Species	No. individuals	Colour pattern category	No. nests	No. bee visits
B. pascuorum	9439 (0.28)	Brown	88 (0.21)	3982 (0.24)
B. lapidarius	6382 (0.19)	Black-bodied, red tails	73 (0.17)	3408 (0.21)
B. pratorum	1804 (0.05)	Banded red tails	39 (0.09)	3337 (0.21)
B. terrestris/lucorum	14704 (0.44)	Two-banded white tails	205 (0.48)	4161 (0.26)
B. hortorum	1501 (0.04)	Three-banded white tails	23 (0.05)	1372 (0.08)

165
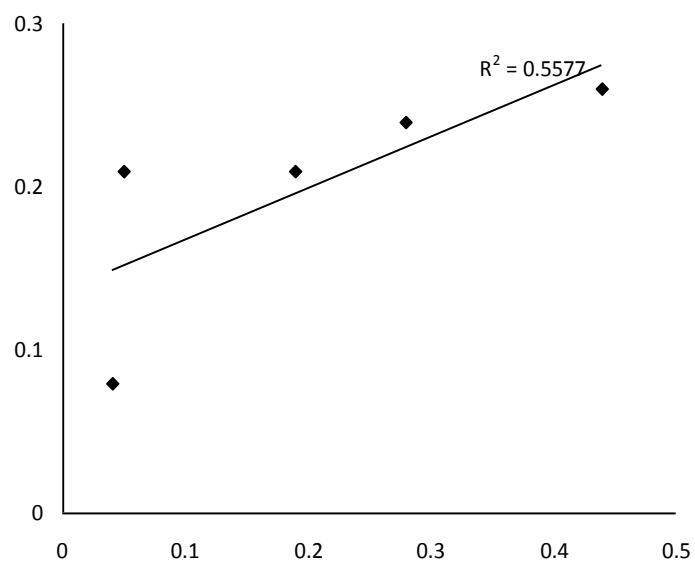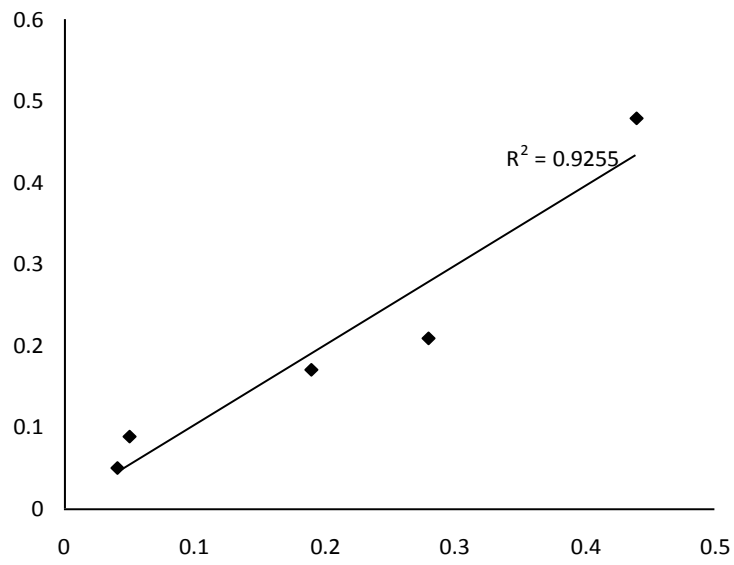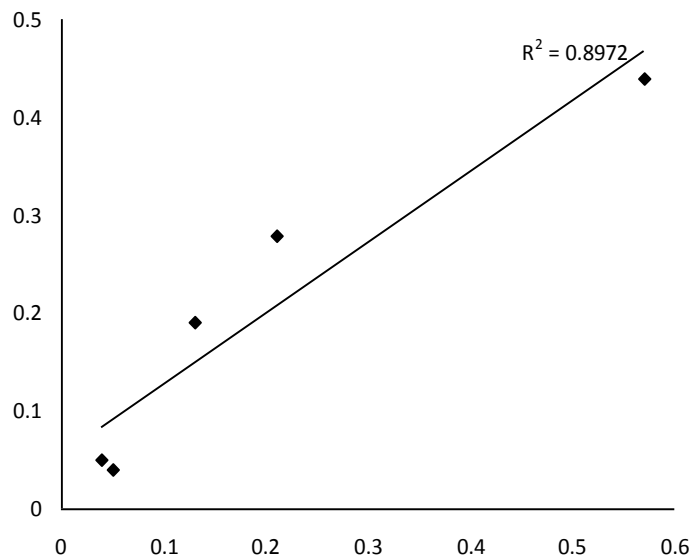
Figure 6.2 Relationship between bumblebee species proportions in the BeeWalk survey (2009-12) and species proportions derived from Fussell and Corbet's (a) nest survey (1989-91), (b) flower visitation survey (1987-88) and (c) Garden BeeWatch survey (2007-14; Chapter 5).

(a)

Legend:
- A. mellifera
- B. hortorum
- B. hypnorum
- B. lapidarius
- B. pascuorum
- B. pratorum
- B. terrestris/lucorum

Average bee density/survey/m

Latitude: 49.91-51.65, 51.66-53.39, 53.4-55.13, 55.14-56.87, 56.87-58.62

Longitude: -7.06- -5.26, -5.27- -3.46, -3.47- -1.66, -1.67- 0.14, 0.15- 1.94

(b)

Legend: A. mellifera, B. hortorum, B. hypnorum, B. lapidarius, B. pascuorum, B. pratorum, B. terrestris/lucorum

Average bee density/survey/m

Habitat: H10, H17, H21, H24, H30, H38, H39, H36, Other

Land Use: L1, L3, L4, L6, L12, L17, L23, L41, Other

Figure 6.3 Bar charts illustrating the relative density of species in relation to (a) Latititude, and longitude (b) habitat variables and (c) land use variables (See Table 6.1 for description of variables). "*" indicates significance of p<.05 (in a least one category for Habitat and Land Use, see also Table S6.2).

6.4.2 Effect of location, habitat and land-use type on individual species abundances.

Location

Bee abundance was significantly affected by the location of transects for all species apart from *B. hortorum* (Supplementary Material S6.1, Fig. 6.3a). Latitude affected species/groups differently with *A. mellifera*, *B. hypnorum* and *B. lapidarius* more abundant in the south while *B. pascuorum* and *B. terrestris/lucorum* were more abundant in the north. Overall bee abundance peaked at intermediate latitudes, being low in the far south but lowest in the north. Only three of the seven species/groups were influenced by longitude with *A. mellifera*, *B. lapidarius* and *B. pratorum* all more abundant in the east (Supplementary Material S6.1, Fig. 6.3a).

Habitat

Habitat had a varying effect on abundance depending on habitat type and species/group (Table 6.2, Supplementary Material S6.1, and Fig. 6.3b). High abundance was positively associated with park and garden habitat for all species/groups. Stands of tall herbs were also associated with higher abundances of all bumblebee species/groups while man-made woodlands were associated with higher abundances of most species (*B. hypnorum, B. lapidarius*, *B. pascuorum* and *B. terrestris/lucorum*). Man-made woodlands were associated with lower abundances

of two species/groups, *A. mellifera* and *B. pratorum*. Three bumblebee species (*B. lapidarius*, *B. pratorum* and *B. terrestris/lucorum*) were highly abundant in flower-rich grassland while inland freshwater vegetation positively affected numbers of *B. terrestris/lucorum* and *B. pratorum*. Field margins of agricultural land had the least positive affect of all habitat types apart from those grouped in the "other" category, associated with higher numbers of only two species/groups, *A. mellifera* and *B. terrestris/lucorum*.

Land-Use

Species densities also varied in their response to land-use type. (Table 6.2, Supplementary Material S6.1, and Fig. 6.3b). Land used for agriculture was associated with lower abundances of most bumblebee species/groups (*B. hypnorum*, *B. pascuorum*, *B. pratorum* and *B. terrestris/lucorum*) and positively associated with higher abundances of *A. mellifera*. Un-used land was associated with lower abundances of all bumblebee species. In contrast, residential areas were positively associated with high abundances of most species/groups (*A. mellifera*, *B. hortorum*, *B. pascuorum* and *B. terrestris/lucorum*). Un-managed forest negatively affected the abundance of most bumblebee species (*B. hortorum*, *B. lapidarius*, *B. pascuorum* and *B. terrestris/lucorum*) while managed forest had a negative effect on three species (*B. pascuorum*, *B. pratorum* and *B. terrestris/lucorum*). Outdoor amenity and open spaces were positively associated with higher abundances of *A. mellifera* and *B. hypnorum* while having a negative effect on *B. hortorum*. Abundances of *B. hypnorum* and *B. terrestris/lucorum* were negatively affected by transport

tracks/ways with *B. terrestris/lucorum* additionally negatively affected by waterways.

6.5 Discussion

A major barrier to assessing the conservation status of UK bees in order to protect against future decline is the paucity of information on their relative abundances due to a lack of monitoring. Here, for the first time a citizen science survey is used to assess the abundances of common UK species on a national scale across a broad variety of different habitats and land use types. The findings reveal interspecific variation across environments but there is a discernible positive effect of urban environments, such as parks, gardens and residential areas on species abundances and a contrasting negative effect of agricultural land. This fits in with the well-established theory that agricultural intensification in the UK as a leading cause of decline in wild bee populations (Williams, 1982; Goulson et al., 2008, 2015; Potts et al., 2010) with urban areas providing refuge in an otherwise impoverished landscape (Goulson et al., 2010; Baldock et al., 2015; Senapathi et al., 2015)

6.5.1 Comparison with earlier studies

Comparison of the relative frequency of species in the BeeWalk survey with previous surveys of bumblebee flower visitation (Fussell and Corbet 1992a) and nest densities (Fussell and Corbet 1992b) reveal a change in the relative abundances of species over time. *B. terrestris/lucorum* is more abundant now compared to a flower visitation study of 1987-88 but similar in abundance to the nest density study of 1989-91. Other studies have found a higher abundance of *B. terrestris/lucorum* in recent years (Osborne et al., 2008; Lye et al., 2012), suggesting that, as a robust set of species that are known for adapting to non-native environments it is more resilient to habitat and land-use change than other species (Chapter 5). *B. pratorum* was less abundant in

the BeeWalk survey compared to previous studies (as in Chapter 5) while *B. pascuorum* showed an increase in relative abundance. It is important to note that these changes may be due to differences in survey methods, for example each Fussell and Corbet study ran for only two seasons while BeeWalk records were collected over a four-year period. Bee populations are highly dynamic with changes in abundance between years (Williams et al., 2001) and shorter-term studies may not account for inter-annual variation. While there are differences for certain species, there is a strong overall correlation between relative species proportions in the BeeWalk data and those in both Fussell and Corbett's nest survey data and Garden BeeWatch data (Fig. 6.2), providing support for the ability of volunteers to collect consistent information on populations. Relative species proportions were less correlated with those in Fussell and Corbett's flower visitation study, a similar pattern to that found for Garden BeeWatch data (Chapter 5). This is likely due to differences in survey methods, for example Fussell and Corbett's flower visitation survey ran from Apr-Oct which potentially led to an underrepresentation of early emerging species, such as *B. terrestris*. The BeeWalk survey is ongoing with an aim to monitor populations in the long term and these initial results will provide a good baseline for comparison of future trends.

6.5.2 Interspecific variation in density across different habitats and land-use types

The results of this study demonstrated that bee species vary in their relative density across different habitats and land use types. Previous studies have found similar differences between bee species in various environments. Carvell (2002) found that UK bumblebee species responded differently to grassland habitat characteristics

based on their foraging and nesting requirements while Carvell et al. (2007) found marked variation in abundance between species in arable field margins under different management regimes. In a study of parks in San Francisco, McFrederick and LeBuhn (2006) also found differences in abundance between species between urban and wild areas, noting the importance of the surrounding landscape as a contributing factor. Interspecific variation across habitat and land use types is most likely due to ecological differences between species with long-tongued bumblebees that specialise on flowers with deeper corollas using different food resources to short tongued generalists (Heinrich, 1979; Inouye, 1978; Goulson and Darvill, 2004). Bumblebees also differ in nesting habitat preferences with carder bees such as *B. pascuorum* utilising on ground sites and requiring sheltered areas of tall grassland or hedgerows. This may explain the finding that lower densities of *B. pascuorum* were associated areas of bare ground, although arable field margins, which could potentially provide shelter, were also included in this habitat category. *B. hypnorum* tends to nest well above ground, often in holes in trees and in bird boxes in urban areas whereas most other common species choose to nest below ground, often in abandoned rodent holes (Carvell, 2002; Goulson et al., 2008). The findings of this study reveal a strong association of high *B. hypnorum* abundances with areas that would provide suitable nesting such as man-made woodlands, gardens and parks. A study of field and forest boundary sites by Kells and Goulson (2003) found similar interspecific variation in nesting habitat preferences of common UK species with *B. pascuorum* and *B. hortorum* favouring tussock-type vegetation and below ground nesters (*Bombus terrestris*, *B. lapidarius* and *B. lucorum*) preferring habitats with raised banks.

Interspecific variation may also be due in part to differences in resource use and/or competition between honeybees and bumblebees. Honeybees are found in similar environments to bumblebees, often utilising similar floral resources yet it is unknown whether or not this leads to competition. Studies investigating potential competition are few and are limited to single habitat types. Steffan-Dewenter and Tscharntke (2000) found no evidence of competition between honeybees, bumblebees and solitary bees in German grassland sites while Walther-Hellwig et al. (2006) found that the introduction of honeybee colonies to agricultural sites had little effect on plant visitation by the short-tongued *B. terrestris* but led to a switch in foraging preferences of the long-tongued *B. pascuorum*. In the UK, Forup and Memmot (2005) found a similar influence of honeybee abundance on bumblebee foraging on lowland heath sites with higher abundance leading to a reduction in the floral host breadth of long tongued species but the authors concluded that although competition cannot be ruled out, further investigation is needed to rule out other potentially contributing factors. Goulson and Sparrow (2009) found that for four species of bumblebee (*B. pascuorum, B. lucorum, B. lapidarius and B. terrestris*), worker size was significantly reduced in areas where honeybees were abundant.

While UK honeybees suffered similar declines to bumblebees following World War 2 due to habitat degradation along with a reduction in beekeeping, population drivers are now likely to vary somewhat across different habitat and land use types. The invasive ectoparasitic mite, *Varroa destructor*, found in Britain in 1991 has led to regional declines in honeybees across Europe, decimating feral populations. Thompson et al. (2014), for example, found that remaining feral honeybee populations in England and Wales had high levels of deformed wing virus (DMV), a

concomitant virus associated with *V. destructor* that leads to colony collapse. Due to this, most remaining honeybee colonies are domesticated and higher abundances of honeybees are likely to be biased towards areas of human activity across both rural and urban habitat and land-use types, as was found in this study where honeybees were positively associated with agricultural areas, residential areas and outdoor amenity spaces.

6.5.3 Spatial patterns of abundance in the UK

Species varied considerably in their patterns of spatial abundance. Three species*, B. hypnorum, A. mellifera* and *B. lapidarius* were found to be more strongly associated with southern latitudes. Two of these species, *A. mellifera* and *B. lapidarius*, along with *B. pratorum* were also found at higher abundances in the east. Although *B. hynorum* has a species distribution that covers a wide range of biotopes, including northern-temperate and southern-montane forests in Europe and Asia (Goulson and Williams, 2001), it is not surprising that it is more abundant in the south of the UK. Despite presence records occurring as far north as central Scotland (BWARS, 2015), its recent arrival to southern UK in 1991 (Goulson and Williams, 2001) means that, while local southern populations have had time to become more established at higher abundances, it is likely northern populations are still growing and expanding. Higher abundances of *B. hypnorum* in the south may also be driven by the species' association with urban habitats with the most densely populated areas in the UK strongly biased towards the southeast (Morton et al., 2011).

While climatic factors may play a certain role the higher abundances of some species in warmer, southern and eastern regions of the UK, it is unlikely that they fully

explain these regional associations. According to Williams' 1988 'marginal mosaic model', species tend to be less abundant towards the edges of their ranges and although *A. mellifera*, *B. lapidarius* and *B. pratorum* have a slightly more southern European distribution limit compared with other species such as *B. hortorum* and *B. pascuorum* they still occur as far north as southern Scandinavia (Rasmont and Iserbyt, 2014).

It is interesting that, of the bumblebee species surveyed, the ones associated with more urban southern and eastern regions are relatively short-tongued, generalist species that emerge earlier than long-tongued species such as *B. hortorum* and *B. pascuorum*, which tend to be more associated with rural habitats (Chapter 4; Goulson et al., 2005; Goulson and Darvill, 2004). These short-tongued generalists may have been more able to adapt quickly in response to the current rapid rate of urbanisation leading to higher population abundances in these areas. As suggested by previous studies on bumblebee distribution and decline, it is likely that a complex combination of these and other potential climatic, ecological and environmental factors drives species population dynamics (Chapter 4; Williams et al., 2007).

6.5.4 Relative abundances across habitat and land-use types.

Higher abundances were positively associated with park and garden habitats for all species, and most species were associated with residential areas. Stands of tall herbs, which are likely to be found within these habitats and residential areas, were also associated with higher species' abundances. This finding supports a number of recent studies that suggest that urban habitats are providing a refuge for pollinators, leading to increases in both species diversity and abundance. Baldock et al. (2015)

compared pollinator communities between cities, farmland and nature reserves finding a higher bee diversity in urban areas. Similarly, Senapathi et al. (2015) found that areas in England surrounded by urban expansion have lost fewer species over the past 80 years compared with other land-use types indicating that more species are able to cope with rapid urbanisation compared with other extensive land use changes such as agricultural intensification. Gardens and parks in particular are increasingly being recognised as important habitats for bees (Chapter 5, Osborne et al., 2008; Chapman et al., 2003; McFrederick and LeBuhn, 2006; Goulson et al., 2010), offering a high diversity of both native and non-native floral resources throughout the foraging season (Gunnarsson and Federsel, 2014). The association between higher bumblebee abundance and gardens may also incorporate a positive effect of rural gardens, which have been shown to provide a refuge for pollinators within an intensively managed agricultural environment (Goulson et al., 2010; Samnegård et al., 2011).

In contrast to urban areas, land used for agriculture was associated with lower abundances for most bumblebee species. This finding is unsurprising since it has long since been established that agricultural intensification is one of the primary causes of bumblebee decline (Goulson et al., 2008, 2015; Williams, 1986). Changes in agricultural practices have led to a loss of floral abundance and diversity and recently, the use of pesticides has been highlighted as having a toxic effect on foraging behaviour, survival and reproduction in both bumblebee (Whitehorn et al., 2012; Feltham et al., 2014; Rundlöf et al., 2015) and honeybee colonies (Henry et al., 2012; Yang et al., 2012). Despite this, results showed that *A. mellifera* was positively associated with agricultural habitats and high abundances of both *A. mellifera* and *B.*

terrestris were associated with margins of agricultural fields and abandoned crops. Both of these species are used commercially, to enhance pollination and increase crop yields (Corbet et al., 1991; Breeze et al., 2011) and managed colonies may increase local counts as volunteers will not differentiate between wild and commercial bees. Field margins have been identified as an important ecological habitat within impoverished agricultural landscapes (Benton et al., 2003) and may increase numbers of such common, short-tongued generalist bees through the provision of flowers and nesting sites. Margins of recently abandoned arable crops (e.g. set aside) in particular may have led to an increase in the abundance of these species which have previously been shown to respond positively to uncropped field margins that have been allowed to regenerate naturally (Kells et al., 2001; Pywell et al., 2005).

Managed woodland had a positive effect on most species and conversely, un-managed forest was associated with lower abundances of most species. This may be an artefact of survey methods since bees will be more visible to recorders in less dense woodland. Numbers may also vary in relation to proximity to the forest or woodland edge with bumblebees displaying a preference for boundaries compared to within woodland areas and clearings (Svensson et al., 2000; Osborne et al., 2008). Traditional coppicing of woodlands is slowly increasing in the UK, particularly on nature reserves, after waning in the 1800s (Fuller and Warren, 1993). This leads to an increase of spring flowers, which may benefit bee populations as it has done with butterflies and moths (Warren and Key, 1991). Managed woodlands also tend to be less dense than forests, allowing more light for visibility and more suitable foraging conditions.

Only three species, *Bombus lapidarius*, *Bombus pratorum* and *Bombus terrestris/lucorum* were positively associated with flower-rich grassland. This is surprising since this habitat is of known importance to bee populations and its degradation is thought to play a key role in species declines (Goulson et al., 2010). It is interesting that all three species are short-tongued generalist bumblebees. Carvell et al., 2006 reported a nationwide decline in key bumblebee forage plants across a wide range of habitats, including unimproved grassland. Fabaceae species, many of which produce flowers with long tubular corollas specialised for pollination by long-tongued bumblebees were among those with high visitation rates that suffered declines at both a local and national scale. Their decline in grassland habitats may have particularly affected abundances of long-tongued bumblebee species since they have a narrower dietary breadth and may adapt less readily than short-tongued species to exploit the remaining floral resources.

6.5.5 Addressing error in data collected by volunteers

Citizen science is invaluable to the field of ecology enabling information to be collected at a scale that would otherwise be impossible, however it is important to note that that there can be some error in this type of volunteer-led data collection. Volunteers differ in their level of experience, motivation and expertise and this variation needs to be addressed and accounted for at both the data collection and analysis stage (Dickinson et al., 2010, Hochachka et al., 2012). This study attempts to address these issues in a number of ways. A standardised protocol designed for collecting information on insect abundance that has proven successful in allowing volunteers to collect long-term scientific information of high ecological value was

used (Pollard and Yates, 1993). Clear instructions were provided to participants and they were encouraged to get in contact with regard to any queries (Supplementary Material S6.2). For the analysis, the dataset was mined for the common, well-known bumblebee species to reduce the level of recorder misidentification. As previously mentioned, the relatively high abundance of these species/groups compared to others means that the inclusion of some misidentified, rare individuals is unlikely to affect overall trends. Even in the remaining fragments of prime habitat for bumblebees in the UK, the vast majority of records are of common species. In a published survey of Salisbury plain, a protected area of 38,000 ha of flower-rich grassland and scrub that is considered the best UK habitat for bumblebees (Carvell, 2002), >80% of records are comprised of the six most common species/groups (Goulson and Darvill, 2004). This strategy has previously been used in other citizen studies involving bumblebee identification by volunteers (Fussell and Corbet, 1992; Osborne et al., 2008; Lye et al., 2012). A potential caveat is the misidentification of honeybees by volunteers who may mistake them for mimic flies such as the drone-fly, *Eristalis tenax*. In a study assessing the use of citizen science to record insect visitors on ivy flowers, Ratnieks et al. (2016) found that most misidentification by volunteers involved mistaking honeybees and wasps for their hoverfly mimics. However, in spite of these misidentifications, volunteer accuracy rates ranged from 79.1-94.3% overall, depending on identification materials and training methods used. This highlights the importance of assessing the accuracy of BeeWalk data in relation to identification materials provided to volunteers and training provision in the future as these factors are likely to affect data reliability (Chapter 2). The final BeeWalk dataset was analysed over a large temporal and spatial scale, looking at

broad trends that were less likely to be affected by variation at a site-specific level, using modelling techniques to account for inter-annual and recorder biases. Even with the application of these techniques, it is important to interpret results with some caution and further studies on both the accuracy of volunteer-collected data and bee population ecology are necessary.

This study highlights the importance of citizen science monitoring in understanding the population dynamics of species at a national scale. It enabled the collection of data on bee abundance data over a wide range of habitats and land use types, enabling assessment of the relative importance of key habitats in terms of population abundance for the first time in the UK. Abundance trends indicate that urban areas are supporting higher numbers of bumblebees and honeybees compared with rural habitats and that short-tongued generalist bumblebees are adapting more readily to land use change than long-tongued specialists. Although this study highlights urban areas, parks and gardens as key habitats for bees, it remains to be seen whether these refuges can offer long-term support for populations that are currently facing extensive habitat and land use change along with the additional stressors of climate change, parasites and pesticides (Goulson et al., 2015). Continued monitoring of these pollinators is crucial in order to confirm these initial trends, understand their importance in relation to other drivers of population change, and protect against future declines.

6.6 Supplementary Material

S6.1 Instructions provided to volunteers

Bumblebee Conservation Trust

Biological and Environmental Sciences

University of Stirling

Stirling, FK9 4LA

Email:Leanne.casey@sussex.ac.uk

Welcome to BeeWalk!

In 2007 the BBCT launched BeeWatch, a survey through which volunteers provide us with digital photograph records of bumblebees. This survey has proven very successful in providing detailed information on the spatial distribution of bumblebee species. However, in order to effectively monitor our declining bumblebee populations it is also important to collect bumblebee *abundance* data. For this reason, a pilot bumblebee transect scheme was launched by the BBCT in 2008. Following positive feedback from this bumblebee transect scheme, we decided to launch "BeeWalk." BeeWalk is a more expansive survey scheme which aims to collect bumblebee abundance data from all across the UK. This type of survey would be impossible without the help of our volunteers.

The information collected by BeeWalk volunteers is integral to monitoring bumblebee population changes and will allow us to detect early warning signs of population declines. All data collected will contribute to important long-term monitoring of bumblebee population changes in response to changes in land-use and climate change.

In order to collect this important information by the transect method you will need to set up a fixed-route walk of 1-2km and take recordings on a monthly basis. It is essential that the walk is a fixed route to allow direct comparisons of bumblebee population trends over time.

This pack provides all the information you will need to set up your transect and begin recording. The following steps outline the main considerations involved:

Step 1: Establish your fixed walk route of 1-2km.

Step 2: Fill out the site description form enclosed, attach a map of your fixed route walk and return it to us.

Step 3: Walk your fixed route monthly recording the bumblebees you observe.

Step 4: Return your records to us by the end of each season.

Thank you for participating in this important survey and for dedicating your time to conserving our native bumblebees.

Best Wishes,

Leanne Casey

BBCT Citizen Science Officer

This step-by-step guide is designed to help you get started by describing the processes involved in collecting your bumblebee abundance data. It is important that you take time to understand these processes so that the important information you collect can be included in a long-term monitoring programme through which results can be compared from year to year. If you have any queries regarding the following steps, please don't hesitate to contact me.

Forms

- **All green forms beginning with letter 'F' require filling out.** F1 should be filled out before you begin recording and a copy sent to us **along with a map of your transect route** so that your site can be registered. F2 is your monthly bumblebee recording form (use one for each monthly walk of the season) copies of which should be returned, preferably using the electronic excel spreadsheet but hard copies are also acceptable, as soon as possible after recording and before November 10th 2012.
- **All blue forms beginning with "G" are guidance forms only.** These forms include examples of how to fill out your F forms (G1 and G2), classification systems (G3 and G4) that you require for filling in details on habitat and land-use types and an example of how to mark your transect route on an OS map (G5).
- **The recorder should retain all original forms.** Copies of filled out forms should be made and sent to us as soon as possible to ensure that information is not lost.

Establishing Your Fixed-Route Transect

- **Transect routes should be approx 1-2km in length, taking about 45-60 minutes to walk**
- **Identify a route that takes in flower-rich habitat.** It is important to consider the location of your route carefully. Your route should easily accessible and located in an area that is convenient for you as the same route will be walked monthly from year to year to enable sightings to be compared.
- **Divide your transect into sections (4-10) according to habitat type** (see Habitat Classification form G3). Note sections in the table provided on Site Description form F1 (see Site Description form G1 for an example). Grid references should be taken from the beginning of each section.
- **Identify the most dominant type of land use in each of your transect sections** (see Land Use Classification form G4). Note land-use types in the

table provided on Site Description form F1 (see Site Description form G1 for an example).

- **Mark your route on a photocopy of an OS map.** You should show clearly where each section of your transect starts and finishes (see Transect Route Map form G5 for an example). This map should be attached to Site Description form F1 and returned to us before recording begins.
- **Notify us if any changes in habitat or land-use occur.**

Walking Your Transect

- **You should walk your transect monthly between and including March and October.**
- **Use a separate monthly recording form (F2) for each walk.**
- **Transects should ideally be walked between 11am and 5pm** and preferably at approximately the same time of day.
- **Transects should only be walked when weather conditions are suitable for bumblebee activity** i.e. warm, sunny days with no more than a light breeze.

Recording Bumblebees

- **Bumblebees should be recorded for on form F2 (see form G2 for an example)**. A separate form should be used for each month. Space is provided for the 6 most common species on the front of the form. Any other species can be recorded on the reverse side. Honeybees should also be noted if possible.
- **Fill in environmental details first.** Before you begin walking fill in name, site, date, weather conditions and start time in the spaces provided on monthly recording form F2 (see monthly recording form G2 for an example).
- **Walk your transect route at a slow steady pace and record all bumblebees you see within 2m of either side of you.** Do not look behind; focus on the area 2m ahead and 2m to either side of you.
- **Maintain a slow steady pace.** Do not linger in hotspots to improve your count, as this will bias results.
- **Nets and pots can be used** to capture bumblebees for closer examination when necessary. For details on suppliers see the Bumblebee Conservation Trust website.
- **Ensure that all recording is completed at the end of each walk.** Double-check for errors, as it will be impossible to accurately fill in any blanks at the end of the season.
- **Where estimates have to be made (when numbers are too large to count accurately) make sure a figure is recorded (e.g.46 rather than 40+).**
- **If something unusual is recorded, add a note at the bottom of the recording sheet to confirm that what you have recorded is correct.** Otherwise anomalous looking data will be omitted.
- **It is very important to note if any changes in habitat or land use occur.**

- **Where possible record the caste (queen, worker, male) of each individual and make a note of any interesting behaviour.**
- **Don't forget to fill in the finish time at the end of your walk.**

Useful Identification References

Field Guide to the bumblebees of Great Britain and Ireland. Revised Edition. Edwards M and Jenner M, 2009. UK: Ocelli.

A Pocket Guide to the Bumblebees of Britain and Ireland. Pinchen BJ, 2006. Forficula Books.

What's that Bumblebee? Bumblebee Conservation Trust, 2010. Laminated identification guide.

Health and Safety
- Take a mobile phone with you.
- Let at least one other person know when and where you are going out and when you will return (let them know when you have returned).
- Wear appropriate footwear and clothing for the terrain and weather conditions.
- Take some water with you.
- Apply sun block if necessary.

Once you have decided on your transect please send a copy of Site Description form F1 along with a map of your fixed route to:

> BeeWalk,
> Bumblebee Conservation Trust,
> Biological and Environmental Sciences
> University of Stirling,
> Stirling
> FK9 4LA

If you are still unsure of anything, please don't hesitate to contact me.

> Happy BeeWalking!!

Best Wishes,

Leanne Casey

BBCT Citizen Science Officer

F1: Site Description Form

(Please refer G1 for an example form)

Habitat and Land Use Details *(Please refer to forms G3 and G4 for codes and descriptions)*

Site Details

Recorder Details:		OS Grid Ref (Centre,6Fig):
Site Name :		OS Map No (1:50000):
County:		Transect Length (m):
Year Transect established:		

Section	Length	Grid Ref	Habitat Description	Code (s)	Land Use Description	Code (s)

G1: Site Description Form

Habitat and Land Use Details *(Please refer to forms G3 and G4 for codes and descriptions)*

Recorder Details: *Leanne Casey*	
	OS Grid Ref (Centre,6Fig): *NT159988*
Site Name : *Vane Farm Nature Reserve*	**OS Map No (1:50000):** *58*
County: *Kinross*	**Transect Length (m):** *1200*
Year Transect established: *2010*	

Section	Length	Grid Ref	Habitat Description *(see G3)*	Code (s)	Land Use Description *(see G4)*	Code (s)
1	316m	NT156988	*BBCT bumblebee reserve, Dry semi unimproved flower rich neutral grassland*	H17	*Unused land, Transport tracks and ways*	L41, L12
2	105m	NT1599O	*Car park, bare ground/woodland herb/grass mosaics of woodland rides, hedgebanks and green lanes and small man made woodland*	H30,H32	*Managed forest*	L3
3	232m	NT160989	*Bracken dominated glades or hillsides and mature broadleaved woodland*	H20,H26	*Un-managed forest*	L4
4	351m	NT161987	*Wet and dry heathland/ dry heather moorland*	H23	*Unused Land*	L41
5	196m	Nt161989	*Bracken dominated glades or hillsides and mature broadleaved woodland*	H20,H26	*Managed forest, Transport tracks and ways*	L3,L12

F2: Monthly Recording Form

Recorder:	Site:
Date:	Temp:
Start Time:	Finish Time:

Wind(please circle):   None   Light   Breezy

Weather conditions(please circle) Sunny   Sunny/Cloudy   Cloudy

Species	Caste	Section 1	Section 2	Section 3	Section 4	Section 5	Section 6	Section 7	Section 8	Section 9	Section 10	Total
Buff-tailed *B.terrestris*	Queen											
	Worker											
	Male											
Red-tailed *B.lapidarius*	Queen											
	Worker											
	Male											
Early *B.pratorum*	Queen											
	Worker											
	Male											
Garden *B. hortorum*	Queen											
	Worker											
	Male											
Common Carder *B. pascuorum*	Queen											
	Worker											
	Male											
White-tailed	Queen											

B. lucorum	Worker											
	Male											

(Please refer to G2 for an example form)

Other Species	Caste	Section 1	Section 2	Section 3	Section 4	Section 5	Section 6	Section 7	Section 8	Section 9	Section 10	Total
	Queen											
	Worker											
	Male											
	Queen											
	Worker											
	Male											
	Queen											
	Worker											
	Male											
	Queen											
	Worker											
	Male											
	Queen											
	Worker											
	Male											
	Queen											
	Worker											
	Male											

Additional Comments (e.g. Has any management such us ploughing, hedge cutting, burning etc. taken place? Were any unusual behaviours observed?)

G2: Monthly Recording Form

Recorder: *Leanne Casey*	Site: *Vane Farm, Kinross*
Date: *13/06/10*	Temp: *15 ° C*
Start Time: *09:00*	Finish Time: *10:30*

Wind(please circle):   None   (Light)   Breezy

Weather conditions(please circle) Sunny   (Sunny/Cloudy)   Cloudy

Species	Caste	Section 1	Section 2	Section 3	Section 4	Section 5	Section 6	Section 7	Section 8	Section 9	Section 10	Total
Buff-tailed *B.terrestris*	Queen	II	I		III	II						**8**
	Worker	II	I	II	IIII							**9**
	Male											**0**
Red-tailed *B.lapidarius*	Queen	I	I		II	I						**5**
	Worker	I	II	I	I	IIII						**9**
	Male											**0**
Early *B.pratorum*	Queen											
	Worker											
	Male											
Garden *B. hortorum*	Queen											
	Worker											
	Male											
	Queen											

Common Carder *B. pascuorum*	Worker											
	Male											
White-tailed *B. lucorum*	Queen											
	Worker											
	Male											

Other Species	Caste	Section 1	Section 2	Section 3	Section 4	Section 5	Section 6	Section 7	Section 8	Section 9	Section 10	Total
Heath B. jonellus	Queen	I			I							**2**
	Worker											
	Male											
Field cuckoo B. campestris	Queen											
	Worker			I								**1**
	Male											
	Queen											
	Worker											
	Male											
	Queen											
	Worker											
	Male											
	Queen											
	Worker											
	Male											
	Queen											
	Worker											
	Male											

G3: Habitat Classification

Code	Habitat Type
H1	Marine saltmarshes/estuaries/saline reedbeds
H2	Coastal dune grassland
H3	Coastal dune and sand heath
H4	Coastal dune and sand scrub
H5	Coastal dune and sand woods
H6	Coastal dune slacks
H7	Coastal Machair
H8	Coastal shingle
H9	Coastal cliffs/undercliffs
H10	Fen/swamp/marsh vegetation of inland freshwater edges
H11	Bare ground/sparse vegetation of inland freshwater edges
H12	Acid bog/mire habitats
H13	Flushes
H14	Inland swamp/fen stands without open water (e.g. reed and sedgebeds)
H15	Dry semi/unimproved (flower-rich) chalk/limestone grassland
H16	Dry semi/unimproved acid grassland
H17	Dry semi/unimproved (flower-rich) neutral grassland
H18	Agriculturally improved/re-seeded/ heavily fertilised grassland
H19	Seasonally wet and wet marshy grasslands
H20	Bracken dominated glades or hillsides -(EUNIS code)
H21	Stands of tall herbs (e.g. nettle and willow-herb beds)
H22	Dry scrub/shrub thickets
H23	Wet and dry heathland/ dry heather moorland
H24	Wet Willow scrub of fen, river and lake-side
H25	Hedgerows
H26	Mature broadleaved woodland
H27	Mature coniferous woodland
H28	Mature mixed broadleaved and coniferous woodland
H29	Lines of trees or scattered trees of parkland
H30	Small man-made woodlands
H31	Recently felled areas/early-stage woodland and coppice
H32	Bare ground/woodland herb/grass mosaics of woodland rides, hedgebanks and green lanes
H33	Orchards, hop gardens and vineyards
H34	Inland screes/cliffs/ rock pavements, and outcrops
H35	Intensive arable crops
H36	Horticultural crops
H37	Organic arable crops
H38	Bare ground/weeds of arable field margins or fallow/recently abandoned arable crops (e.g. set-aside)
H39	Ornamental shrubs/trees/lawns of churches/parks/domestic gardens etc
H40	Bare ground/weed communities of post-industrial sites

G4: Land Use Classification

Code	Land Use Type
L1	Agriculture
L2	Fisheries
L3	Managed forest
L4	Un-managed forest
L5	Mineral workings and quarries
L6	Outdoor amenity and open spaces
L7	Amusement and show places
L8	Libraries, museums and galleries
L9	Sports facilities and grounds
L10	Holiday parks and camps
L11	Allotments and city farms
L12	Transport tracks and ways
L13	Transport terminals and interchanges
L14	Car parks
L15	Vehicle storage
L16	Goods and freight terminals
L17	Waterways
L18	Energy production and distribution
L19	Water storage and treatment
L20	Refuse disposal
L21	Cemeteries and cremetoria
L22	Post and telecommunications
L23	Residential
L24	Hotels
L25	Residential Institutions
L26	Medical and healthcare services
L27	Places of worship
L28	Education
L29	Community services
L30	Shops
L31	Financial and professional services
L32	Restaurants and cafes
L33	Public houses and bars
L34	Manufacturing
L35	Offices
L36	Storage
L37	Wholesale distribution
L38	Vacant
L39	Derelict
L40	Defence
L41	Unused Land

G5: Transect route map (example)
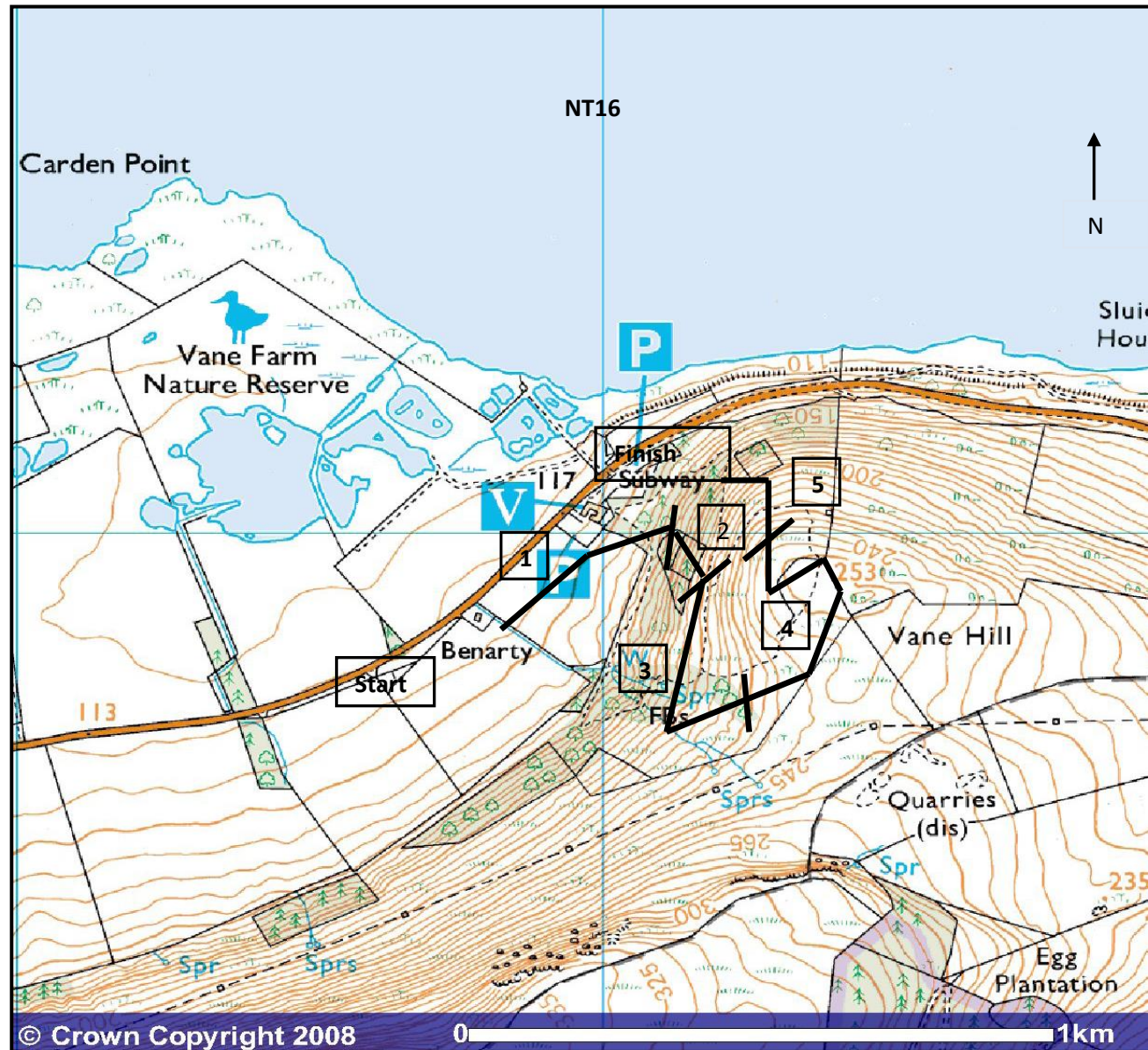
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S6.2 Minimal model summary for each species where number of bees observed is fitted as the response variable in a general linear mixed model. Latitude and Longitude of the midpoint of each transect along with (a) habitat variable and (b) land use variables were fitted as fixed factors. Year and transect length were included in each model as random factors. Habitat and land-use variables are compared to all other categories grouped under "Other" (see Methods, Table 6.1).

Species

    Fixed Effects

	Estimate	S.E.	z-value	P	AIC	Loglik
(a) Habitat Variables						
A. mellifera						
Latitude	-0.407	0.072	-5.639	1.71e-08*	3619.1	-1795.57
Longitude	0.148	0.069	2.143	0.032*		
H10 (Fen/swamp/marsh vegetation of inland freshwater edges)	-0.574	0.630	-0.911	0.362		
H17 (Dry semi/unimproved (flower-rich) neutral grassland)	-0.587	0.366	-1.603	0.109		
H21 (Stands of tall herbs (e.g. nettle and willow-herb beds))	0.276	0.378	0.731	0.465		
H24 (Wet Willow scrub of fen, river and lake-side)	0.154	1.178	0.130	0.896		
H30 (Small man-made woodlands)	-2.020	0.702	-2.875	0.004*		
H36 (Horticultural crops)	1.816	1.104	1.645	0.1		
H38 (Bare ground/weeds of arable field margins or fallow/recently abandoned arable crops)	2.041	0.737	2.768	0.006*		
H39 (Ornamental shrubs/trees/lawns of churches/parks/domestic gardens)	0.871	0.282	3.095	0.002*		
B. hortorum						
H10 (Fen/swamp/marsh vegetation of inland freshwater edges)	0.346	0.528	0.656	0.512	3198.2	-1587.1

H17 (Dry semi/unimproved (flower-rich) neutral grassland)	0.135	0.311	0.434	0.664		
H21 (Stands of tall herbs (e.g. nettle and willow-herb beds))	1.899	0.324	5.867	4.43e-09*		
H24 (Wet Willow scrub of fen, river and lake-side)	1.349	0.945	1.428	0.153		
H30 (Small man-made woodlands)	0.243	0.550	0.442	0.659		
H36 (Horticultural crops)	0.867	0.931	0.932	0.351		
H38 (Bare ground/weeds of arable field margins or fallow/recently abandoned arable crops)	0.317	0.648	0.490	0.624		
H39 (Ornamental shrubs/trees/lawns of churches/parks/domestic gardens)	1.669	0.237	7.042	1.90e-12*		
B. hypnorum						
Latitude	-0.430	0.081	-5.313	1.08e-07*	1828	-900.981
H10 (Fen/swamp/marsh vegetation of inland freshwater edges)	-0.482	0.711	-0.678	0.498		
H17 (Dry semi/unimproved (flower-rich) neutral grassland)	0.064	0.417	0.153	0.878		
H21 (Stands of tall herbs (e.g. nettle and willow-herb beds))	1.123	0.380	2.957	0.003*		
H24 (Wet Willow scrub of fen, river and lake-side)	0.758	1.224	0.620	0.536		
H30 (Small man-made woodlands)	1.381	0.644	2.144	0.032*		
H36 (Horticultural crops)	-0.335	1.513	-0.221	0.825		
H38 (Bare ground/weeds of arable field margins or fallow/recently abandoned arable crops)	0.220	0.846	0.260	0.795		
H39 (Ornamental shrubs/trees/lawns of churches/parks/domestic gardens)	1.869	0.288	6.482	9.06e-11*		
B. lapidarius						
Latitude	-0.074	0.034	-2.217	0.027*	6708.5	-3340.27
Longitude	0.159	0.030	5.237	1.63e-07*		
H10 (Fen/swamp/marsh vegetation of inland freshwater edges)	0.617	0.318	1.941	0.052		

H17 (Dry semi/unimproved (flower-rich) neutral grassland)	0.751	0.182	4.133	3.57e-05*		
H21 (Stands of tall herbs (e.g. nettle and willow-herb beds))	0.638	0.197	3.234	0.001*		
H24 (Wet Willow scrub of fen, river and lake-side)	0.150	0.587	0.255	0.799		
H30 (Small man-made woodlands)	0.782	0.368	2.122	0.034*		
H36 (Horticultural crops)	0.927	0.569	1.627	0.104		
H38 (Bare ground/weeds of arable field margins or fallow/recently abandoned arable crops)	0.541	0.400	1.353	0.176		
H39 (Ornamental shrubs/trees/lawns of churches/parks/domestic gardens)	0.450	0.156	2.886	0.004*		
B. pascuorum						
Latitude	0.108	0.026	4.135	3.56e-05*	8240.3	-4107.15
H10 (Fen/swamp/marsh vegetation of inland freshwater edges)	0.487	0.285	1.708	0.088		
H17 (Dry semi/unimproved (flower-rich) neutral grassland)	0.220	0.165	1.331	0.183		
H21 (Stands of tall herbs (e.g. nettle and willow-herb beds))	0.968	0.180	5.387	7.16e-08*		
H24 (Wet Willow scrub of fen, river and lake-side)	0.404	0.532	0.759	0.448		
H30 (Small man-made woodlands)	1.028	0.298	3.454	0.001*		
H36 (Horticultural crops)	0.812	0.506	1.603	0.109		
H38 (Bare ground/weeds of arable field margins or fallow/recently abandoned arable crops)	-0.050	0.358	-0.140	0.889		
H39 (Ornamental shrubs/trees/lawns of churches/parks/domestic gardens)	0.880	0.135	6.541	6.12e-11*		
B. pratorum						
Longitude	0.088	0.043	2.021	0.043*	3501.3	-1737.65
H10 (Fen/swamp/marsh vegetation of inland freshwater edges)	1.031	0.470	2.194	0.028*		
H17 (Dry semi/unimproved (flower-rich) neutral grassland)	0.441	0.278	1.587	0.113		

	Estimate	Std. Error	t value	p value		
H21 (Stands of tall herbs (e.g. nettle and willow-herb beds))	0.892	0.291	3.069	0.002*		
H24 (Wet Willow scrub of fen, river and lake-side)	-0.096	0.916	-0.105	0.917		
H30 (Small man-made woodlands)	-1.745	0.698	-2.499	0.012*		
H36 (Horticultural crops)	0.506	0.865	0.585	0.559		
H38 (Bare ground/weeds of arable field margins or fallow/recently abandoned arable crops)	0.067	0.609	0.110	0.912		
H39 (Ornamental shrubs/trees/lawns of churches/parks/domestic gardens)	1.301	0.224	5.806	6.38e-09*		
B. terrestris/lucorum						
Latitude	0.065	0.019	3.472	0.001*	10285	-5129.51
H10 (Fen/swamp/marsh vegetation of inland freshwater edges)	0.429	0.215	1.997	0.046*		
H17 (Dry semi/unimproved (flower-rich) neutral grassland)	0.330	0.125	2.651	0.008*		
H21 (Stands of tall herbs (e.g. nettle and willow-herb beds))	0.690	0.133	5.175	2.27e-07*		
H24 (Wet Willow scrub of fen, river and lake-side)	0.045	0.405	0.111	0.912		
H30 (Small man-made woodlands)	0.598	0.240	2.491	0.013*		
H36 (Horticultural crops)	0.617	0.385	1.603	0.109		
H38 (Bare ground/weeds of arable field margins or fallow/recently abandoned arable crops)	0.809	0.265	3.057	0.002*		
H39 (Ornamental shrubs/trees/lawns of churches/parks/domestic gardens)	0.878	0.102	8.577	9.77e-18*		
(b) Land Use Variables						
A. mellifera						
Latitude	-0.277	0.072	-3.817	1.35e-04*	3625.1	-1798.56
Longitude	0.199	0.069	2.875	0.004*		
L1 (Agriculture)	1.113	0.348	3.198	0.001*		

L12 (Transport tracks and ways)	-0.183	0.390	-0.470	0.638		
L17 (Waterways)	-0.217	0.700	-0.310	0.756		
L23 (Residential)	1.700	0.451	3.769	1.64e-04*		
L3 (Managed forest)	0.610	0.459	1.329	0.184		
L4 (Un-managed forest)	0.756	0.666	1.135	0.256		
L41 (Unused Land)	0.169	0.343	0.492	0.623		
L6 (Outdoor amenity and open spaces)	0.649	0.311	2.088	0.037*		
B. hortorum						
L1 (Agriculture)	-0.521	0.307	-1.697	0.090	3231.1	-1603.55
L12 (Transport tracks and ways)	-0.600	0.347	-1.730	0.084		
L17 (Waterways)	-1.031	0.613	-1.682	0.092		
L23 (Residential)	1.164	0.401	2.902	0.004*		
L3 (Managed forest)	-0.700	0.417	-1.676	0.094		
L4 (Un-managed forest)	-1.577	0.648	-2.432	0.015*		
L41 (Unused Land)	-0.949	0.313	-3.033	0.002*		
L6 (Outdoor amenity and open spaces)	-0.711	0.278	-2.553	0.011*		
B. hypnorum						
Latitude	-0.432	0.088	-4.920	8.64e-07*	1846.6	-909.292
L1 (Agriculture)	-0.897	0.373	-2.401	0.016*		
L12 (Transport tracks and ways)	-0.968	0.439	-2.202	0.028*		
L17 (Waterways)	1.150	0.669	1.718	0.086		

L23 (Residential)	0.650	0.476	1.366	0.172		
L3 (Managed forest)	0.467	0.485	0.964	0.335		
L4 (Un-managed forest)	0.040	0.727	0.054	0.957		
L41 (Unused Land)	-1.405	0.393	-3.574	3.52e-04*		
L6 (Outdoor amenity and open spaces)	-0.407	0.327	-1.245	0.213		
B. lapidarius						
Longitude	0.161	0.028	5.685	1.31e-08*	6722.3	-3348.15
L1 (Agriculture)	0.162	0.191	0.847	0.397		
L12 (Transport tracks and ways)	-0.055	0.216	-0.256	0.798		
L17 (Waterways)	-0.251	0.359	-0.700	0.484		
L23 (Residential)	-0.058	0.257	-0.224	0.822		
L3 (Managed forest)	-0.111	0.257	-0.433	0.665		
L4 (Un-managed forest)	-0.692	0.375	-1.843	0.065		
L41 (Unused Land)	-0.007	0.196	-0.037	0.971		
L6 (Outdoor amenity and open spaces)	0.446	0.174	2.565	0.010*		
B. pascuorum						
Latitude	0.092	0.028	3.257	0.001*	8271.6	-4122.79
L1 (Agriculture)	-0.337	0.165	-2.037	0.042*		
L12 (Transport tracks and ways)	0.152	0.189	0.800	0.424		
L17 (Waterways)	-0.354	0.314	-1.126	0.260		
L23 (Residential)	0.516	0.222	2.327	0.020*		

L3 (Managed forest)	-0.595	0.226	-2.629	0.009*		
L4 (Un-managed forest)	-0.798	0.332	-2.403	0.016*		
L41 (Unused Land)	-0.342	0.163	-2.099	0.036*		
L6 (Outdoor amenity and open spaces)	-0.225	0.154	-1.459	0.145		
B. pratorum						
Longitude	0.083	0.042	1.968	0.049*	3510.4	-1742.21
L1 (Agriculture)	-1.030	0.266	-3.872	1.08e-04		
L12 (Transport tracks and ways)	-0.183	0.296	-0.619	0.536		
L17 (Waterways)	-1.089	0.535	-2.038	0.042*		
L23 (Residential)	0.612	0.359	1.706	0.088		
L3 (Managed forest)	-0.785	0.367	-2.137	0.033*		
L4 (Un-managed forest)	-0.873	0.549	-1.592	0.111		
L41 (Unused Land)	-1.247	0.269	-4.635	3.57e-06*		
L6 (Outdoor amenity and open spaces)	-0.381	0.236	-1.616	0.106		
B. terrestris/lucorum						
Latitude	0.086	0.021	4.135	3.55e-05*	10338.7	-5156.37
L1 (Agriculture)	-0.313	0.124	-2.526	0.012*		
L12 (Transport tracks and ways)	-0.377	0.137	-2.744	0.006*		
L17 (Waterways)	-0.328	0.233	-1.412	0.158		
L23 (Residential)	0.431	0.161	2.678	0.007*		
L3 (Managed forest)	-0.388	0.167	-2.325	0.020*		

L4 (Un-managed forest)	-0.509	0.242	-2.103	0.035*
L41 (Unused Land)	-0.454	0.129	-3.529	4.18e-04*
L6 (Outdoor amenity and open spaces)	-0.195	0.124	-1.576	0.115

* P-value at a significance level of <0.05.

Chapter 7

GENERAL DISCUSSION

7.1 Research purpose

Bumblebees are currently in global decline and honeybees are in decline in Europe and N. America threatening the ecosystem service of pollination (Chapter 4; Goulson et al., 2008, 2015; Potts et al., 2010). Range contractions are evident for a number of bee species and some have become locally or globally extinct in recent years (Williams, 1982; Goulson et al., 2008, 2015; Potts et al., 2010) but due to a lack of monitoring, patterns of decline are poorly understood and long-term abundance data is entirely lacking. A recent report on the status of European bees (Nieto et al., 2014) found that over half of 1,965 European species were classed as 'data deficient' and their population trends remain unknown. Given the importance of wild bees as pollinators (Williams 1994; Goulson et al., 2008; Goulson et al., 2015), experts have called for more widespread monitoring of their populations to elucidate drivers of decline and guide effective conservation action (Steffan-Dewenter et al., 2005; Holden, 2006; Nieto et al., 2014; Goulson et al., 2015). Therefore, this thesis first reports my findings from evaluating training methods for citizen scientists (Chapter 2) and then explores the use of large-scale citizen science datasets to fill this knowledge gap, monitor bumblebee and honeybee populations, and elucidate drivers of population change (Chapters 3, 4, 5 and 6).

7.2 The value of citizen science in monitoring bumblebee and honeybee populations

Bumblebees and honeybees are popular, charismatic, visible insects, traits that make them particularly suitable for citizen science surveys (Dickinson et al, 2010; Silverton et

al, 2009; Lye et al., 2012). This thesis demonstrates the scale on which volunteer-led monitoring of these taxa is possible with tens of thousands of records collected by the public over multiple years (Chapters 3, 4, 5 and 6). While broad-scale data collection is possible, biases are often inherent in data collected by volunteers due to differences in individuals' expertise, effort and experience. These issues need to be addressed at each stage of the scientific process; data collection, data analysis through to the interpretation of results, in order to draw any dependable conclusions relating to ecological trends (Dickinson *et al.*, 2010, Hochachka *et al.*, 2012). In this thesis, techniques used to address these issues are applied to bumblebee and honey bee citizen science datasets to derive much need information on species distribution and abundance trends.

The provision of adequate training for volunteers is often cited as critical to data accuracy in any volunteer-led monitoring programme (Dickinson et. al., 2010; Brandon et al. 2003; Bell 2007; Kremen et al. 2010), yet there is a lack of information available on what type of training to provide and its efficacy. Understanding the level and extent of training required to produce the most accurate information on species trends is crucial, particularly where there is a need to produce high quality data with limited resources. In Chapter 2, I showed that training can have a significantly positive effect on bumblebee species identification, even after a short 30-minute session. Furthermore, I found that type of training matters, where a simple training type, focusing on just seven common species, was more efficacious for producing accurate species identification than when volunteers were introduced to a larger suite of species. This was valuable in informing subsequent studies where untrained volunteers were asked to focus on only the six

most common species/groups, along with *A. mellifera* to ensure identification accuracy (Chapter 5 and 6).

Broad-scale surveys aiming to gather data on species population trends often benefit from collaboration between regional and national organisations that share data standards (Silvertown, 2009). In this thesis, the benefits of collaboration are highlighted through the use of already-established citizen science networks and datasets to assess and monitor UK bumblebee populations. In Chapter 4, a collaboration with BWARS (Bees, Wasps and Ants Recording Society) and the National Biodiversity Data Centre (Ireland) facilitated access to historical data, which is comprised of presence-only records that have been validated by senior members of each society and made available through the National Biodiversity Network. This enabled the assessment of populations over a broad spatial and temporal scale using a reliable species records database. The outcomes revealed serious species range contractions during the 1960s-80s that supported Williams' (1982) previous findings. My analysis highlighted recent population trends, which may be of conservation concern with common species expanding in distribution while endangered UKBAP species retreating towards their climatic optimum.

The use of rigorous, standardised protocols by volunteers is considered imperative for the collection of reliable citizen science data (Dickinson et al., 2010, Silvertown, 2009; Matteson et al., 2012). In Chapters 3 and 5, data derived from a collaboration with a long-established citizen science scheme, BTO's Garden BirdWatch, which utilised a standardised protocol and a consistent network of volunteers, was used to investigate species trends. Other advantages to this collaboration included an online system, which

used threshold validation alerting to flag-up unusual records, thereby alerting observers and scientists to potential errors, which were removed from the dataset. It also allowed the assessment of trends at a national scale over multiple years, accounting for some spatial and temporal bias in species trends, in garden habitats which are of known importance to bumblebees (Chapter 5 and 6; Fussell and Corbet, 1992a, b; Goulson et al., 2002; Osborne et al., 2008; Lye et al., 2012). In Chapter 6, data were derived from a collaboration with the Bumblebee Conservation Trust, which has established network of volunteers that can be used to gather much needed information on honeybee and bumblebee abundance trends. A standardised transect monitoring protocol, previously used in published smaller-scale studies on bumblebee abundance trends, (Kells and Goulson, 2003; Redpath et al., 2010; Persson and Smith, 2013) was provided to volunteers. Monitoring methods closely follow the highly successful volunteer-led butterfly monitoring survey, the UK Butterfly Monitoring Scheme (Pollard and Yates, 1993). Using a tried and tested protocol, the collection of reliable information on species abundances and comparison to earlier studies was made possible, and highlighted urban areas as one of most important habitats for these declining taxa (Chapter 6).

The value of citizen science in monitoring population trends often depends on the opportunity to mine data for subsets that are less prone to volunteer error, while having the potential to reveal ecologically interesting trends (Dickinson *et al.*, 2010, Hochachka *et al.*, 2012). My research highlights the benefits of applying data mining techniques to volunteer-collected bumblebee datasets. In Chapter 3, for example, BTO's Garden BeeWatch dataset was mined for records of two species that have recently been observed foraging during the winter months, an unusual phenomenon since until these sightings, winter hibernation was thought to be typical for all UK bumblebees. The data

was further mined with seasonal restrictions for winter records, when all other species were inactive, and spring records when only queens were active. Since these two species are morphologically dissimilar to one another, being assigned to two separate colour morphs in previous studies (Fussell and Corbet 1992a,b; Lye et al., 2012), misidentification of winter records is improbable. The queens are more distinctive than workers, particularly for *B. terrestris* (Wolf et al., 2010) and are less prone to misidentification during the spring queen flight period than later in the year when worker bumblebees predominate. Mining the dataset for these subsets that were likely to be comprised of more accurate records while still incorporating species and time-periods of interest enabled a reliable analysis of the distribution of this phenomenon for the first time, revealing a southerly bias of winter records. In Chapters 5 and 6, datasets were mined for common species only since these most likely comprise the vast majority of UK bumblebee records, and the odd rare species included by untrained volunteers is unlikely to affect overall trends that are measured on a national scale over multiple years. This allowed a reliable assessment of population abundances of these seven species in relation to environmental variables for the first time, and revealed interspecific differences in location and habitat associations.

The value of citizen science in monitoring is also dependant on the application of statistical techniques that account for variation in recorder effort along with the spatial and temporal variation inherent in these broad-scale datasets (Hochachka et al, 2012; Dickinson et al, 2010). Modern analytical approaches, such as the use of general linear models and their extensions in R Statistical Software and species distribution modelling in Maxent, have great capability in accounting for these issues to reveal accurate patterns in citizen science datasets (Hochachka et al., 2012; Bird et al., 2014). In

Chapters 3 and 6, general linear models extensions were applied (Chapter 3: general linear model with binomial distribution; Chapter 6: general linear mixed models) to bee data collected by volunteers, allowing me to incorporate factors such as recorder id, number of recorders (Chapter 3), year and transect length (Chapter 6) into the models to account for potentially confounding sources of variation and increasing the reliability of my outcomes and conclusions. In Chapter 5, I used a hurdle model approach with general linear models, modelling presence/absence and abundance separately, to account for the high proportion of zeros in the dataset, which could obscure interesting trends, a common problem in citizen science datasets of species records (Hochachka et al., 2012; Bird et al., 2014). The resulting analysis revealed a concerning decline in some common bumblebee species and interspecific differences in responses to levels of urbanisation, both issues of importance to bumblebee conservation.

Collaborating with organisations that share data standards and/or have established successful citizen science projects, using standardised protocols, mining data for reliable subsets, and applying appropriate statistical techniques to volunteer collected datasets, enabled the successful application of citizen science to bumblebee and honeybee monitoring, helping to fill some of the current knowledge gaps in their population ecology.

A notable drawback of the use of citizen science in monitoring species populations is that the spatial extent and resolution of data, as well as the structure of the program and the simplicity of the protocol limits the questions that can be addressed (Tulloch et al., 2013). Many citizen science programs are spatially restricted to areas near to where people reside. Garden BeeWatch (Chapter 5) is one example where the survey habitat

is easily accessible to volunteers possibly leading to to a high number of records and level of volunteer retention. However, a notable drawback to this is that the survey is restricted to common garden visitors and that other species that may be suitable for inclusion in volunteer surveys in terms of their ease of identification, such as *B. monticola*, an upland moorland specialist (Edwards and Jenner, 2001), are unsuitable due to their association with more remote habitats. Species that are rarely encountered are often incompatible with volunteer monitoring unless more complex protocols are used. An increased effort in terms of training and volunteer engagement in areas where these species occur is often required. An example of this is the Great Yellow Bumblebee (*B. distinguendus*) Species Action Framework (SAF) plan implementation (2007-12; Tonhasca and MacDonald, 2016) in the north west of Scotland. Implementation involved the production of species information packs, recruitment and direct training of local volunteers in a variety of monitoring methods along with the verification of preserved specimens by experts. This was highly successful, leading to the production of a public database of verified records on the National Biodiversity Network (NBN) website and continuation of species specific monitoring and habitat management after the SAF plan timeframe had ended (Tonhasca and MacDonald, 2016). Unfortunately, it is not possible to monitor such rarer species using broadscale, national surveys with more straightforward protocols, such as BeeWalk and Garden BeeWatch (Chapter 5 and 6). It is often impossible to include species that easily mistaken for others in volunteer-led surveys. Even with targeted effort, as in the case of the SAF plan for *B. distinguendus*, some species simply cannot be monitored using volunteers. An example is *Bombus muscuorum* a rare species that is impossible to separate from the common *B. pascuorum* in the field whose identification requires lab dissection by experts (Edwards and Jenner,

2001). My analysis of the effect of training type on volunteer identification of bumblebees (Chapter 2) highlights the importance of introducing a small suite of species that can be identified in the field to volunteers when monitoring UK bumblebees using citizen science. While it is a powerful monitoring tool, the limitations of volunteer collected data, suggest that it needs to be combined with studies by trained scientists and professionals in order to successfully monitor and protect all of the UK's bumblebee populations.

7.3 Population trends of UK bumblebees and honeybees

While Williams (1982) revealed severe range contractions in several UK bumblebee species in the 1960s-80s compared with pre1960, his is the only published national study on the range dynamics of UK bumblebees and more recent information on population trends is necessary to understand the status and conservation requirements of these species. My analysis of UK bumblebee range dynamics in Chapter 4 substantiated Williams' findings, revealing significant range contractions in those species that were awarded UKBAP status based on his earlier study. It also highlighted severe range contractions in two additional species, *B. rupestris* and *B. soroeensis* during this time period, trends that may previously have been masked by the coarser scale of Williams' analysis. Comparison of more recent data (1981-12) to these time periods (Chapter 4) suggest that UKBAP species' ranges have remained stable while the most common species have expanded by 25-65% of the area they occupied during 1960-80. However, it is important to note that, despite attempts to account for variations in survey effort across time periods by only analysing areas for which at least one bumblebee had been recorded in the earliest time period (Chapter 4), the apparent stabilisation and/or

expansion of bumblebee species' ranges could be an artefact of more intensive sampling in recent years. This could potentially create artefactual apparent increases in range of common species and mask further decline of rare species; continued monitoring of the status of all bumblebees is necessary to ensure their protection.

While range contractions are evident for a number of bumblebee species with some becoming locally or globally extinct in recent years (Williams, 1982; Goulson et al., 2008, 2015; Potts et al., 2010), there is a paucity of information on abundance trends of bumblebees and honeybees (Nieto et al., 2014; Goulson et al., 2008; 2015). It is important to consider abundance trends along with range dynamics when assessing the status of populations since the relationship between range size and abundance is not always positive (Blackburn et al., 1998; Gaston et al., 1998a; Gaston et al., 1998b). In this thesis, abundances of common bumblebees (Chapters 5 and 6) and honeybees (Chapter 6) are analysed at a national scale over multiple years for the first time using two separate citizen science surveys, Garden BeeWatch (2007-14; Chapter 5) and BeeWalk (2009-12; Chapter 6). The bumblebee species proportions derived from these surveys are highly correlated with one another (Chapter 6) supporting the validity of using citizen science to collect consistent and accurate data on populations. The analysis of both surveys also revealed an overall positive effect of parks and gardens on bumblebee abundances (Chapters 5 and 6). There are, however some contrasting findings, for example analysis of Garden BeeWatch data indicates that *B. lapidarius* and *B. terrestris/lucorum* are associated with southern areas whereas BeeWalk data reveals an association of these species with higher latitudes. Specific, contrasting trends are to be expected when comparing surveys with differing protocols that span different time periods and habitat ranges and further monitoring is necessary to reveal which of these

trends remain constant over time. It is however, encouraging that overall species proportions and the main habitat asscoiation are consistent across both Garden BeeWatch and BeeWalk surveys.

Comparing abundances of bumblebees derived from these surveys to those presented in previous smaller-scale surveys carried on nest density (1989-91; Fussell and Corbet, 1992b) and flower visits (1987-88; Fussell and Corbet 1992a) suggests a notable increase in the relative abundance of *B. terrestris/lucorum* and a decrease in the relative abundances of *B. pratorum* (Chapters 5 and 6). Comparisons with other studies (Osborne et al., 2008; Lye et al., 2012) to Fussell and Corbet's nest density survey have also revealed an increase in *B. terrestris/lucorum* suggesting that, as a robust taxonomic group that is known for adapting to non-native environments, it is more resilient to habitat and land-use change than other species. However, this is the first evidence of decline in *B. pratorum*.

More recent trends derived from Garden BeeWatch records (2007-14) suggest that *B. terrestris/lucorum* is now decreasing in abundance over time (Chapter 5). A potential explanation for the recent decrease in *B. terrestris/lucorum* could be competition with *B. hypnorum*, also a robust species capable of invading non-native environments that has been spreading quickly through the UK since its arrival in 2001 (Goulson and Williams, 2001; Crowther et al., 2014). My results from analysing both Garden BeeWatch (Chapter 5) and BeeWalk (Chapter 6) records show that *B. hypnorum* is increasing in abundance over time (Chapter 5), that higher abundances of both *B. hypnorum* and *B. terrestris/lucorum* are associated with urban habitats (Chapter 5 and 6) and that abundances of both species are higher in the south (Chapter 5 and 6). Occupation of

similar habitats may lead to competition for nesting and foraging resources. While this is a possible explanation, there is no other quantitative evidence to suggest that *B. hypnorum* is competing with native species and further monitoring is required to ascertain whether or not it is a contributing factor in their decline.

Garden BeeWatch records (2007-14) also suggest a decline in abundance of long-tongued specialist bumblebee species with numbers of both *B. hortorum* and *B. pascuorum* declining between 2007 and 2014 (Chapter 5). Lye et al (2012) and Osborne et al., (2008) found a lower relative abundance of *B. pascuorum* when comparing smaller-scale surveys to Fussell and Corbet (1992b) nest density survey, however this is the first evidence for decline in *B. hortorum.* It is of particular concern that the last remaining long-tongued species, previously thought to be common, are now showing signs of threat as this is likely to impact on the pollination of wild plants with deep corollas specialised for pollination by these species, many of which are already in decline (e.g. *Trifolium pratense*, *Rhinanthus minor*; Carvell *et al.,* 2006), providing a potential circle of positive feedback or 'extinction vortex'.

It is important to note that care must be taken when interpreting the results of comparisons among these studies due to spatial and temporal differences between surveys. The exact geographic location of Fussell and Corbet's (1992b) nest density survey is unknown and their survey on flower visits by bumblebees (1992a) is comprised predominantly of southerly records. Additionally both studies run for two seasons representing a temporal snapshot that may be influenced by chance variations in environmental conditions, pressure from natural enemies and other short-term factors. Since the BeeWalk and Garden BeeWatch surveys are ongoing with an aim to monitor

populations in the long term, these initial outcomes will provide a good baseline for comparison of future trends.

7.4 Species population trends in relation to environmental drivers

7.4.1 Distribution trends indicate climate associations of bumblebees

Climate change has a significant impact on many invertebrates (Walther et al. 2002; Robinet and Rocques, 2010; Pöyry et al. 2011) with the highly successful citizen science survey, the UK Butterfly Monitoring Scheme (UKBMS) revealing large-scale evidence of range shifts and changes in first and peak emergence dates of species (Parmesan et al., 1999; Roy and Sparks, 2000; Hodgson et al., 2011). Compared with butterflies, there is a paucity of information available on the effect of climate change on UK bumblebees and it is likely that a combination of climate and habitat associations determine population trends (Goulson et al, 2015; Williams et al., 2007). My findings support the theory that bumblebee populations are, at least in part, influenced by climate. In Chapter 3, my analysis of Garden BeeWatch records revealed that winter-active bumblebees, *B.terrestris/lucorum* and *B. pratorum* were disproportionately more common in the south of the UK compared with spring populations with no clear influence of urbanisation in the surrounding landscape on their distribution, indicating that climate may play a role in this phenomenon. In Chapter 4, Maxent models revealed that all rare, UKBAP species apart from *B. muscorum* have retreated to areas of higher predicted climatic suitability in the 1981-12 time period, supporting the theory that species retreat to their climatic optimum as they decline (Williams et al., 2007) and that climate may be influencing patterns of decline in the bumblebees of Britain and Ireland. *B. soroeensis*, which showed similar range contractions to UKBAP species in the 1960-80

time period compared to pre1960, has also retreated to areas of higher predicted climatic suitability in recent years, indicating that its population may be more unstable than previously thought (Chapter 4).

7.4.2 Habitat associations of honeybees and bumblebees

Habitat loss due to agricultural intensification, which has led to a reduction in food-plants and nesting opportunities, has been a major driver of honeybee and bumblebee declines over the last 50 years (Williams, 1982; Goulson et al., 2003; Goulson et al., 2008; Goulson et al., 2015). In order to protect remaining populations we need to understand which habitats best support them but information on habitat-associations is lacking making it difficult to assess the health of populations and target conservation measures (Goulson et al., 2015; Convention on Biological Diversity, 2016). My analysis highlights several main habitats as important conservation areas for bees, including marshes (Chapter 5), coastal habitats (Chapter 4 and 5) and urban gardens and parks (Chapter 5 and 6). Analysis of the Garden BeeWatch dataset in Chapter 5 revealed that gardens close to marsh habitat were more likely to record bumblebee species and have a higher abundance of most species. Williams (1988) had previously highlighted marshes as important bumblebee habitat as they are less affected by agricultural intensification due to their unsuitability for farming, and tendency to be high in floral richness and abundance with a long growing season. Coastal areas were also highlighted as a key bumblebee habitat in my study with higher abundances of common species, *B. lapidarius, B. pascuorum, B. pratorum,* and *B. terrestris/lucorum* found in gardens near to the coast, and Maxent models in Chapter 4 showed that rare species, *B. muscorum*, *B. distinguendus* and *B. soroeensis* have retracted towards the coast in recent years.

Urbanisation has increased in recent years (United Nations, 2014) and several studies have indicated that urban and suburban parks and gardens are supporting pollinator populations (Goulson et al., 2010; Baldock et al., 2015; Senapathi et al., 2015). My analysis illustrated interspecific variation across different habitats (Chapter 4, 5 and 6) but there is a pronounced effect of urban habitat on species populations. In Chapter 3, analysis of BeeWalk records revealed an overall positive effect of urban habitat with higher abundances of all common bumblebee species and *A. mellifera* associated with parks and gardens, supporting evidence that urban areas provide refuge for bees in an otherwise impoverished landscape (Chapters 5 and 6; Goulson et al., 2002, Goulson et al., 2010, Osborne et al., 2008; Chapman et al., 2003; McFrederick and LeBuhn, 2006). However, populations of short-tongued, generalist species were associated with the more urbanised southern and eastern regions of the UK (Chapter 5). Additionally, results of the Garden BeeWatch survey highlighted urban gardens as having higher abundances of short-tongued common bumblebee species only while long-tongued specialists, *B. hortorum* and *B. pascuorum,* were more likely to occur in rural gardens (Chapter 5). These findings are of concern given that the Garden BeeWatch analysis also showed a recent decline in the abundance of these long-tongued specialists (Section 7.3; Chapter 5), suggesting that short-tongued generalists may be outcompeting long-tongued specialists as they adapt more readily to rapidly expanding urban environments.

7.5 Further research and management recommendations

- A short, targeted bumblebee identification session can increase record reliability. It is therefore recommended that the number of species that are introduced per training session is kept to a minimum, focusing on just the six

common bumblebee species groups, and honeybees, and providing additional targeted sessions in areas where UKBAP species are present and/or in areas of key bumblebee habitat. Further research into training types, including assessing the efficacy of online training, is also recommended.

- Further research is required into the accuracy to which individual bee species that are targeted as part of citizen science projects can be identified without training, following training and following experience of taking part in surveys. This information could be used to apply confidence limits to species data and incorporate measures of volunteer expertise into statistical modelling.

- Since *Bombus hypnorum* is the most distinctive species in terms of identification by volunteers (Chapter 2), the current Garden BeeWatch dataset could reliably be used to analyse its spread northwards in the UK and assess possible effects of its expansion on the occurrence and abundance of other bumblebee species.

- Continue long-term monitoring of bumblebee and honeybee populations using citizen surveys, BeeWalk and Garden BeeWatch particularly in light of the evidence for decline of some common species (Chapters 5 and 6) and the recent retraction of rare species to their climatic optima (Chapter 4). These surveys are reliable and can act as a baseline for future comparisons. *B. soroeensis* needs more recognition as a rare species given evidence for range contractions similar to those observed for UKBAP species along with its retraction to areas of higher predicted climatic suitability (Chapter 4).

- Further research is required into how urban habitats support bee populations and whether expanding urban areas are leading to homogenisation of

communities by favouring generalist species. Urban green space should be managed sympathetically for declining, specialist pollinators such as long-tongued bumblebee species by providing continuity of forage with suitable native flowers, particularly from the Fabaceae family (e.g. *Trifolium pratense*, *Vicia cracca*, *Lamium album*)

- In addition to providing suitable forage for long-tongued bumblebee species in flowerbeds, other recommendations to manage gardens beneficially for bumblebees are the inclusion of vegetable plots and berry plants for additional forage rewards and the use of hedges as boundaries to provide linear features for navigation, forage material, potential nesting sites and shelter

References

Aizen, M.A., Garibaldi, L.A., Cunningham, S.A. and Klein, A.M. 2008. Long-term global trends in crop yield and production reveal no current pollination shortage but increasing pollinator dependency. *Current Biology*, **18:** 1572-1575.

Aizen, M.A. and Harder, L.D. 2009. The global stock of domesticated honeybees is growing slower than agricultural demand for pollination. *Current Biology*, **19:** 915-918.

Ahrne, K., Bengtsson, J. and Elmqvist, T., 2009. Bumble bees (*Bombus* spp.) along a gradient of increasing urbanization. *PLoS One*, **4:** e5574.

Alford, D.V. 1975. Bumblebees. Davis-Poynter, London.

Alford, D.V. 1980. *Atlas of the bumblebees of the British Isles*. 32 pp. Cambridge.

Arbetman, M. P., Meeus, I., Morales, C. L., Aizen, M. A., and Smagghe, G. 2013. Alien parasite hitchhikes to Patagonia on invasive bumblebee. *Biological Invasions*, **15**: 489-494.

Ayres M.P. and Lombardero M.J. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *The Science of the Total Environment,* **262:** 263–286.

Baldock, K.C., Goddard, M.A., Hicks, D.M., Kunin, W.E., Mitschunas, N., Osgathorpe, L.M., Potts, S.G., Robertson, K.M., Scott, A.V., Stone, G.N. and Vaughan, I.P. 2015. Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects. *Proceedings of the Royal Society of London B: Biological Sciences*, **282:** 20142849.

Balvenera, P., Pfisterer, A.B., Buchmann, N., He, J.S., Nakashizuka, T., Raffaelli, D. and Schmid, B. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, **9:** 1146-1156.

Bates, A., Sadler, J.P., Fairbrass, A.J., Falk, S.J., Hale, J.D. and Matthews, T.J. 2011. Changing bee and hoverfly pollinator assemblages along an urban-rural gradient. *PLoS one*, **6**: e23459.

Bates, D., Maechler, M., Bolker, B. and Walker, S. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-6. URL http://CRAN.R-project.org/package=lme4

Bell, J. J. 2007. The use of volunteers for conducting sponge biodiversity assessments and monitoring using a morphological approach on Indo-Pacific coral reefs. *Aquatic Conservation: Marine and Freshwater Ecosystems,* **17:** 133–145.

Bell, S., Marzano, M., Cent, J., Kobierska, H., Podjed, D., Vandzinskaite, D., Reinert, H., Armaitiene, A., Grodzińska-Jurczak, M. and Muršič, R. 2008. What counts? Volunteers and their organisations in the recording and monitoring of biodiversity. *Biodiversity and Conservation*, **17:** 3443-3454.

Benton, T.G., Vickery, J.A. and Wilson. J.D. 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution,* **18**: 182-188.

Berman, M.G., Jonides, J., Kaplan, S. 2008. The cognitive benefits of interacting with nature. *Psychological Science*, **19**: 1207–1212.

Bibby, C. J. 2003. Fifty years of bird study: Capsule field ornithology is alive and well, and in the future can contribute much more in Britain and elsewhere. *Bird Study*, **50**: 194–210.

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, 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**: 351-354.

Bird, T.J., Bates, A.E., Lefcheck, J.S., Hill, N.A., Thomson, R.J., Edgar, G.J., Stuart-Smith, R.D., Wotherspoon, S., Krkosek, M., Stuart-Smith, J.F. and Pecl, G.T., 2014. Statistical solutions for error and bias in global citizen science datasets. *Biological Conservation*, **173:** 144-154.

Blackburn, T.M., Gaston, K.J., Greenwood, J.J.D. & Gregory, R.D. 1998. The anatomy of the interspecific abundance–range size relationship for the British avifauna. II. Temporal dynamics. *Ecology Letters*, **1:** 47–55.

Blüthgen, N. and Klein, A.M. 2011. Functional complementarity and specialisation: the role of biodiversity in plant–pollinator interactions. *Basic and Applied Ecology*, **12:** 282-291.

Bonney, R., Cooper, C. B., Dickinson, J., Kelling, S., Phillips, T., Rosenberg, K. V. and Shirk, J. 2009. Citizen Science: A Developing Tool for Expanding Science Knowledge and Scientific Literacy. *Bioscience,* **59:** 977-984.

Branchini, S., Pensa, F., Neri, P. Tonucci, B.M., Mattielli, L., Collavo, A., Sillingardi, M.E., Piccinetti, C., Zaccanti, F. and Goffredo, S. 2015. Using a citizen science program

to monitor coral reef biodiversity through space and time. *Biodiversity and Conservation*, **24**: 319-336.

Brandon, A., Spyreas, G., Molano-Flores, B., Carroll, C. and Ellis, J. 2003. Can volunteers provide reliable data for forest vegetation surveys? *Natural Areas Journal,* **23:** 254-261.

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 and Environment,* **142:** 137-143.

Brittain, C., Kremen, C. and Klein, A.M. 2013. Biodiversity buffers pollination from changes in environmental conditions. *Global Change Biology*, **19:** 540-547.

Bronstein, J.L., Alarcón, R. and Geber, M. 2006. The evolution of plant-insect mutualisms. *New Phytologist,* **172:** 412-428.

Brosi, B.J. 2016. Pollinator specialization: from the individual to the community. *New Phytologist*, **210**: 1190-1194.

Buchmann, S.L., Nabhan, G.P. 1996. *The Forgotten Pollinators*, Island Press, Washington D.C.

Büchs, W. 2003. *Biotic indicators for biodiversity and sustainable agriculture*. Elsevier.

Burkle, L.A., Marlin, J.C. and Knight, T.M. 2013. Plant-pollinator interactions over 120 years: loss of species, co-occurrence, and function. *Science*, **339:** 1611-1615.

BWARS, 2015. *Bombus hypnorum* (Linnaeus, 1758). Avaliable from: <http://www.bwars.com/index.php?q=bee/apidae/bombus-hypnorum> [01 February 2016].

BWARS, 2015. *Bombus hypnorum* mapping project. [Online] Available from: http://www.bwars.com/index.php?q=content/bombus-hypnorum-mapping-project. [Accessed: 02 September 2015].

Cameron, S. A., Lozier, J. D., Strange, J. P., Koch, J. B., Cordes, N., Solter, L. F. and Griswold, T. L. 2011. Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences*, **108**: 662-667.

Cannon, A. 1999. The significance of private gardens for bird conservation. *Bird Conservation International*, **9**:287-297.

Cannon, A.R., Chamberlain, D.E., Toms, M.P., Hatchwell, B.J. and Gaston, K.J. 2005. Trends in the use of private gardens by wild birds in Great Britain 1995-2002. *Journal of Applied Ecology,* **42:** 659-671.

Cardoso, P., Erwin, T.L., Borges, P.A., & New, T.R. 2011. The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation*, **144:** 2647-2655.

Carper, A.L., Adler, L.S., Warren, P.S., & Irwin, R.E. 2014. Effects of suburbanization on forest bee communities. *Environmental Entomology*, **43:** 253-262.

Carroll, A., Taylor, S.W., Re´gnie`re, J. and Safranyik, L. 2003. Effects of climate change on range expansion by the mountain pine beetle in British Columbia. In: Mountain Pine Beetle Symposium: Challenges and Solutions (eds Shore TL,

Brooks JE, Stone JE), October 30–31, 2003, Kelowna, BC. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Information Report BC-X-399, Victoria, BC, pp. 223–232.

Carvalheiro L.G., Kunin W.E., Keil P., Aguirre-Gutiérrez, J., Ellis, W.N., Fox, R., Groom, Q., Hennekens, S., Van Landuyt, W., Maes, D., Van de Meutter, F., Michez, D., Rasmont, P., Ode, B., Potts, S.G., Reemer, M., Roberts, S.G., Schaminee, J., WallisDeVries M.F. and Biesmeijer, J.C. 2013. Species richness declines and biotic homogenization have slowed down for NW-European pollinators and plants. *Ecology Letters*, **16**: 870-878.

Carvell, C. 2002. Habitat use and conservation of bumblebees (*Bombus* spp.) under different grassland management regimes. *Biological Conservation,* **103**: 33-49.

Carvell, C., Meek, W. R., Pywell, R. F., Goulson, D., and Nowakowski, M. 2007. Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *Journal of Applied Ecology*, **44:** 29-40.

Carvell, C., Roy, D.B., Smart, S.M., Pywell, R.F., Preston, C.D. and Goulson, D. 2006. Declines in forage availability for bumblebees at a national scale. *Biological Conservation* **132**: 481-489.

Chamberlain, D.E., Cannon, A.R. and Toms, M.P. 2004. Associations of garden birds with gradients in garden habitat and local habitat. *Ecography*, **27:** 589-600.

Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C., and Shrubb, M. 2000. Changes in the abundance of farmland birds in relation to the timing of

agricultural intensification in England and Wales. *Journal of Applied Ecology*, **35:** 771-788.

Chamberlain, D.E., Toms, M.P., Cleary-McHarg, R. and Banks, A.N. 2007a. House Sparrow (*Passer domesticus*) habitat use in urbanized landscapes. *Journal of Ornithology,* **148:** 453-462.

Chapman, F. M. 1900. A Christmas bird-census. *Bird-Lore*, **2:** 192.

Chapman, R.E., Wang, J. and Bourke, A.F.G. 2003. Genetic analysis of spatial foraging patterns and resource sharing in bumble bee pollinators. *Molecular Ecology*, **12**: 2801–2808.

Cincotta, R.P., Wisnewski, J. and Engelman, R. 2000. Human population in the biodiversity hotspots. *Nature*, **404:** 990-992.

Clavel, J., Julliard, R. and Devictor, V. 2011. Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment*, **9**: 222–228.

Cleland, E. E., Chuine, I., Maenzel, A., Mooney, H. A. and Scwartz, M. D. 2007. Shifting plant phenology in response to global change. *Trends in Ecology and Evolution,* **22:** 357-365.

Cohn, J.P. 2008. Citizen science: Can volunteers do real research? *BioScience*, **58:** 192-197.

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**: 1379-1391.

Collen, B, Kock, R, Heinrich, M, Smith, L, and Mace, G. 2015. Biodiversity and ecosystems. In: Waage, J. and Yap, C. (eds.) *Thinking Beyond Sectors for Sustainable Development,* pp. 3–9. London: Ubiquity Press.

Concepción, E.D., Moretti, M., Altermatt, F., Nobis, M.P. and Obrist, M.K. 2015. Impacts of urbanisation on biodiversity: the role of species mobility, degree of specialisation and spatial scale. *Oikos*, **124:** 1571-1582.

Conrad, C. C. and Hilchey, K. G. 2011. A review of citizen science and community based environmental monitoring. *Environmental Monitoring and Assessment,* **176:** 273-291.

Convention on Biological Diversity, 2016. *Implications of the IPBEs Assessment on Pollinators, Pollination and Food Production for the Work of the Convention. (UNEP/CBD/SBSTTA/20/9).*

Cooper, C.B., Dickinson, J., Phillips, T. and Bonney, R. 2007. Citizen science as a tool for conservation in residential ecosystems. *Ecology and Society*, **12:** 11.

Corbet, S. A., Williams, I.H. and Osborne, J.L. 1991. Bees and the pollination of crops and wild flowers in the European Community. *Bee world,* **72**: 47-59.

Corbet, S.A., Fussell, M., Ake, R., Fraser, A., Gunson, C., Savage, A. and Smith, M. 1993. Temperature and the pollinating activity of social bees. *Ecological Entomology,* **18**: 17-30

Cordellier, M. and Pfenninger, M. 2009. Inferring the past to predict the future: climate modelling predictions and phylogeography for the freshwater gastropod *Radix balthica* (Pulmonata, Basommatophora). *Molecular Ecology*, **18**: 534-544.

Costanza, R., d'Arge, R., De Groot, R., Faber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O' Neill, R.V. and Raskin, R.G. 1997. The value of the world's ecosystem services and natural capital.

Couvet, D., Jiguet, F., Julliard, R., Levrel, H. and Teyssedre, A. 2008. Enhancing citizen science contributions to biodiversity science and public policy. *Interdisciplinary Science Reviews,* **33:** 95-103.

Cragg, J.G., 1971. Some statistical models for limited dependent variables with application to the demand for durable goods. *Econometrica,* **39**: 829–844.

Cranmer, L. 2004. *The influence of linear landscape features on pollinator behaviour*. PhD thesis, University of Leicester, Leicester, UK.

Cranmer, L., McCollin, D. and Ollerton, J. 2012. Landscape structure influences pollinator movements and directly affects plant reproductive success. *Oikos.* **121:** 562-568.

Crowther, L.P., Hein, P.L. and Bourke, A.F., 2014. Habitat and forage associations of a naturally colonising insect pollinator, the tree bumblebee *Bombus hypnorum*. *PloS one*, **9:** p.e107568.

Daily, G.C. 1997. Nature's Services: Societal Dependence on Natural Ecosystems. Island Press, Washington.

Daily, G.C. and Karp, D.S., 2015. Nature's bounties: reliance on pollinators for health. *The Lancet*, **386:** 1925-1927.

Dallimer, M., Irvine, K.N., Skinner, A.M.J., Davies, Z.G., Rouquette, J.R., Maltby, L.L., Warren, P.H., Armsworth, P.R. and Gaston, K.J. 2012. Biodiversity and the feel-

good factor: understanding associations between self-reported human well-being and species richness. *BioScience,* **62**: 47-55.

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**: 761-771.

Dearborn, D.C., and Kark, S. 2010. Motivations for conserving urban biodiversity. *Conservation Biology*, **24:** 432-440.

Deguines, N., Julliard, R., De Flores, M., and Fontaine, C. 2012. The whereabouts of flower visitors: contrasting land-use preferences revealed by a country-wide survey based on citizen science. *PloS one*, **7:** e45822.

Delaney, D.G., Sperling, C.D., Adams, C.S. and Leung, B. 2008. Marine invasive species: validation of citizen science and implications for national monitoring networks. *Biological Invasions*, **10:** 117-128.

Devictor, V., van Swaay, C., Brereton, T., Chamberlain, D., Heliölä, J., Herrando, S., Julliard, R., Kuussaari, M., Lindström, Å., Reif, J., Roy, D.B., Schweiger, O., Settele, J., Stefanescu, C., Van Strien, A., Van Turnhout, C., Vermouzek, Z., WallisDeVries, M.,Wynhoff, I. and Jiguet, F. 2012. Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change*, **2**: 121-124.

Devictor, V., Whittaker, R.J., & Beltrame, C. 2010. Beyond scarcity: citizen science programmes as useful tools for conservation biogeography. *Diversity and Distributions*, **16:** 354-362.

Dickinson, J. L., Zuckerberg, B. and Bonter, B.N. 2010. Citizen science as an ecological research tool: challenges and benefits. *Annual Review of Ecology, Evolution, and Systematics,* **41**: 149-172.

Dickinson, J.L., Shirk, J., Bonter, D., Bonney, R., Crain, R.L., Martin, J., Phillips, T. and Purcell, K. 2012. The current state of citizen science as a tool for ecological research and public engagement. *Frontiers in Ecology and the Environment,* **10**: 291-297.

Eaton, M.A., Brown, A.F., Noble, D.G., Musgrove, A.J., Hearn, R.D., Aebischer, N.J., Evans, A. and Gregory, R.D. 2009. Birds of conservation concern 3. *British Birds*, **102**: 296-341.

E-bird, 2016. Audubon and Cornell Lab of Ornithology. Accessed 07 May 2016. <htpp://ebird.org>

Edwards, M. 2001. UK Biodiversity Action Plan Bumblebee Working Group report 2001. Unpublished report of the UKBAP working group, Midhurst, UK.

Eilers, E.J., Kremen, C., Greenleaf, S.S., Garber, A.K. and Klein, A.M. 2011. Contribution of pollinator-mediated crops to nutrients in the human food supply. *PLoS one*, **6:** p.e21363.

Eiswerth, M.E. and Haney, J.C. 2001. Maximizing conserved biodiversity: why ecosystem indicators and thresholds matter. *Ecological Economics*, **38:** 259-274.

Elith, J., Ferrier, S., Guisan, A., Graham, C.H., Anderson, R.P., Dudík, M., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., McC Overton, J., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S., Wisz, M.S. and Zimmermann, N.E. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**: 129–151.

ESRI [Environmental Systems Research Institute], 2011. ArcGIS version 10. ESRI, Redlands, California, USA.

ESRI. 2012. ArcMap: Release 10.1. Redlands, CA: Environmental Systems Research Institute.

Evans, K.L., Chamberlain, D.E., Hatchwell, B.J., Gregory, R.D. and Gaston, K.J. 2011. What makes an urban bird? *Global Change Biology*, **17:** 32-44.

Faegri, K. and Van Der Pijl, L. 2013. *Principles of pollination ecology*. Elsevier.

Feltham, H., Park, K. and Goulson, D. 2014. Field realistic doses of pesticide imidacloprid reduce bumblebee pollen foraging efficiency. *Ecotoxicology,* **23**: 317-323.

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:** 1067–1077.

Fielding A.H. and Bell F.J. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**: 38–49.

Fitzpatrick Ú., 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**: 185–194.

Fortel, L., Henry, M., Guilbaud, L., Guirao, A.L., Kuhlmann, M., Mouret, H., Rollin, O. and Vaissière, B.E. 2014. Decreasing abundance, increasing diversity and changing structure of the wild bee community (Hymenoptera: Anthophila) along an urbanization gradient. *PloS one*, **9:** e104679.

Forup, M. L. and Memmott, J. 2005. The relationship between the abundances of bumblebees and honeybees in a native habitat. *Ecological Entomology*, **30:** 47-57.

Fourcade, Y., Engler, J.O., Besnard, A.G. and Rödder, D. 2013. Confronting expert-based and modelled distributions for species with uncertain conservation status: a case study from the Corncrake (*Crex crex*). *Biological Conservation*, **167**: 161-171.

Fournier D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M., Nielsen, A. and Sibert, J. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software*, **27**: 233-249.

Fox, R., Randle, Z., Hill L., Anders, S., Wiffen, L. and Parsons, M. S. 2011. Moths count: recording moths for conservation in the UK. *Journal of Insect Conservation,* **15**: 55-68.

Fox, R. 2013. The decline of moths in Great Britain: a review of possible causes. *Insect Conservation and Diversity*, **6**:5-19.

Fox, R., Brereton, T.M., Asher, J., August, T.A., Botham, M.S., Bourn, N.A.D., Cruickshanks, K.L., Bulman, C.R., Ellis, S., Harrower, C.A. and Middlebrook, I. 2015. The State of the UK's Butterflies 2015.

Frankham, R., Ballou, J.D. and Briscoe, D.A. 2004. *A primer of conservation genetics.* Cambridge University Press. Cambridge, UK.

Fredericks, T. K., Choi, S. D., Hart, J., Butt, S. E. and Mital, A. 2005. An investigation of myocardial aerobic capacity as a measure of both physical and cognitive workloads. *International Journal of Industrial Ergonomics,* **35:** 1097-1107.

Free, J.B. 1993. *Insect Pollination of Crops.* Academic Press, London.

Fründ, J., Dormann, C.F., Holzschuh, A. and Tscharntke, T. 2013. Bee diversity effects on pollination depend on functional complementarity and niche shifts. *Ecology*, **94:** 2042-2054.

Fuccillo, Kerissa K., Theresa M. Crimmins, Catherine E. de Rivera, and Timothy S. Elder. 2015. Assessing accuracy in citizen science-based plant phenology monitoring. *International Journal of Biometeorology,* **59:** 917-926.

Fuller, R.J. and Warren, M.S., 1991. Conservation management in ancient and modern woodlands: responses of fauna to edges and rotations. In: The scientific management of temperate communities for conservation, ed. by I.F. Spellerberg, F.B. Goldsmith and M.G. Morris, 445-471. Oxford, Blackwell, Scientific Publications. British Ecological Society Symposium No. 31.

Fussell, M. and Corbet, S.A. 1992a. Flower usage by bumble-bees: a basis for forage plant management. *Journal of Applied Ecology*, 451-465.

Fussell, M. and Corbet, S.A. 1992b. The nesting places of some British bumble bees. *Journal of Apicultural Research,* **31**: 32-41.

Gallai, N., Salles, J.M., Settele, J. and Vaissière, B.E. 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological Economics*, **68:** 810-821.

Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A., Kremen, C., Carvalheiro, L.G., Harder, L.D., Afik, O. and Bartomeus, I. 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science*, **339:** 1608-1611.

Gaston, K.J. and Fuller, R.A. 2007. Biodiversity and extinction: losing the common and the widespread. *Progress in Physical Geography*, **31**: 213.

Gaston, K.J. and Spicer, J.I. 2013. *Biodiversity: an introduction*. John Wiley & Sons.

Gaston, K.J., 1996. Biodiversity-congruence. *Progress in Physical Geography*, **20:** 105-112.

Gaston, K.J., Blackburn, T.M. and Gregory, R.D. 1998. Interspecific differences in intraspecific abundance–range size relationships of British breeding birds. *Ecography,* **21**: 149–158.

Gaston, K.J., Warren, P.H., Thompson, K. and Smith, R.M. 2005. Urban Domestic Gardens (IV): The Extent of the Resource and its Associated Features. *Biodiversity and Conservation,* **14:** 3327-3349.

Geslin, B., Gauzens, B., Thébault, E., and Dajoz, I. 2013. Plant pollinator networks along a gradient of urbanisation. *PloS one*, **8**: e63421.

Ghazoul, J. 2005. Buzziness as usual? Questioning the global pollination crisis. *Trends in Ecology and Evolution*, **20:** 367-373.

Ghazoul, J. 2015. Qualifying pollinator decline evidence. *Science*, **348:** 981-982.

Gill, R. J., Ramos-Rodriguez, O., and Raine, N. E. 2012. Combined pesticide exposure severely affects individual-and colony-level traits in bees. *Nature*, **491**: 105-108.

Goddard, M.A., Dougill, A.J. and Benton, T.G. 2010. Scaling up from gardens: biodiversity conservation in urban environments. *Trends in Ecology and Evolution*, **25:** 90-98.

Gooch, M. 2005. Voices of the volunteers: an exploration of the experiences of catchment volunteers in coastal Queensland, Australia. *Local Environment*, **10:** 5-19.

Goulson, D. 2003. *Bumblebees: Behaviour and Ecology*, 2nd edn. Oxford University Press, Oxford.

Goulson, D. 2013. An overview of the environmental risks posed by neonicotinoid insecticides. *Journal of Applied Ecology,* **50**: 977-987.

Goulson D. and Darvill B. 2004. Niche overlap and diet breadth in bumblebees: are rare species more specialized in their choice of flowers? *Apidologie* **35**: 55–63.

Goulson, D., Hanley, M.E., Darvill, B. and Ellis, J.S. 2006. Biotope associations and the decline of bumblebees (*Bombus* spp.). *Journal of Insect Conservation*, **10**: 95-103.

Goulson D., Hanley M.E., Darvill B., Ellis J.S. and Knight M.E. 2005. Causes of rarity in bumblebees. *Biological Conservation*, **122**: 1–8.

Goulson, D. and Hughes, W.O. 2015. Mitigating the anthropogenic spread of bee parasites to protect wild pollinators. *Biological Conservation*, **191**: 10-19.

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: 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,* **46**: 1207-1215.

Goulson, D., Nicholls, E., Botías, C. and Rotheray, E.L. 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science,* **347**: 1255957.

Goulson, D., Lye, G.C. and Darvill, B., 2008. Diet breadth, coexistence and rarity in bumblebees. *Biodiversity and Conservation*, **17: 3269-3288.

Goulson, D. and Sparrow, K.R. 2009. Evidence for competition between honeybees and bumblebees; effects on bumblebee worker size. *Journal of Insect Conservation*, **13:** 177-181.

Goulson, D. and Williams, P., 2001. *Bombus hypnorum* (L.)(Hymenoptera: Apidae), a new British bumblebee? *British Journal of Entomology and Natural History*, **14:** 129-131.

Graham, J., Newman, G., Jarnevich, C., Shory, R. and Stohlgren T. J. 2007. A global organism detection and monitoring system for non-native species. *Ecological Informatics,* **2:** 177-183.

Greenwood, J.J. 2007. Citizens, science and bird conservation. *Journal of Ornithology*, **148:** 77-124.

Grimaldi, D. 1999. The co-radiators of pollinating insects and angiosperms in the Cretaceous. *Annals of the Missouri Botanical Garden*, **86:** 373-406.

Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, X. and Briggs, J. M. 2008. Global change and the ecology of cities. *Science*, **319:** 756-760.

Grixti, J.C., Wong, S.A., Cameron, S.A. and Favret, C. 2009. Decline of bumble bees (*Bombus*) in the North American Midwest. *Biological Conservation,* **142**: 75-84.

Gross, M., 2008. Bee gloom deepens. *Current Biology*, **18:** 1073.

Gunnarsson, B. and Federsel, L. 2014. Bumblebees in the city: abundance, species richness and diversity in two urban habitats. *Journal of Insect Conservation,* **18:** 1185-1191.

Gürel, F., Gösterit, A. and Eren. O. 2008. Life cycle and foraging patterns of native *Bombus terrestris* (L.) (Hymenoptera: Apidae) in the Mediterranean region. *Insectes Sociaux,* **55:** 123–128.

Hanley, M.E., Amanda J.A., and Franco, M. 2014. Going native? Flower use by bumblebees in English urban gardens. *Annals of Botany,* **113**: 799-806.

Heinrich, B. 1979. *Bumblebee Economics*. Harvard University Press, Cambridge, MA.

Henry, M., Beguin, M., Requier, F., Rollin, O., Odoux, J-F, Aupinel, P., Aptel, J., Tchamitchian, S. and Decourtye, A. 2012. A common pesticide decreases foraging success and survival in honey bees. *Science,* **336**: 348-350.

Hernandez, J.L., Frankie, G.W. and Thorp, R.W. 2009. Ecology of urban bees: a review of current knowledge and directions for future study. *Cities and the Environment (CATE)*, **2: 3.**

Hernandez, P.A., Graham, C.H., Master, L.L. and Albert, D.L. 2006. The effect of sample size and species characteristics on performance of different species distribution models. *Ecography*, **29:** 773-785.

Hijmans, R.J., Cameron, S.E., Parra, J. L., Jones, P.G. and Jarvis, A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology,* **25**: 1965–1978.

Hilty, J. and Merenlender, A. 2000. Faunal indicator taxa selection for monitoring ecosystem health. *Biological Conservation*, **92:** 185-197.

Hirzel, A.H., Hausser, J., Chessel, D. and Perrin, N. 2002. Ecological niche-factor analysis: How to compute habitat suitability maps without absence data? *Ecology,* **83**: 2027-2036.

Hochachka, W. M., Fink, D., Hutchinson, R.A., Sheldon, D., Wong, W-K and Kelling, S. 2012. Data-intensive science applied to broad-scale citizen science. *Trends in Ecology and Evolution,* **27**: 130-137.

Hodgson, J.A., Thomas, C.D., Oliver, T.H., Anderson, B.J., Brereton, T.M. and Crone, E.E. 2011. Predicting insect phenology across space and time. *Global Change Biology,* **17:** 1289-1300.

Hoehn, P., Tscharntke, T., Tylianakis, J.M. and Steffan-Dewenter, I. 2008. Functional group diversity of bee pollinators increases crop yield. *Proceedings of the Royal Society of London B: Biological Sciences*, **275:** 2283-2291.

Holden, C., 2006. Report warns of looming pollination crisis in North America. *Science*, **314:** 397-397.

Hooper, D.U., Chapin Iii, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S. and Schmid, B. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological monographs*, **75:** 3-35.

Hortal, J., Jiménez-Valverde, A., Gómez, J.F., Lobo, J.M. and Baselga, A. 2008. Historical bias in biodiversity inventories affects the observed environmental niche of the species. *Oikos*, **117**: 847-858.

Ings, T.C., Ward, N.L. and Chittka, L. 2006. Can commercially imported bumblebees out-compete their native conspecifics? *Journal of Applied Ecology*, **43:** 940–948.

Inoue, M. N., and Yokoyama, J. 2010. Competition for flower resources and nest sites between *Bombus terrestris* (L.) and Japanese native bumblebees. *Applied Entomology and Zoology*, **45**: 29-35.

Inoue, M.N., Yokoyama, J. and Washitani, I. 2008. Displacement of Japanese native bumblebees by the recently introduced *Bombus terrestris* (L.)(Hymenoptera: Apidae). *Journal of Insect Conservation*, **12:** 135-146.

Inouye, D.W. 1978. Resource partitioning in bumblebees: experimental studies of foraging behavior. *Ecology*, 672-678.

IPBES, 2016. Summary for policymakers of the assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production. S.G. Potts, V. L. Imperatriz-Fonseca, H. T. Ngo, J. C. Biesmeijer, T. D. Breeze, L. V. Dicks, L. A. Garibaldi, R. Hill, J. Settele, A. J. Vanbergen, M. A. Aizen, S. A. Cunningham, C. Eardley, B. M. Freitas, N. Gallai, P. G. Kevan, A. Kovács-Hostyánszki, P. K. Kwapong, J. Li, X. Li, D. J. Martins, G. Nates-Parra, J. S. Pettis, and B. F. Viana (eds.).

IPCC, 2013. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Stocker, T. F., D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P. M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, 1535 pp.

Isaac, N.J., Strien, A.J., August, T.A., Zeeuw, M.P. and Roy, D.B. 2014. Statistics for citizen science: extracting signals of change from noisy ecological data. *Methods in Ecology and Evolution*, **5:** 1052-1060.

Jacobs, J.H., Clark, S.J., Denholm, I., Goulson, D., Stoate, C. and Osborne, J.L. 2009. Pollination biology of fruit-bearing hedgerow plants and the role of flower-visiting insects in fruit-set. *Annals of Botany*, **104:** 1397-1404.

Jacobs, J.H., Clark, S.J., Denholm, I., Goulson, D., Stoate, C. and Osborne, J.L. 2010. Pollinator effectiveness and fruit set in common ivy, *Hedera helix* (Araliaceae). *Arthropod-Plant Interactions*, **4:** 19-28.

Jiménez-Valverde, A., 2014. Threshold-dependence as a desirable attribute for discrimination assessment: implications for the evaluation of species distribution models. *Biodiversity and Conservation,* **23**: 369-385.

JNCC. 2007. Report on the Species and Habitat Review. Joint Nature Conservation Committee, Peterborough. Available at:

http://jncc.defra.gov.uk/pdf/UKBAP_Species-HabitatsReview-2007.pdf

(Accessed 19 April 2014).

Johnson, S.D. 1996. Pollination, adaptation and speciation models in the Cape flora of South Africa. *Taxon*, 59-66.

Johnson, S.D. and Steiner, K.E. 2000. Generalization versus specialization in plant pollination systems. *Trends in Ecology & Evolution*, **15:** 140-143.

Kearns, C.A. and Inouye, D.W. 1997. Pollinators, Flowering Plants, and Conservation Biology: Much remains to be learned about pollinators and plants. *Bioscience,* **47:** 297-307.

Kearns, C.A., Inouye, D.W. and Waser, N.M., 1998. Endangered mutualisms: the conservation of plant-pollinator interactions. *Annual Review of Ecology and Systematics*, 83-112.

Keil, P., Biesmeijer, J.C., Barendregt, A., Reemer, M. and Kunin, W.E. 2010. Biodiversity change is scale-dependent: an example from Dutch and UK hoverflies (Diptera, Syrphidae). *Ecography*, **33**: 1–10.

Kells, A.R. and Goulson, D., 2003. Preferred nesting sites of bumblebee queens (Hymenoptera: Apidae) in agroecosystems in the UK. *Biological Conservation*, **109:** 165-174.

Kenta, T., Inari, N., Nagamitsu, T., Goka, K. and Hiura, T. 2007. Commercialized European bumblebee can cause pollination disturbance: an experiment on seven native plant species in Japan. *Biological Conservation*, **134:** 298-309.

Kleijn, D. and Raemakers, I. 2008. A retrospective analysis of pollen host plant use by stable and declining bumble bee species. *Ecology,* **89:** 1811-1823.

Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L.G., Henry, M., Isaacs, R., Klein, A.M., Kremen, C., M'gonigle, L.K., Rader, R. and Ricketts, T.H. 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nature Communications*, **6**.

Klein, A.M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I.,Cunnigham, S.A., Kremen, C. and Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society*, **274:** 303–313.

Kodra E., Steinhaeuser K., Ganguly A.R. 2011. Persisting cold extremes under 21st century warming scenarios. *Geophysical Research Letters*, **38:** p.L08705.

Kondo, N. I., Yamanaka, D., Kanbe, Y., Kunitake, Y. K., Yoneda, M., Tsuchida, K. and Goka, K. 2009. Reproductive disturbance of Japanese bumblebees by the introduced European bumblebee *Bombus terrestris*. *Naturwissenschaften*, **96**: 467-475.

Kosier, A. Celary, W., Oloejniczak, P., Fijal, J., Król, W., Solarz, W. and Plonka, P. 2007. The decline of the bumble bees and cuckoo bees (Hymenoptera: Apidae: Bombini) of western and central Europe. *Oryx,* **41**: 79-88.

Koss, R.S. 2010. Volunteer health and emotional wellbeing in marine protected areas. *Ocean and Coastal Management,* **53**: 447-453.

Kremen, C. Ullmann, K. S. and Thorp, R. W. 2010. Evaluating the quality of citizen scientist data on pollinator communities. *Conservation Biology,* **25:** 607–617.

Kwak, M.M., Kremer, P., Boerrichter, E. and van den Brand, C. 1991a. Pollination of the rare species *Phyteuma nigrum* (Campanulaceae): Flight distances of bumblebees. *Proceedings of Experimental and Applied Entomology,* **2**: 131-163.

Kwak, M., van den Brand, C., Kremer, P. and Boerrigter, E. 1991b. Visitation, flight distances and seed set in the species *Phyteuma nigrum* (Campanulaceae). *Acta Horticulturae,* **288**: 303-307.

Lange, H., Økland, B. and Krokene, P. 2006. Thresholds in the life cycle of the spruce bark beetle under climate change. *Interjournal for Complex Systems,* **1648:** 1–10.

Lawson, B., Robinson, R.A., Colvile, K.M., Peck, K.M., Chantrey, J., Pennycott, T.W., Simpson, V.R., Toms, M.P. and Cunningham, A.A. 2012. The emergence and spread of finch trichomonosis in the British Isles. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **367:** 2852-2863.

Lepage, M., Courois and R., Daigle, C. 1997. Surveying calling anurans in Que´bec using volunteers. In: Green D.M. (Ed.), Amphibians in Decline: Canadian Studies of a

Global Problem, Herpetological Conservation Volume 1. Society for the Study of Amphibians and Reptiles, St. Louis, Missouri, USA, Pp. 128–140.

Lepais, O., Darvill, B., O'Connor, S., Osborne, J.L., Sanderson, R.A., Cussans, J., Goffe, L. and Goulson, D. 2010. Estimation of bumblebee queen dispersal distances and a comparison of reconstruction methods for haplodiploid organisms. *Molecular Ecology,* **19**: 819-831.

Lopezaraiza-Mikel, M.E., Hayes, R.B., Whalley, M.R. and Memmott, J. 2007. The impact of an alien plant on a native plant-pollinator network: an experimental approach. *Ecology Letters*, **10**: 539–550.

Loram A., Tratalos J., Warren P.H., Gaston K.J. 2007. Urban domestic gardens (X): the extent and structure of the resource in five major cities. *Landscape Ecology,* 22: 601-615.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B. and Tilman, D. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, **294:** 804-808.

Lowenstein, D.M., Matteson, K.C. and Minor, E.S. 2015. Diversity of wild bees supports pollination services in an urbanized landscape. *Oecologia*, **179**: 811-821.

Luck, G.W. 2007. The relationships between net primary productivity, human population density and species conservation. *Journal of Biogeography*, **34:** 201-212.

Lye, G.C., Osborne, J.L., Park, K.J. and Goulson, D. 2012 Using citizen science to monitor *Bombus* populations in the UK: nesting ecology and relative abundance in the urban environment. *Journal of Insect Conservation,* **16**: 697-707.

MA, 2005. Millennium Ecosystem Assessment (2005) Ecosystems and Human Well-being: Synthesis, World Resources Institute.

Mace, G.M., Norris, K. and Fitter, A.H. 2012. Biodiversity and ecosystem services: a multilayered relationship. *Trends in Ecology and Evolution*, **27:** 19-26.

Magurran, A.E. 2013. *Measuring biological diversity*. John Wiley & Sons.

Margaret, P., Bernhardt, E., Chornesky, E., Collins, S., Dobson, A., Duke, C., Gold, B., Jacobson, R., Kingsland, S. and Kranz, R., 2004. Ecology for a Crowded Planet. *Science*, **304**: 1251-1252.

Mathieu, R., Freeman, C. and Aryal, J. 2007. Mapping private gardens in urban areas using object-oriented techniques and very high-resolution satellite imagery. *Landscape and Urban Planning,* **81:** 179-192.

Matsumara, C., Nakajima, M., Yokoyama, J. and Waishitini, I. 2004. High reproductive ability of an alien bumblebee invader, *Bombus terrestris*, L., in the Hidaka region of southern Hokkaido, Japan. *Japanese Journal of Conservation Ecology,* **9**: 93-102.

Matteson, K. C., Taron, D. J. and Minor, E. S. 2012. Assessing citizen contributions to butterfly monitoring in two large cities. *Conservation Biology*, **26:** 557-564.

Maxwell, S.L., Fuller, R.A., Brooks, T.M. and Watson, J.E. 2016. Biodiversity: The ravages of guns, nets and bulldozers. *Nature*, **536**: 143-145.

Mayer, R. E., Heiser, J. and Lonn, S. 2001. Cognitive constraints on multimedia learning: when presenting more material results in less understanding. *Journal of Educational Psychology,* **93:** 187-198.

McFrederick, Q.S. and LeBuhn, G. 2006. Are urban parks refuges for bumble bees *Bombus* spp. (Hymenoptera: Apidae)? *Biological Conservation*, **129:** 372-382.

McGregor, S.E. 1976. *Insect pollination of cultivated crops.* USDA Agriculture Handbook No. 496, US Government Printing Office, Washington, D.C.

McKenzie, A.J., Petty, S.J., Toms, M.P. and Furness, R.W. 2007. Importance of Sitka Spruce Picea sitchensis seed and garden bird-feeders for Siskins *Carduelis spinus* and Coal Tits *Periparus ater*. *Bird Study*, **54:** 236-247.

McKinney, M.L. 2002. Urbanization, Biodiversity, and Conservation: The impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. *BioScience,* **52**: 883-890.

McKinney, M.L. 2006. Urbanization as a major cause of biotic homogenization. *Biological Conservation*, **127**: 247-260.

McKinney, M.L. 2008. Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems*, **11**: 161-176.

Menzel, A., Sparks, T.H., Estrella N., Koch, E., Aasa, A., Ahas, R., Alm-Kubler, K., Bissolli, P., Braslavská, O.G., Briede, A., Chmielewski, F.M., Crepinsek, Z, Curnel, Y., Dahl, A., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Mage, F., Mestre, A., Nordli, O., Penuelas, J., Pirinen, P., Remisova, V., Schiefinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wielgolaski, F-E., Zach, S. and Zust, A. 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology,* **12:** 1969–1976.

Merow, C., Smith, M.J. and Silander, J. A. 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography*: **36**: 1058–1069.

Millennium Ecosystem Assessment. 2005. *Ecosystems and human well-being: Biodiversity synthesis*. Washington (D.C.): World Resources Institute. 86 p.

Miller, G. A. 1956. The magic number seven plus or minus two: some limits on our capacity to process information. *Psychological review*, **63:** 81-97.

Miller, J.R. 2005. Biodiversity conservation and the extinction of experience. *Trends in Ecology & Evolution*, **20:** 430-434.

Miller, J.R. 2006. Restoration, reconciliation, and reconnecting with nature nearby. *Biological Conservation*, **127**: 356-361.

Miller-Rushing, A., Primack, R. and Bonney, R. 2012. The history of public participation in ecological research. *Frontiers in Ecology and the Environment*, **10:** 285-290.

Moonen, A.C. and Barberi, P. 2008. Functional biodiversity: an agroecosystem approach. *Agriculture, Ecosystems & Environment*, **127:** 7-21.

Morales, C.L., Arbetman, M.P., Cameron, S.A. and Aizen, M.A. 2013. Rapid ecological replacement of a native bumble bee by invasive species. *Frontiers in Ecology and the Environment*, **11:** 529-534.

Morrison, C.A., Robinson, R.A., Leech, D.I., Dadam, D., and Toms, M.P. 2014. Using citizen science to investigate the role of productivity in House Sparrow *Passer domesticus* population trends. *Bird Study,* **61**: 91-100.

Morton, D., Rowland, C. Wood, C., Meek, L., Marston, C., Smith, G., Wadsworth, R. and Simpson, I. 2011. Final Report for LCM2007-the new UK land cover map. Countryside Survey Technical Report No 11/07.

Nabhan, G.P. and Buchmann, S.L., 1997. Services provided by pollinators. *Nature's Services: societal dependence on natural ecosystems*, pp.133-150.

National Biodiversity Network, 2015. Available from: http://data.nbn.org.uk. [20 July 2015].

National Biodiversity Network, 2017. Available from: http://data.nbn.org.uk. [04 February 2017]

Newman, G., Crall, A., Laituri, M., Graham, J., Stohlgren, T., Moore, J.C., Kodrich, K. and Holfelder, K.A. 2010. Teaching citizen science skills online: Implications for invasive species training programs. *Applied Environmental Education and Communication*, **9:** 276-286.

Newson, S. E., Ockendon, N., Joys, A., Noble, D.G. and Baillie, S.R. 2009. Comparison of habitat-specific trends in the abundance of breeding birds in the UK. *Bird Study*, **56**: 233-243.

Nieto, A., Roberts, S.P., Kemp, J., Rasmont, P., Kuhlmann, M., García Criado, M., Biesmeijer, J.C., Bogusch, P., Dathe, H.H., De la Rúa, P. and De Meulemeester, T., 2014. European red list of bees. *Luxembourg: Publication Office of the European Union*.

Oberhauser, K. and Prysby, M. 2008. Citizen science: creating a research army for conservation. *American Entomologist,* **54:** 97-99.

Ockendon, N., Davis, S.E., Miyar, T. and Toms, M.P. 2009. Urbanization and time of arrival of common birds at garden feeding stations. *Bird Study,* **56:** 405-410.

Öckinger, E. and Smith, H.G. 2007. Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology,* **44**: 50–59.

Oliver, T.H., Roy, D.B., Hill, J.K., Brereton, T. and Thomas, C.D. 2010. Heterogeneous landscapes promote population stability. *Ecology Letters,* **13**: 473-484.

Oliver, T.H., Thomas, C.D., Hill, J.K., Brereton, T. and Roy, D.B. 2012. Habitat associations of thermophilous butterflies are reduced despite climatic warming. *Global Change Biology,* **18**: 2720-2729.

Ollerton, J. and Coulthard, E. 2009. Evolution of animal pollination. *Science*, **326**: 808-809.

Ollerton, J., Erenler, H., Edwards, M. and Crockett, R., 2014. Extinctions of aculeate pollinators in Britain and the role of large-scale agricultural changes. *Science*, **346:** 1360-1362.

Ollerton, J., Winfree, R. and Tarrant, S., 2011. How many flowering plants are pollinated by animals? *Oikos*, **120:** 321-326.

Osawa, T. 2015. Importance of Farmland in Urbanized Areas as a Landscape Component for Barn Swallows (*Hirundo rustica*) Nesting on Concrete Buildings. *Environmental Management,* **55**: 1160-1167.

Osborne J.L., Martin A.P., Shortall C.R., Todd A.D., Goulson D., Knight M.E., Hale R.J. and Sanderson R.A. 2008. Quantifying and comparing bumblebee nest densities in gardens and countryside habitats. *Journal of Applied Ecology,* **45**: 784–792.

Osborne, J.L. and Corbet, S.A. 1994. Managing habitats for pollinators in farmland. *Aspects of Applied Biology,* **40**: 207–15.

Osborne, J.L. and Williams, I.H. 1996. Bumble bees as pollinators of crops and wild flowers. *Bumblebees for pleasure and profit,* pp. 24-32. (Ed. A. Matheson), International Bee Research Organisation, Cardiff.

Osborne, J.L., Williams, I.H. and Corbet, S.A. 1991. Bees, pollination and habitat change in the European community. *Bee World,* **72**: 99-116.

Owen, E.L., Bale, J.S. and Hayward, S.A. 2013. Can winter-active bumblebees survive the cold? Assessing the cold tolerance of Bombus terrestris audax and the effects of pollen feeding. *PloS one*, **8:** p.e80061.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T. and Tennent, W.J., 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399:** 579–83.

Parsons R., Tassinary L.G., Ulrich R.S., Hebl M.R. and Grossman-Alexander, M. 1998. The view from the road: Implications for stress recovery and immunization. *Journal of Environmental Psychology*, **18**: 113–140.

Pastore, R. 2012. The effect of time-compressed instruction and redundancy on learning and learners' perceptions of cognitive load. *Computers and Education,* **58:** 641-651.

Pateman, R.M., Hill, J.K., Roy, D.B., Fox, R. and Thomas, C.D. 2012. Temperature-dependent alterations in host use drive rapid change expansion in a butterfly. *Science,* **6084**: 1028-1030.

Pauw, A. 2007. Collapse of a pollination web in small conservation areas. *Ecology*, **88:** 1759-1769.

Pearce-Higgins, J.W., Eglington, S.M., Martay, B., and Chamberlain, D.E. 2015. Drivers of climate change impacts on bird communities. *Journal of Animal Ecology*, **84**: 943–954.

Peat, J., Tucker, J. and Goulson, D. 2005. Does intraspecific size variation in bumblebees allow colonies to efficiently exploit different flowers? *Ecological Entomology*, **30:** 176–181

Peat. J. and Goulson, D. 2005. Effects of experience and weather on foraging efficiency and pollen versus nectar collection in the bumblebee, *Bombus terrestris. Behavioural Ecology and Sociobiology*, **58**: 152-156.

Persson, A.S. and Smith, H.G., 2013. Seasonal persistence of bumblebee populations is affected by landscape context. *Agriculture, Ecosystems & Environment*, **165:** 201-209.

Phillips, S.J., Anderson, R.P. and Schapire, R. 2006. Maximum entropy modelling of species geographic distributions. *Ecological Modelling*, **190:** 231-259.

Pillemer, K., Fuller-Rowell, T.E., Reid, M.C. and Wells, N.M. 2010. Environmental volunteering and health outcomes over a 20-year period. *The Gerontologist,* **50**: 594-602.

Plummer, K.E., Siriwardena, G.M., Conway, G.J., Risely, K. and Toms, M.P. 2015. Is supplementary feeding in gardens a driver of evolutionary change in a migratory bird species? *Global Change Biology*, **21:** 4353-4363.

Pollard, E. and Yates, T.J. 1993. *Monitoring Butterflies for Ecology and Conservation*. Chapman and Hall, London.

Potts, J.M. and Elith, J. 2006. Comparing species abundance models. *Ecological Modelling,* **199**: 153-163.

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**: 345-353.

Pöyry, J., Leinonen, R., Söderman, G., Nieminen, M., Heikkinen, R.K. and Carter, T.R. 2011. Climate-induced increase of moth multivoltinism in boreal regions. *Global Ecology and Biogeography,* **20:** 289–298.

Prather, C.M., Pelini, S.L., Laws, A., Rivest, E., Woltz, M., Bloch, C.P., Del Toro, I., Ho C-K, Kominoski, J., Newbold, T.A.S., Parsons, S. and Joern, A. 2012. Invertebrates, ecosystem services and climate change. *Biological Reviews,* **88**: 327–348.

Prys-Jones, O. 2014. The tree bumble bee (*Bombus hypnorum*) as a house sparrow equivalent? Comments on colonizing success in Britain in the context of declining native species. *Bee World*, **91**: 98-101.

Pyle, R.M. 1978. The extinction of experience. *Horticulture*, **56**: 64–67.

Pywell, R. F., Warman, E.A., Carvell, C., Sparks, T.H., Dicks, L.V., Bennett, D., Wright, A., Critchley, C.N.R. and Sherwood, A. 2005. Providing foraging resources for bumblebees in intensively farmed landscapes. *Biological Conservation,* **121**: 479-494.

R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

R Development Core Team, 2011. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. ISBN 3-900051-07-0. URL http://www.R-project.org/.

Rasmont, P. and Iserbyt, I. 2014. *Atlas of the European Bees: genus Bombus*. 3d Edition. STEP Project, Atlas Hymenoptera, Mons, Gembloux. URL http://www.zoologie.umh.ac.be//hymenoptera/ page.asp?ID=169.

Rasmont, P., Coppee, A., Michez, D. and De Meulemeester, T. 2008. An overview of the *Bombus terrestris* (L. 1758) subspecies (Hymenoptera: Apidae). *Annales de la Société Entomologique de France,* **44:** 243-250.

Randler, C. 2008. Teaching species identification—a prerequisite for learning biodiversity and understanding ecology. *Eurasia Journal of Mathematics, Science and Technology Education*, **4:** 223-231.

Randler, C. and Bogner, F.X. 2002. Comparing methods of instruction using bird species identification skills as indicators. *Journal of Biological Education,* **36:** 181-188.

Randler, C. and Bogner, F.X. 2006. Cognitive achievements in identification skills. *Journal of Biological Education*, **40**: 161-165.

Ratcliff, J. 2008. *The Transit of Venus Enterprise in Victorian Britain*. London: Pickering & Chatto.

Rathcke, B.J. and Jules, E.S. 1993. Habitat fragmentation and plant-pollinator interactions. *Current Science,* **65**: 273-277.

Ratnieks, F.L., Schrell, F., Sheppard, R.C., Brown, E., Bristow, O.E. and Garbuzov, M. 2016. Data reliability in citizen science: learning curve and the effects of training method, volunteer background and experience on identification accuracy of insects visiting ivy flowers. *Methods in Ecology and Evolution*, **7:** 1226-1235.

Rebelo, H. and Jones, G. 2010. Ground validation of presence-only modelling with rare species: a case study on barbastelles *Barbastella barbastellus* (Chiroptera: Vespertilionidae). *Journal of Applied Ecology*, **47**: 410–420.

Redpath, N., Osgathorpe, L.M., Park, K. and Goulson, D., 2010. Crofting and bumblebee conservation: the impact of land management practices on bumblebee populations in northwest Scotland. *Biological Conservation*, **143:** 492-500.

Regan, E.C., Santini, L., Ingwall-King, L., Hoffmann, M., Rondinini, C., Symes, A., Taylor, J. and Butchart, S.H. 2015. Global trends in the status of bird and mammal pollinators. *Conservation Letters*, **8:** 397-403.

Ren, D. and Makarkin, V.N. 2009. Ascalochrysidae–a new lacewing family from the Mesozoic of China (Insecta: Neuroptera: Chrysopoidea). *Cretaceous Research*, **30:** 1217-1222.

Renwick, A. R., Massimino, D., Newson, S. E., Chamberlain, D. E., Pearce-Higgins, J. W. and Johnston, A. 2012 Modelling changes in species' abundance in response to projected climate change. *Diversity and Distributions,* **18:** 121-132.

Richards, A.J. 1997. *Plant Breeding Systems*, 2nd edn. Chapman & Hall, London.

Rissler L. J., Hijmans R. J., Graham C. H., Moritz C. and Wake D. B. 2006. Phylogeographic lineages and species comparisons in conservation analysis: a case study of California herpetofauna. *The American Naturalist*, **167:** 655-666.

Robertson, A. 1991. A mid-winter colony of *Bombus terrestris* L. (Hym., Apidae) in Devon. *Entomology Monthly Magazine,* **127:** 165–166.

Robinet, C. and Roques, A. 2010. Direct impact of recent climate warming on insect populations. *Integrative Zoology,* **5:** 132-142.

Robinson, R.A., Lawson, B., Toms, M.P., Peck, K.M., Kirkwood, J.K., Chantrey, J., Clatworthy, I.R., Evans, A.D., Hughes, L.A., Hutchinson, O.C. and John, S.K., 2010. Emerging infectious disease leads to rapid population declines of common British birds. *PLoS one*, **5:** p.e12215.

Rotman, D., Preece, J., Hammock, J., Procita, K., Hansen, D., Parr, C., Lewis, D. and Jacobs, D. 2012. Dynamic changes in motivation in collaborative citizen-science

projects. In *Proceedings of the ACM 2012 conference on Computer Supported Cooperative Work* (pp. 217-226). ACM.

Roy, D. B. and Sparks, T. H. 2000. Phenology of British butterflies and climate change. *Global Change Biology,* **6:** 407-416.

Rundlöf, M., Andersson, G.K., Bommarco, R., Fries, I., Hederström, V., Herbertsson, L., Jonsson, O., Klatt, B.K., Pedersen, T.R., Yourstone, J. and Smith, H.G., 2015. Seed coating with a neonicotinoid insecticide negatively affects wild bees. *Nature*, **51:** 77-80.

Samnegård, U., Persson, A.S. and Smith, H.G. 2011. Gardens benefit bees and enhance pollination in intensively managed farmland. *Biological Conservation*, **144**: 2602-2606.

Sarkar, S. and Margules, C. 2002. Operationalizing biodiversity for conservation planning. *Journal of Biosciences*, **27:** 299-308.

Savard, J-P.L., Clergeau, P. and Mennechez, G. 2000. Biodiversity concepts and urban ecosystems. *Landscape and Urban Planning*, **48**: 131-142

Schmeller, D.S. and Bridgewater, P. 2016. The Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES): progress and next steps. *Biodiversity and Conservation*, **25:** 801-805.

Schmid-Hempel, R., Eckhardt, M., Goulson, D., Heinzmann, D., Lange, C., Plischuk, S., Escudero, L. R., Salathé, R., Scriven, J. J. and Schmid-Hempel, P. 2014. The invasion of southern South America by imported bumblebees and associated parasites. *Journal of Animal Ecology,* **83:** 823-837.

Scriven, J.J., Woodall, L.C., Tinsley, M.C., Knight, M.E., Williams, P.H., Carolan, J.C., Brown, M.J.F. and Goulson, D. 2015. Revealing the hidden niches of cryptic bumblebees in Great Britain: implications for conservation. *Biological Conservation*, **182**: 126-133.

Senapathi, D., Carvalheiro, L.G., Biesmeijer, J. C., Dodson, C, Evans, R.L., McKerchar, M. Morton, R.D., Moss, E.D., Roberts, S.P.M., Kunin, W.E. and Potts, S.G. 2015. The impact of over 80 years of land cover changes on bee and wasp pollinator communities in England. *Proceedings of the Royal Society B: Biological Sciences*, **282:** 20150294.

Shochat, E., Warren, P.S., Faeth, S.H., McIntyre, N.E. and Hope, D. 2006. From patterns to emerging processes in mechanistic urban ecology. *Trends in Ecology & Evolution,* **21**: 186-191.

Silvertown, J. 2009. A new dawn for citizen science. *Trends in Ecology & Evolution*, **24:** 467-471.

Sladen, F.W.L. 1912. *The Humble-bee, its life history and how to domesticate it.* Macmillan and Co. Ltd.

Smith, M.R., Singh, G.M., Mozaffarian, D. and Myers, S.S. 2015. Effects of decreases of animal pollinators on human nutrition and global health: a modelling analysis. *The Lancet*, **386:** 1964-1972.

Stanghellini, M.S., Ambrose, J.T. and Schulthei, J.R. 1997. The effects of *A. mellifera* and *B. impatiens* pollination on fruit set and abortion of cucumber and watermelon. *American Bee Journal,* **137**: 386-391.

Stanghellini, M.S., Ambrose, J.T. and Schulthei, J.R. 1998. Seed production in watermelon: a comparison between two commercially available pollinators. *HortScience,* **33**: 28-30.

Steffan-Dewenter, I., and Tscharntke, T. 2000. Resource overlap and possible competition between honey bees and wild bees in central Europe. *Oecologia*, **122:** 288-296.

Steffan-Dewenter, I., Potts, S.G., and Packer, L. 2005. Pollinator diversity and crop pollination services are at risk. *Trends in Ecology & Evolution*, **20:** 651-651.

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:** e9559.

Stepenuck, K.F., and Green, L.T. 2015. Individual-and community-level impacts of volunteer environmental monitoring: a synthesis of peer-reviewed literature. *Ecology and Society,* **20**: 19.

Stoddard, F.L. and Bond, D.A. 1987. The pollination requirements of the faba bean. *Bee World,* **68**: 564-577.

Stout J.C. and Casey L.M. 2014. Relative abundance of an invasive alien plant affects insect-flower interaction networks in Ireland. *Acta Oecologia*, **55**: 78–85.

Stout J.C., Parnell J.A.N., Arroyo J., Crowe T.P. 2006 Pollination ecology and seed production of *Rhododendron ponticum* in native and exotic habitats. *Biodiversity and Conservation*, **15**: 755–777.

Sullivan, B.L., Aycrigg, J.L., Barry, J.H., Bonney, R.E., Bruns, N., Cooper, C.B., Damoulas, T., Dhondt, A.A., Dietterich, T., Farnsworth, A. and Fink, D. 2014. The eBird enterprise: an integrated approach to development and application of citizen science. *Biological Conservation*, **169:** 31-40.

Svensson, B., Lagerlöf, J. and Svensson, B.G. 2000. Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. *Agriculture, Ecosystems & Environment,* **77**: 247-255.

Sweller, J. 1988. Cognitive load during problem solving: effects on learning. *Cognitive Science,* **12:** 257-285.

Thomas, C.D., Aldina, M.A. and Hill, J.K. 2006. Range retractions and extinction in the face of climate warming. *Trends in Ecology and Evolution,* **21**: 415-416.

Thomas, J.A. 2005. Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **360:** 339-357.

Thomas, J.A., Telfer, M.G., Roy, D.B., Preston, C.D., Greenwood, J.J.D., Asher, J., Fox, R., Clarke, R.T. and Lawton, J.H. 2004. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science*, **303**: 1879-1881.

Thompson, C.E., Biesmeijer, J.C., Allnutt, T.R., Pietravalle, S. and Budge, G.E. 2014. Parasite pressures on feral honey bees (*Apis mellifera sp.*). *PLoS one*, **9:** e105164. doi:10.1371/journal.pone.0105164.

Thompson, J.D. and Goodell, K. 2001. Pollen removal and deposition by honeybee and bumblebee visitors to apple and almond flowers. *Journal of Applied Ecology*, **38**: 1032-1044.

Tommasi, D., Miro, A., Higo, H.A. and Winston, M.L. 2004. Bee diversity and abundance in an urban setting. *The Canadian Entomologist* **136**: 851-869.

Toms, M.P. and Newson, S.E. 2006. Volunteer surveys as a means of inferring trends in garden mammal populations. *Mammal Review*, **36:** 309-317.

Tonhasca, A and Macdonald, M.A. 2016. Great yellow bumblebee. Version 1.0. In The Species Action Framework Handbook, Gaywood, M.J., Boon, P.J., Thompson, D.B.A., Strachan, I.M. (eds). Scottish Natural Heritage, Battleby, Perth.

Tonietto, R., Fant, J., Ascher, J., Ellis, K. and Larkin, D. 2011. A comparison of bee communities of Chicago green roofs, parks and prairies. *Landscape and Urban Planning*, **103:** 102-108.

Trumbull, D.J., Bonney, R., Bascom, D. and Cabral, A. 2000. Thinking scientifically during participation in a citizen-science project. *Science Education,* **84**: 265-275.

Tsuchida, K., Ito Kondo, N., Inoue, M. N. and Goka, K. 2010. Reproductive disturbance risks to indigenous Japanese bumblebees from introduced *Bombus terrestris*. *Applied Entomology and Zoology*, **45**: 49-58.

Tulloch, A. I., Possingham, H. P., Joseph, L. N., Szabo, J., and Martin, T. G. 2013. Realising the full potential of citizen science monitoring programs. *Biological Conservation*, **165:** 128-138.

Tylianakis, J.M., 2013. The global plight of pollinators. *Science*, **339:** 1532-1533.

UK Meteorological Office, 2012. Met Office Integrated Data Archive System (MIDAS) Land and Marine Surface Stations Data (1853-current). NCAS British Atmospheric Data Centre, 2012. 08/11/2012. Available from http://badc.nerc.ac.uk/view/badc.nerc.ac.uk__ATOM__dataent_ukmo-midas

UK National Ecosystem Assessment, 2011. The UK National Ecosystem Assessment: Synthesis of the Key Findings. UNEP-WCMC, Cambridge.

Ulrich, R.S, Simons, R.F., Losito, B.D. and Fiorito, E. 1991. Stress recovery during exposure to natural and urban environments. *Journal of Environmental Psychology*, **11**: 201–230.

United Nations, 1992. Convention on Biological Diversity, www.biodiv.org/convention/articles.asp.

United Nations, Department of Economic and Social Affairs, Population Division 2014. World Urbanization Prospects: The 2014 Revision, Highlights (ST/ESA/SER.A/352).

Van den Eijende, J., de Ruijter, A. and Van der Steen, J. 1991. Method for rearing *Bombus terrestris* continuously and the production of bumble bee colonies for pollination purposes. *Acta Horticulturae,* **288**: 154-158.

van Swaay, C. and Warren, M. S. 2006. Biotope use and trends of European butterflies. *Journal of Insect Conservation,* **10**: 189–209.

Vanbergen, A.J., Baude, M., Biesmeijer, J.C., Britton, N.F., Brown, M.J., Brown, M., Bryden, J., Budge, G.E., Bull, J.C., Carvell, C. and Challinor, A.J., 2013. Threats to an ecosystem service: pressures on pollinators. *Frontiers in Ecology and the Environment*, **11:** 251-259.

Visconti, P., Bakkenes, M., Baisero, D., Brooks, T., Butchart, S.H., Joppa, L., Alkemade, R., Di Marco, M., Santini, L., Hoffmann, M. and Maiorano, L., 2015. Projecting global biodiversity indicators under future development scenarios. *Conservation Letters*, **9:** 5-13.

Wal, R., Sharma, N., Mellish, C., Robinson, A. and Siddharthan, A. 2016. The role of automated feedback in training and retaining biological recorders for citizen science. *Conservation Biology*, **30:** 550-561.

Walther, G-R, Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J-M., Hoegh-Guldberg, O. and Bairlein, F. 2002. Ecological responses to recent climate change. *Nature,* **416:** 389-395.

Walther-Hellwig, K., Fokul G., Frankl, R., Buechler, R., Ekschmitt, K. and Wolters, V. 2006. Increased density of honeybee colonies affects foraging bumblebees. *Apidologie,* **37:** 517-532.

Warren, M. S., Hill, J. K., Thomas, J. A., Asher, J., Fox, R., Huntley, B., Roy, D. B., Telfer, M. G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S. G., Greatorex-Davies, J. N., Moss, D. and Thomas, C. D. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature,* **414:** 65-69.

Warren, M.S. and Key, R.S. 1991. Woodlands: past, present and potential for insects. In: *The conservation of insects and their habitats*, eds. N.M. Collins & J.A.

Thomas, 155-211. London, Academic Press. (Royal Entomological Society of London, Symposium No. 15.)

Whitehorn, P.R., O' Connor, S., Wackers, F.L. and Goulson, D. 2012 Neonicotinoid pesticide use reduces bumblebee colony growth and queen production. *Science,* **336**: 351-352.

Wilcock, C. and Neiland, R. 2002. Pollination failure in plants: why it happens and when it matters. *Trends in Plant Science,* **7:** 270-277.

Williams I.H., 1994. The dependences of crop production within the European Union on pollination by honey bees. *Agricultural Zoology Reviews,* **6:** 229–257*.*

Williams, I.H., Martin, A.P. and White, R.P. 1987. The effect of insect pollination on plant development and seed production in winter oilseed rape (*Brassica napus* L.). *The Journal of Agricultural Science* **109**: 135-139.

Williams, N.M., Minckley, R.L. and Silveira, F.A., 2001. Variation in native bee faunas and its implications for detecting community changes. *Conservation Ecology*, **5:** 7.

Williams P.H. 1982. The distribution and decline of British bumble bees (*Bombus* Latr.). *Journal of Apicultural Research,* **21**: 236:245

Williams P.H. 1986 Environmental change and the distributions of British bumble bees (*Bombus* Latr.). *Bee World*, **67**: 50–61.

Williams, P. H. 1988. Habitat use by bumble bees *Bombus* spp. *Ecological Entomology*, **13:** 223-237.

Williams P.H., Araújo M.B. and Rasmont P. 2007 Can vulnerability among British bumblebee (*Bombus*) species be explained by niche position and breadth? *Biological Conservation,* **138**: 493–505.

Williams, P.H and Osborne, J.L. 2009 Bumblebee vulnerability and conservation world-wide. *Apidologie*, **40**: 367-387.

Williams P.H., Tang Y., Yao J. and Cameron S. 2009. The bumblebees of Sichuan (Hymenoptera: Apidae, Bombini), *Systematics and Biodiversity,* **7**: 101-190.

Williams, C.S. 1995. Conserving Europe's bees: why all the buzz? *Trends in Ecology & Evolution,* **10**: 309-310

Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H. and Guisan, A. 2008. Effects of sample size on the performance of species distribution models. *Diversity and Distributions*, **14:** 763-773.

Wolf, S., Rohde, M. and Moritz, R.F., 2010. The reliability of morphological traits in the differentiation of *Bombus terrestris* and *B. lucorum* (Hymenoptera: Apidae). *Apidologie*, **41:** 45-53.

Woodcock, B.A., Edwards, M., Redhead, J., Meek, W.R., Nuttall, P., Falk, S., Nowakowski, M. and Pywell, R.F. 2013. Crop flower visitation by honeybees, bumblebees and solitary bees: Behavioural differences and diversity responses to landscape. *Agriculture, Ecosystems & Environment*, **171:** 1-8.

Xie, Z., Williams, P.H. and Tang Y. 2008. The effect of grazing on bumblebees in the high rangelands of the eastern Tibetan Plateau of Sichuan. Journal of Insect Conservation, **12:** 695–703.

Yang, E-C., Chang, H-C., Wu, W-Y. and Chen, Y-W. 2012. Impaired olfactory associative behavior of honeybee workers due to contamination of imidacloprid in the larval stage. *PLoS ONE*, **7:** e49472.

Zipkin, E.F., Ries, L., Reeves, R., Regetz, J. and Oberhauser, K.S. 2012. Tracking climate impacts on the migratory monarch butterfly. *Global Change Biology*, **18**: 3039–3049.