Biodiversity climate change impacts report card technical paper

3. Implications of climate change for UK invertebrates (excluding butterflies and moths)

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Executive summary

- The invertebrate biodiversity of Britain is substantial, with more than 24,000 species of insect alone. However, there were significant declines in many species over the past century. Data regarding the status of invertebrate species are patchy and incomplete. There are few systematically collected, long-term data sets. The biological recording network is good, providing data on distributions (presence only) and can be used to changes in range. However, the available data only provide limited power to assess trends in the population size.
- Species have recently colonised southern England from continental Europe and are expanding northwards rapidly. There is medium evidence (with high levels of agreement) that climate warming has resulted in increases in the range sizes of southern invertebrates and shifts northwards in the range of highly mobile species, such as dragonflies, and those considered to be more limited by dispersal, e.g. woodlice. There is only limited evidence that the southern range margins of species have also shifted north and the ranges of northern species have contracted; the evidence may be more limited because detecting colonisations only requires a single record, but reliably detecting absences (i.e. local extinctions) of a species is challenging. Warmer temperatures are likely to cause species to shift their habitat associations to cooler microclimates.
- There is limited evidence that climate changes are resulting in declines in the abundance of some invertebrate species; observed declines are site and/or habitat specific and generally greatest in upland areas and in habitat-specialist species. Habitat quality and extent may also be contributing to these declines. In contrast, there is limited evidence of increases in the relative abundance of common and habitat generalist species.
- There is medium evidence, with high levels of agreement, that spring and summer phenological events have advanced significantly, with average rates of change consistent with observed warming trends. There is limited, but growing, evidence these advances have not occurred at the same rate between trophic groups. Such asynchrony could alter trophic interactions between plants, herbivores, pollinators, predators and parasitoids. Advances in spring emergence could lengthen the season suitable for reproduction and increase the number of generations per year, thus potentially increasing population size; however there is limited evidence regarding the success of such additional generations.
- The effects of predicted decreases in summer rainfall and increases in winter rainfall are likely to be contrasting, but the relative importance of each is unknown. Changes in rainfall patterns are likely to affect flight period, food availability, may cause direct mortality (e.g. through droughting and flooding) and result in significant changes in habitat quality, particularly in aquatic habitats.
- Sea level rise will have significant impacts on coastal margin habitats, which contain highly adapted, specialist fauna and losses of coastal habitats are very likely to have severe effects on these invertebrates.
- There is good evidence that changes in habitat extent and quality are important drivers of invertebrate populations. However, there is considerable uncertainty of the relative importance of changes in climate and changes in habitat extent and quality on trends in invertebrate populations; further uncertainty is caused by complex interactions between climate and habitat quality.
- Rising temperatures is likely to make the climate in the UK suitable for an unknown number of invertebrate pests. Whilst many species will be unable to naturally disperse to the UK, human-assisted introduction is likely.
- Colonisations, changes in species ranges and phenology, and potential habitat shifts are likely to alter local assemblage composition. However, there is little evidence of the consequences of these changes. Furthermore, our understanding of current

ecosystem functioning and the role of individual invertebrate species is very poor and therefore the direction and magnitude of alterations in ecosystem functions due to climate-change induced changes in invertebrate communities cannot currently be predicted.

Invertebrate biodiversity in the UK

Invertebrates are extremely numerous and diverse but, despite being acknowledged to play important roles in ecosystem services and functions, our knowledge of the status, ecology, interactions and sensitivity to change of many species is poor (Cardoso *et al.* 2011).

Britain's invertebrate biodiversity resource is substantial. Approximately 24,000 species of insect are estimated to occur in Britain (Barnard 2011), plus (largely) unquantified but presumably thousands of other invertebrate species; non-arthropod invertebrates are particularly poorly quantified. This compares to 312 bird species (Dudley *et al.* 2006) and approximately 2000 flowering plants and ferns (Preston, Pearson & Dimes 2002). Much of the UK's invertebrate biodiversity has suffered significant declines over the past century; 9% of insects are currently listed in Red Data Books (RDB, Table 1). However, our understanding and therefore conservation efforts are biased towards a small subset of invertebrate taxa. For example, Lepidoptera comprise 41% of the invertebrates designated as UK Biodiversity Action Plan (BAP) priority species, but only 9% of UK RDB invertebrates. Only 8% of UK Hymenopteran species are Aculeates but they comprise all BAP and RDB listed Hymenopteran.

Lepidopteran species were excluded from this paper because they are unusual in the quality and quantity of data available regarding them; they are covered in other papers on the effects of climate change on their population size (Pearce-Higgins 2013) and distribution change (Pateman 2013).

Fifty-nine invertebrates, including ten Lepidopterans, were identified as species for which the UK has an International Responsibility (Table 1, Appendix 1), defined as 1) species occurring in UK that are listed as global Red Data Book species (31 species); 2) species listed in Annexes II and/or IV of the EU Habitats Directive (13 species); and 3) Biodiversity Action Plan (BAP) species for which designation criteria mention that the species is endemic in the UK or that the UK holds significant proportion of the global population (25 species). The extent to which this list is exhaustive is not known. However, it is likely that all species endemic to the UK, or for which the UK holds a significant proportion of the global population, were identified as priority species during the BAP process.

Table 1. *UK invertebrate biodiversity within selected groups for which at least one species has a conservation designation, showing the estimated numbers of: invertebrate taxa, including marine taxa, occurring in the UK; those listed in Red Data Books (UK and Global RDB (GRDB) lists, excluding Least Concern, totalling 3951 taxa, GRDB numbers shown in parentheses); those designated as nationally Rare, Scarce or Notable (Na and Nb); those listed by the UK Biodiversity Action Plan (total number of BAP priority species, 1150). Also shown are the number for which the UK has International Responsibility, defined as species listed in GRDB, in Annexes II and/or IV of the EU Habitat Directive, and BAP priority species known to be endemic in the UK or for which the UK holds a significant proportion of the global population. Note: designations are not mutually exclusive. Source of taxa designations (JNCC 2011).*

	No. of taxa in UK	**No. of RDB (GRDB) taxa**	**No. of rare taxa**	**No. of BAP taxa**	**International Responsibility**
Sponge (Porifera)	Unknown	0	8	0	
Cnidaria (coelenterate)	Unknown	3 (3)	21	14	3
Nemertea	Unknown				1
Mollusca[1]	1100	34 (9)	22	22	10
Annelida	Unknown	3 (1)	6	2	1
Arthropoda					
Arachnida					
Spider (Araneae)[2]	648	87	0	31	2
False scorpion (Pseudoscorpiones)[3]	27	1	0	0	
Crustacea	Unknown	11 (2)	14	8	3
Millipede (Diplopoda)[4]	72	2	0	3	
Centipede (Chilopoda)[4]	73	3	0	1	1
Insecta					
Mayfly (Ephemeroptera)[5]	51	4	1	2	
Dragonfly (Odonata) [5]	49	16 (2)	0	2	2
Stonefly (Plecoptera) [5]	34	4	3	2	1
Orthopteran[5]	33	6	0	4	
Tue bug (Hemiptera) [5]	1830	84	158	10	
Alderfly (Megaloptera) [5]	3	0	1	0	
Lacewing (Neuroptera) [5]	69	0	9	1	
Beetle (Coleoptera) [5]	4000	838 (6)	1021	78	10
Caddis fly (Trichoptera) [5]	198	31	16	4	
Lepidoptera[5]	2570	211 (1)	71	176	10
True fly (Diptera) [5]	7000	814	660	35	8
Hymenopteran[5]	7000	144 (6)	106	35	6
Bryozoa	Unknown	1	11	2	
Echinodermata	Unknown	1 (1)	3	0	1
Total		2298	2131	432	59

Sources of the estimated number of species in the UK: [1] Conchological Society of Great Britain and Ireland, [2] (Harvey, Nellist & Telfer 2002), [3] (Legg & Jones 1988), [4] British Myriapod & Isopod Group (www.bmig.org.uk), [5] (Barnard 2011)

Current status and trends in invertebrate biodiversity

Overview

There has been no comprehensive documentation of invertebrate gains and losses in the UK. Extinctions are notoriously difficult to confirm due to intermittent species records, particularly for poorly recorded invertebrates groups. Natural England's Lost Life report identified 290 invertebrates (including 110 Lepidoptera) that have been extirpated in England (Brown *et al.* 2010); a small number of these may still occur elsewhere in the UK. However, the Lost Life report was limited in that it only considered records collated within NBN. Assessments of the accuracy of Lost Life in two bio-regions found recent records for 42% of 'extinct' invertebrate species identified by Lost Life (Dolman, Panter & Mossman 2010; Panter, Mossman & Dolman 2011). Conversely, the Lost Life estimate is likely to under-estimate recent losses since invertebrate extinctions are poorly documented. For example, globally only 70 insect extinctions are recognised, but are estimated at 44,000 from the extinction rates of other taxa (Dunn 2005).

Data regarding the status of invertebrate species are patchy and incomplete. Evidence of expansions or declines can be measured or deduced from changes in population size or, more usually, range or number of occupied sites or squares. Recent trends have been assessed for a small number of species during the selection of Priority species to include in the UK BAP. There was some evidence of a marked decline (>50% of range and or abundance) in the UK for 59% of the 414 BAP terrestrial invertebrates. Where these trends had been quantified, the average decline in abundance or distribution over the past 25 was 67±22% (JNCC 2011). The majority of these declines were based on changes in the number of sites or grid squares in which a species was recorded.

Data availability

There are few systematically collected, long-term data sets that can be used to assess trends in the relative abundance or population sizes of invertebrates. There is therefore *a significant knowledge gap* regarding the population status of most invertebrate groups, comprising the majority of the UK's invertebrate species.

The Butterfly Monitoring Scheme and the Wider Countryside Butterfly Survey provide standardised long-term abundance data across much of the country for butterflies, but data for non-Lepidopteran invertebrates are scant. Long-term studies of single species or sites can be used to understand changes in phenology, e.g. hoverflies in a garden (Graham-Taylor, Stubbs & Brooke 2009), and further efforts should be made to identify sources of such data. However, such studies are likely to be rare and, where they do exist, cannot provide a national view. Long-term surveillance schemes that monitor non-Lepidopteran invertebrates include the Rothamsted Insect Survey (RIS) and the UK Environmental Change Network (ECN). The RIS has operated a network of 16 suction traps since 1965, which sample biomass at landscape- rather than at local or site-scales (Harrington & Woiwod 2007). The UK ECN is a series of 45 river and lake and 12 terrestrial sites throughout the UK; most sites were established in 1992, with the remaining by 1998. At each site, the abundance of butterflies, moths and some other invertebrates (including spiders, carabids and spittle bugs) are monitored, as well as a range of climatic and environmental variables. The frequency of sampling varies with taxa, but pitfall traps are run fortnightly (www.ecn.ac.uk). In contrast to terrestrial habitats, there are relatively abundant data, both geographically and temporally, on river macroinvertebrates. For example, the Environment Agency BIOSYS data base contains information of macroinvertebrate families from 27,000 sites in England and Wales, with some records available from 1970 and the majority from 1990.

Whilst there is a paucity of systematically collected data that can be reliably used to assess population sizes of most invertebrate groups, the biological recording network in the UK (e.g. county recorders, national recording schemes and biological records centres) is generally good. It can provide useful data on species' distribution, the richness of a particular group per 10 km grid square and, to a lesser extent, temporal changes in species distribution or richness. In contrast to systematic long-term monitoring schemes, such as ECN, the biological recording network provides presence only data (i.e. not quantitative and does not indicate true absences), contains no systematic resurveying and locations are usually accurate to grid square level. By comparing the distribution of recent and historic records, it is possible to assess changes in the extent of occurrence (i.e. the geographic range) and the area of occupancy (usually the number of 10 km grid squares occupied), and thus to investigate range shifts and changes in range size. Such data are particularly suited to monitoring expansions because are arrivals more easily observed than losses. However, data quality and recorder coverage varies considerably among species and taxonomic groups. Further limitations to this approach are discussed in a later section. Novel approaches may be needed to plug the data availability gap. For example, museum and herbarium collections have been used to demonstrate the changes in phenology of a plant and its pollinator (Robbirt *et al.* 2011; Robbirt *et al.* 2014).

Detecting colonisations of species is relatively simple since it only requires a single record. In contrast, detecting local extinctions of a species as it moves northwards is challenging; range shifts are usually analysed using long time periods in order to ensure sufficient data and a species may be almost extinct in a hectad but a single record at any point in the time period counts as an occupancy. The difficultly in detecting local extinctions is likely to result in a significant time lag before we are able to estimate losses occurring now. The identification of shifting ranges requires good quality data of the area of occupancy, e.g. the number of occupied 10 km grid squares. The quality and availability of such data is highly variable between taxonomic groups, with a general bias towards larger, mobile species, such as butterflies, dragonflies and grasshoppers. Poorly recorded groups are often those that are regarded as sedentary and poorly dispersing, such as molluscs and annelids. Thus, the evidence base may be heavily biased towards those groups most able to adjust their range margins in response to changing climate.

Trends in abundance, area of occupancy and diversity

Analyses of catches from RIS and ECN sites have shown long-term changes in invertebrate abundance. Total aerial insect biomass declined significantly between 1973-2002 at one of four southern RIS suction trap sites (Shortall *et al.* 2009). However, the total catch at that site, particularly in the 1970s, was much greater than at the other sites, possibly indicating that significant declines had taken place at the other sites prior to trap installation in the mid-1960s. Total aerial invertebrate biomass also declined significantly at the RIS site in Stirling (Benton *et al.* 2002). Changes in the population dynamics of the social wasp *Vespula vulgaris* and abrupt declines in the abundance of *V. germanica,* beginning in c. 1980, have been observed at seven RIS suction trap sites (Archer 2001). There have been substantial overall declines in the abundance of a number of carabid species across the ECN network between 1993 and 2008; half of the species studied underwent declines of more than 30% (Brooks *et al.* 2012). However, there were significant differences between regions and habitats, with declines greatest in montane, northern upland and western pasture sites (Brooks *et al.* 2012). There has also been a significant decline in the abundance of specialist moorland and carnivorous carabids (Morecroft *et al.* 2009; Pozsgai & Littlewood 2014). In contrast, carabid populations increased in the southern downland sites (Brooks *et al.* 2012). Changes in abundance and community composition of river macroinvertebrates have been reported in a number of upland and lowland watercourses (e.g. (Durance & Ormerod 2007; Durance & Ormerod 2009; Clews & Ormerod 2010).

Reduced populations sizes and substantial range declines have been documented in bumble bees, including the loss of three of the UK's 25 species (Williams 1982; Williams 2005; Goulson, Lye & Darvill 2008). Declines have also been observed in the species richness of all bees (Biesmeijer *et al.* 2006); bee species richness was lower in 52% of 81 UK 10-km cells post-1980 compared to pre-1980, but richness increased in only 10% of cells. No significant change in the richness of hoverflies was observed over the same period (Biesmeijer *et al.* 2006). However, across both groups there was an increase in the relative abundance of common, ubiquitous species.

Drivers of population change – relative impacts of climate change

Detecting climate responses of poorly monitored groups is problematic. However, evidence of recent colonisations of the south east of England by species from mainland Europe, shifts in the range of UK species and changes in phenology all indicate responses to changing climate.

There have been changes in the climate of the UK over the past 30 years; however, over the same period there have been dramatic reductions in habitat availability and changes in habitat quality and physical and functional connectivity of landscapes (Table 2). There is uncertainty in the relative importance to invertebrate populations of the observed changes in climate and compared to the changes in habitat extent and quality, with further uncertainty caused by complex interactions between climate and habitat quality.

Table. 2. *Changes in extent and quality of selected habitats*

Habitat	Change in habitat extent		Change in habitat quality
	c.1940-1990	Recent	
Lowland Neutral Grassland	↓95%	↑6% (98-07)	42% in favourable condition Under-grazing, scrub encroachment
Chalk & Limestone grassland	↓80%	No change	26% in favourable condition Under-grazing (lowland) Over-grazing (upland)
Lowland heath	↓40%	↑slowly (05-08)	17% in favourable condition Scrub encroachment, loss of early successional micro-habitats, eutrophication
Lowland fen	↓50%	↓slowly (02-08)	38% in favourable condition Under-grazing, water management, eutrophication 20% reduction in plant species richness

Sources: Warren & Goldsmith (1983); Blunden & Curry (1988); Carey *et al.* (2008); JNCC (2009).

Signal from warming temperatures

Recent colonists

A number of continental European invertebrates have established in the south of the UK in the past 100 years and are expanding their range northwards (e.g. Table 3). It is not known if some of these species arrived following human-assisted introduction, but others, such as the Southern Emerald Damselfly, were regular migrants prior to establishment as a breeding species. Non-Lepidopteran colonising species that have been recognised to date are dominated by relatively strongly flying species such as Hymenoptera and Odonata; the extent to which less mobile species will be able to colonise from the continent is not clear. Most of these insects are relatively large and conspicuous and belong to groups with active recording schemes, and hence it is likely that other additions to the British invertebrate fauna have gone undetected.

Table 3. *Examples of species that have colonised the UK from mainland Europe within the last 100 years.*

Species	Year of first record	Location of first record	Spread	Reference
Wasp Spider *Argiope bruennichi*	1922	Sussex	Largely restricted to south coast until 1970s when it underwent a considerable range expansion. It is now widespread in the south of England and has been recorded as far north as Nottingham	(British Arachnological Society 2012)
Median Wasp *Dolichovespula media*	1980	Sussex	Rapidly spread northwards with scattered records in northern England and Scotland	(Phillips & Roberts 2010)
Small Red-eyed Damselfly *Erythromma viridulum*	1999 2000	Essex Isle of Wight: 2 distinct colonisation events	Spread throughout SE England to reach Devon in the west and North Yorkshire in the north. Expansion has slowed.	(Watts, Keat & Thompson 2010; British Dragonfly Society 2012)
Tree Bumblebee *Bombus hypnorum*	2001	Wiltshire	Throughout south and central England and as far north as the Scottish border	(BWARS 2012)
Southern Emerald Damselfly *Lestes barbarus*	2002	Norfolk	Since first record regular migrants seen at scattered locations on SE England coast. Ovipositing females have been observed at Cliffe marshes	
Willow Emerald Damselfly *Lestes viridis*	2009	Suffolk	Records from Suffolk, Norfolk, Essex and north Kent. More common than *L. barbarous*	(British Dragonfly Society 2012)

Range expansions and shifts north

Climate warming has resulted in increases in the range sizes of southern and ‘ubiquitous’ British Odonata species as their distribution has shifted northwards at the range margin (Hickling *et al.* 2005; Hickling *et al.* 2006). In contrast, two of the four northern species declined in range size and the remaining two expanded in range size but retracted northwards at their southern margin, further indicating that the range shifts are linked to climatic suitability (Hickling *et al.* 2005). Range shifting species include those that are highly mobile, such as the Long-winged Conehead *Conocephalus discolour* and Roesel’s bush-cricket *Metrioptera roeselii*, which have rapidly expanded northwards from the south coast over the past 30 years (Thomas *et al.* 2001). However, shifts northwards may be a common phenomenon; northward movement of the northern range margins were observed in all of the 12 invertebrate groups investigated by (Hickling *et al.* 2006), including Orthoptera, longhorn beetles, carabid beetles, aquatic bugs, millipedes, woodlice, spiders, soldier beetles, butterflies, Odonata, lacewings and harvestmen, although range shifts of lacewings and harvestmen were not significant. Species also moved to higher altitudes (Hickling *et al.* 2006; see also Menendez *et al.* 2014). There is also evidence of shifts northwards of southerly coastal and intertidal species, for example in recent decades the rocky shore molluscs *Osilinus lineatus* and *Gibbula umbilicalis* have extended northwards and have increased in abundance (Mieszkowska *et al.* 2006). *Coelopa pilipes*, a coastal strandline fly with a southern distribution, has expanded its UK range northwards and has become more abundant; however, the similar, previously dominant, northern species has reduced in abundance (Edward *et al.* 2007).

The MONARCH project modelled the future climate suitability of the UK for 120 BAP species, including 16 non-Lepidopteran invertebrates, using current European occupied climate space (Berry *et al.* 2007). However, for the majority of invertebrates, their potentially suitable climate space in the UK was much larger than their current distributions (Berry *et al.* 2007). This suggests that either climate is not the major constraint on their UK distribution (i.e. factors such as habitat availability, quality or connectivity are more important), or there is geographic variation in climate tolerance, with UK populations locally adapted to different climate space compared to the wider European population. So whilst large changes in potential climate space may occur, their implications for the UK distributions are unclear.

The assessment of the likely impacts of future climate changes on populations in fragmented landscapes requires understanding the relative frequency of habitat specialists and the proportion of the UK invertebrate fauna that have a northerly rather than southerly distribution (Hill *et al.* 2002). However, both are poorly known. To provide an initial assessment, we quantified the number of species from selected groups (Odonata, three spider families and Carabids) that were habitat specialists or generalists, and the number that had a northerly, southerly or widespread distribution in the UK (Table 4). Whilst a relatively small proportion of the invertebrates assessed had northerly distributions (8%, compared to 48% that were southern), if this 8% is representative of the more than 24,000 invertebrate species in Britain, then at least 2000 species might be expected to decline, with some at risk of regional extinction. However, a large proportion of both southern and northern species were habitat specialists (70%, 78% respectively, Fisher Exact test p = 0.331), compared to only 45% of species found across a wide range of latitudes within the UK. This assessment is far from exhaustive and we recommend further groups are investigated. There is some interaction between climate and habitat associations of butterfly species (Suggitt *et al.* 2012), with warming winters potentially allowing butterflies to occupy a broader range of habitats (Oliver *et al.* 2009). However, this was not enough to ameliorate the effects of habitat degradation (Oliver *et al.* 2012). This suggests that reductions in habitat extent and or quality would cause a serious problem for large numbers of species. However, much of this work has studied butterflies and it is unclear how this transfers to other taxa. Furthermore, with the exception of butterflies, our understanding of dispersal distances in invertebrate groups is generally very poor. Most species are thought to disperse distances of a maximum of a few kilometres per generation (Hardman 2010). Although climate suitability might increase for some species, it cannot be assumed that all taxa will be able to shift with that changing climate, particularly in fragmented landscapes.

Table 4. *Number of habitat generalist and specialist* [1] *species from selected taxon groups with northern* [2] *or southern* [3] *UK distribution or that are widespread* [4] *across the UK.*

		Habitat association	Northern species	Southern species	Widespread species	Total
Odonata		Generalist	0	11	10	
		Specialist	4	10	3	
Araneae	Theridiidae	Generalist	1	7	14	
		Specialist	3	16	5	
	Lycosidae	Generalist	0	5	10	
		Specialist	3	4	9	
	Thomisidae	Generalist	0	5	5	
		Specialist	0	11	5	
Coleoptera	Carabidae	Generalist	7	36	70	
		Specialist	19	107	66	
Total		Generalist	8	64	109	191
		Specialist	29	148	88	265
			37	212	197	446

[1] Habitat specialists: are known in the UK from only one or two habitats

[2] Northern: restricted to Scotland, Northern England and uplands at southern latitudes; assumed to have a southern range margin within the UK

[3] Southern: range does not extend to Northern England or Scotland; assumed to have a northern range margin within the UK

[4] Widespread: includes widely distributed and ubiquitous species, but also rare species with a scattered distribution across a broad range of latitudes

Sources: Odonata (British Dragonfly Society 2012); Araneae (Harvey, Nellist & Telfer 2002); Carabidae (Luff 1998).

Changes in phenology

Spring and summer phenological events have advanced significantly across a wide range of UK terrestrial, freshwater and marine taxa, including a range of invertebrate groups, with average rates of change consistent with observed warming trends (Thackeray *et al.* 2010). Intertidal mollusc species have responded to increases in sea surface temperature with changes in their reproductive development; the southerly species advancing the date of its reproductive development, lengthening its reproductive season and by more of the population being reproductively active, and the northerly species delaying the timing of its development and reducing the proportion of the population reaching advanced reproductive stages (Moore, Thompson & Hawkins 2011). Some ground beetle species have ceased activity earlier in the season leading to a shortening of their activity window. This has been linked to population declines; however, other species may have benefited from an earlier onset of activity in spring (Pozsgai & Littlewood 2014).

Diapause plays an important role in cold stress tolerance and almost all insects in the temperate zone rely on it to overwinter. Photoperiod is the primary cue for entering diapause (Bale & Hayward 2010). Whilst climate change will not affect day length patterns, it may alter the effectiveness of photoperiod as an indicator of seasonal changes in temperature (Bale & Hayward 2010). Warmer conditions at the beginning of diapause may reduce diapause incidence and duration. If diapause is crucial for overwintering survival, late entrance increases the risk of encountering cold stress outside of diapause. However, if species can complete another generation prior to winter, or can survive winter outside of diapause, there may be a selective advantage in not entering diapause as temperatures increase (Bale & Hayward 2010). In some species, cold-tolerance mechanisms require exposure to cold conditions in order to be most effective; higher temperatures in early winter may therefore increase mortality if the winter then becomes more severe.

There has been a significant advance in the early flight period of Odonata, with ‘spring’ species advancing their phenology more than those with flight periods later in the year (Hassall *et al.* 2007). Warmer winter temperatures are thought to have advanced the date of first appearance of several species of hoverfly and lengthened the flight period of others (Graham-Taylor, Stubbs & Brooke 2009). The duration of diapause is shorter at higher temperatures, possibly because metabolic rates are higher at raised temperatures and this depletes stored resources more quickly (Hahn & Denlinger 2007); there has been little research on the comparative fitness of early and late emerging individuals (Bale & Hayward 2010).

Habitat extent, quality and connectivity

Extent and quality of protected areas are vital to habitat specialist invertebrates, which comprise much of the UK biodiversity (Table 4). The rapid and severe losses of semi-natural habitats during the 1940s-1980s (Table 2) has abated and the destruction of designated sites is now rare; the extent of some habitats has also increased (e.g. broadleaved woodland (Carey *et al.* 2008)). However, in contrast to a slowing in the rate of habitat loss, the quality of most UK semi-natural habitats has continued to change due to a combination of cessation of traditional land-use practices, insufficient resources for conservation management (particularly for small or isolated fragments, and non-designated sites), edge effects, nitrogen deposition, eutrophication and hydrological change. In the latest assessment, 43% of SSSIs and 63% of SACs were in unfavourable condition (Williams 2006; Natural England 2012). There has also been a decline in the quality of habitat resource provided by the wider countryside. For example, loss of flower-rich meadows and declines in food availability across the wider countryside are thought to have caused declines in many bumblebee species (Goulson *et al.* 2005b). Habitat degradation due to changes in agricultural practices was assessed as the most significant threat to priority species in the UK (JNCC 2009). Whilst climate warming is resulting in range expansions of a range of southern invertebrate species, these may be retarded, prevented, or in some cases, reversed by reduced habitat extent, quality and connectivity (Oliver *et al.* 2012); both habitat changes and climate may jointly generate negative trends in northern species.

Many invertebrate species require complexes of microhabitats and vegetation structures to provide contrasting the microclimate and conditions that are required by differing life cycle stages. However, management regimes may be designed without understanding of which species are present, or of the range of interventions required by the full complement of species of conservation concern (Dolman, Panter & Mossman 2012) and generic prescriptions for habitat management can fail to provide the structural complexity required by invertebrates (Webb, Drewitt & Measures 2010). Vegetation structure and site topography are also important determinants of local microclimate and can potentially buffer species from adverse climates. Future habitat management may need to be adaptive as climate change alters the suitability vegetation structures; warmer temperatures are likely to increase use of taller vegetation and later successional stages (Thomas *et al.* 1999; Suggitt *et al.* 2012). Additional protected areas with varied topography and aspect, including shaded, north-facing slopes, may be needed (Thomas *et al.* 1999).

Habitat connectivity

Colonising species, particularly some habitat specialists, have been found to favour protected areas (Thomas *et al.* 2012). The majority of remaining semi-natural habitat in the UK occurs in small patches, for example 77% of SSSIs are less than 100 ha in size (Lawton *et al.* 2010). Smaller patch sizes support smaller populations and some patches may be too small to sustain viable populations. This may be particularly important for specialist species, those that occur at low density, species with complex requirements for complementing resources and species that forage at landscape scales (e.g. Hymenoptera). Smaller habitat fragments suffer increased edge effects and distance to habitat edge can have a greater impact on invertebrate communities than habitat area (Ewers, Thorpe & Didham 2007). Fragmentation can also have significant impacts on ecosystem functioning. For example, litter decomposition rates have been found to be lower in a woodland edge compared to the interior, due to lower moisture conditions resulting from higher evapotranspiration (Riutta *et al.* 2012).

Remaining habitat fragments are poorly connected, for example the connectivity of most grassland types in Dorset dropped to almost zero beyond a few hundred metres (Hooftman & Bullock 2012). Many invertebrate species are thought to be poor dispersers (e.g. freshwater gastropods) for which inter-patch distances may be considerably greater than the maximum dispersal distance in a generation (Niggebrugge *et al.* 2007). Furthermore, most semi-natural habitat fragments are located in impermeable landscapes, predominantly intensive agriculture. Future change in land use and management will affect the permeability of landscapes, but future land use is subject to large uncertainties. The majority of invertebrate species are habitat specialists and may be unable to disperse through large tracts of unsuitable habitat. The connectivity of suitable habitat may be further reduced for species with very specialised requirements, e.g. for only a small subset of vegetation types. There is poor understanding of the dispersal abilities of individual species or the effects of landscape configuration on invertebrate dispersal, resulting in considerable uncertainty. Recently established populations of two rapidly expanding Orthoptera have been shown to have higher frequencies of longer-winged, more dispersive forms (Thomas *et al.* 2001; Simmons & Thomas 2004), although these changes are transient, with the incidence of long-winged forms becoming similar to that in the core of the range within 5-10 yrs. Ecological and evolutionary processes may be responsible and new dispersive phenotypes may further increase the speed of colonisation (Thomas *et al.* 2001). However, the evolution of increased dispersal can only begin once expansion has started and some habitat patches may be too isolated for some species to achieve this. Flightless species, species with high degrees of host-plant specialisation and those with rare host plants may be particularly slow to disperse (Woodcock *et al.* 2012). There is also concern whether rare and isolated wetland habitats, such as relict fen, ombrotrophic mire or saline lagoons, can be sufficiently connected to allow movement of dispersal-limited species. Isolation may lead to a reduction in genetic diversity, as observed in some rare bumblebees (Darvill *et al.* 2006; Ellis *et al.* 2006) – although *Bombus terrestris* has been able to rapidly invade Tasmania despite a drastic genetic bottleneck (Schmid-Hempel *et al.* 2007). Poor dispersal ability however, is not a universal trait of invertebrates, for example the range shifts of tens of kilometres observed in a range of invertebrate groups (Hickling *et al.* 2006). Rare species that disperse greater distances show less evidence of reduced genetic diversity, e.g. Great Silver Beetle *Hydrophilus piceus* (Beebee 2007).

Nitrogen deposition

Elevated levels of nitrogen is considered one of the most important threats to terrestrial biodiversity, with critical loads currently exceeded in about 58% of the area of sensitive habitat (RoTAP 2012) and uplands particularly badly affected (Lawton *et al.* 2010). There is strong evidence that elevated nitrogen has reduced plant species richness (Wilby *et al.* 2006; Field *et al.* 2014), altered plant community composition (Braune *et al.* 2008) and vegetation structure (Ellwood *et al.* 2012), with increases in competitive and nitrophilous plant species (Carey *et al.* 2008). There are few studies investigating the effects of nutrient enrichment on terrestrial invertebrates at biogeographic scales, but they are may be substantial. Losses of food/host plants will affect obligate invertebrate species. Increased dominance and biomass of grasses encourages closed swards that, without management, become unsuitable for many specialist species (e.g. ground-hunting arthropods, or carabids dependent on abundant ruderal seeds). However, dense, tall swards resulting from elevated nitrogen provide cool, moist microclimates, which may counteract warming effects (Wallisdevries & van Swaay 2006).

There may be considerable interaction between the effects of nitrogen deposition, climate warming and potential changes in rainfall. Climate scenarios for the UK indicate that winters are likely to become wetter, particularly in the west of the UK, and summers drier, particularly in southern England. Increased winter rainfall, coupled with milder winter temperatures, may extend the growing season and lead to increases in competitive plant species and declines in smaller forb species, exacerbating the effects of nutrient enrichment (Wallisdevries & van Swaay 2006). Conversely, the predicted decrease in summer rainfall and potential increase in drought frequency may counteract effects of elevated nitrogen. The balance of these opposing effects is currently unknown. Experimental summer drought has been demonstrated to alter the soil invertebrate assemblage, but the effects are short-lived. However, species varied in their response to the droughts and long term effects of an increase in incidence of summer droughts will be species-specific (Staley *et al.* 2007a). Experimental work has also shown drought can reduce the survival of herbivorous insects (Scherber *et al.* 2013).

Water quality and flow

Whilst poor water quality and eutrophication is still a major threat to many aquatic systems, in recent decades there have been improvements in overall water quality, e.g. declining phosphate and biochemical oxygen demand. This has resulted in an increase in species richness (including nutrient sensitive taxa) in lake macroinvertebrate and zooplankton assemblages (Gunn *et al.* 2012), and a general increase in abundance of river macroinvertebrates, with a shift in communities towards those typical of well-oxygenated conditions (Durance & Ormerod 2009; Vaughan & Ormerod 2012).

There have been significant increases in the winter water temperature of rivers over the past 25 years (>1.5 °C) (Durance & Ormerod 2007; Durance & Ormerod 2009). Experimental work has found that warming had no effect on total emergent insect biomass but did result in altered community structure, with few Chironomidae (Jonsson *et al.* 2015). However, concurrent with changes in water temperatures have been changes in water quality or river management (Clews & Ormerod 2010) and these are currently outweighing the effects of climate change (Vaughan & Ormerod 2014). There may also be complex interactions between climate change and other factors, such as water quality. Increased water temperatures will alter the metabolic rate of organisms and the availability of dissolved oxygen and, if eutrophication continues, this will be confounded by increased prevalence of algal blooms (Wilby *et al.* 2006). Lower summer water levels and reduced river flows, resulting from low summer rainfall, further concentrate pollutants and elevate water temperatures – increasing oxygen demand. Projected increases in heavy rainfall events (Kendon *et al.* 2014) may increase surface flooding, leading to increased diffuse pollution and more frequent flushing of sewer outflows (Wilby *et al.* 2006).

The relative importance of potential decreases in summer rainfall, increases in winter rainfall and increases in heavy rain events on wetland habitats is not known. However, geographic variations in seasonal rainfall and other factors, such as water abstraction, are likely to be critical. Reductions in rainfall, coupled with increased abstraction, could lead to low flow conditions in rivers and streams, resulting in changes in the macroinvertebrate assemblage composition (e.g. Extence 1981; Stubbington *et al.* 2009), which are most marked when surface water disappears (Boulton 2003). Flood events also have significant effects on the freshwater invertebrate abundance and community composition (e.g. Stubbington *et al.* 2009). During flooding, fine sediments may be suspended, larger bed materials moved and invertebrates killed or displaced (Lake 2000). Infrequent, catastrophic flooding events may pose conservation threat to some species, for example 4-8% of an internationally important freshwater pearl mussel (*Margaritifera margaritifera*) population were killed by a single flood event in 1998 (Hastie *et al.* 2001). Whilst fluctuating water levels are important for many wetland invertebrates, severe flooding may result in drowning of wetland invertebrate communities, particularly those associated with wetland-terrestrial interfaces. The effects of drought and flooding may be greater in highly modified watercourses due to a reduction in the habitat complexity and the availability of suitable refugia (Dunbar *et al.* 2010). Re-colonisation following drought or flooding depends on the length and severity of the disturbance (and its effects), stream bed composition, water chemistry and connectivity to less affected habitat (Boulton 2003). Summer droughts could also lead to losses of standing water, premature and exaggerated drying out of wetlands and soils more generally, and loss of humidity from within woods and other damp habitats.

Sea level rise

Sea level around the UK coast is predicted to rise by 13–76 cm by 2095 (Jenkins *et al*. 2009). This rise will have significant impacts on coastal margin habitats, such as sand dune and vegetated shingle, and intertidal habitats, such as saltmarsh and mudflat; the effects of climate change on coastal and intertidal habitats is discussed in more detail in Mossman, Grant & Davy (2013), Mieszkowska (2010) and Rees *et al.* (2010). These habitats contain highly adapted, specialist fauna and losses of coastal habitats may have severe effects on these invertebrates; for example the endemic fly *Botanophila fonsecai* is only currently known from one site, Dornoch Sands. Saline and brackish lagoons are a particularly rare habitat in the UK, which support a suite of rare and specialist invertebrate species, such as the Lagoon sea slug (*Tenellia adspersa*) and the Lagoonal sea-snout cranefly *(Geranomyia bezzi*), but many are highly vulnerable to changes in salinity or coastal retreat. Habitat restoration or creation may mitigate the effects of rising sea levels by increasing habitat extent, e.g. through managed realignment. However, restored or created habitat is often not equivalent to natural areas, for example restored saltmarshes have reduced abundance of important host plant species (Mossman, Davy & Grant 2012) and impoverished benthic invertebrate abundance (Mazik *et al.* 2010).

Invertebrate adaptations to climate changes

In most multivoltine species, the start of diapause is triggered by the shortening of the days following the summer solstice, which will not vary in response to climate change, and therefore warmer summer days will have little effect on voltinism (Bale *et al.* 2002). However, warmer temperatures in late winter and early spring could result in advances in emergence or flight date of first generation adults, lengthening the season suitable for reproduction and increasing the number of generations per year (Bale *et al.* 2002). Furthermore, warmer temperatures may result in faster completion of insect life-cycles at northern latitudes (Braune *et al.* 2008); this may also increase the number of generations completed (Dalin 2011). Over the recent warming period, there has been an increase in the frequency of second and subsequent generations of a range of European butterfly and moth species (Altermatt 2010). However, the failure of late season generations may have significant negative effects on a population but there is relatively little evidence regarding the viability of the new additional generations compared to earlier generations. There may be asynchrony in the phenology of the insect species and its host plant (Altermatt 2010), food resources may restrict the possibility of increased voltinism (Bale *et al.* 2002) or there may be insufficient resources to complete generations instigated late in the season. Very early and late emerging individuals will be vulnerable to occasional frosts. A large proportion of the climate-threatened northern species are univoltine, and increased temperatures may reduce viability by requiring a longer dormant period at times when conditions are suitable for development. Changes in voltinism and overwintering patterns may have knock on effects at higher trophic levels if predators and parasitoids are slower to change their phenology (Wermelinger *et al.* 2012).

Whilst warmer temperatures may provide benefits for some species in periods of increased activity and the completion of additional generations, other insects may be negatively affected by increases in temperature due to higher costs of thermoregulation. For example, in Germany adult stag beetle activity has been shown to be inversely related to average air temperature, and body condition was poorer in warmer summers (Rink & Sinsch 2011). Wetter, warmer winters may lead to increases in larvae and pupae succumbing to fungal attack (Cannon 1998).

Some invertebrate species may adapt their habitat associations as the climate changes. For example, as a result of increases in temperature, the requirements of some thermophilous species for sparse or short vegetation may be reduced, and denser vegetation may provide shaded, cooler microclimates. There may also be morphological adaptations to changing conditions, for example warmer temperatures may alter the frequency of melanic morphs (Cowie & Jones 1998; Brakefield & de Jong 2011).

Trophic interactions

Trophic interactions between plants, herbivorous invertebrates, pollinators, predators and parasitoids can be affected by climate change. There is evidence for shifts in the start and end of diapause, with which many other processes, such as pollination, are synchronous (Bale & Hayward 2010). Differences in the rate of change of species' phenology could lead to mismatched timing between trophic levels; range shifts and invading species could impact on food web composition; and invading species could alter host-parasite or predator-prey interactions.

Recent advances in the phenology of many species have not occurred at the same rate between trophic groups, with disparity increasing at higher trophic levels across marine, freshwater and terrestrial environments (Both *et al.* 2009; Thackeray *et al.* 2010). Mis-matches in phenological shifts have been shown between golden plover and tipulid prey (Pearce-Higgins, Yalden & Whittingham 2005); although the overall decline in tipulid numbers is thought to be responsible for golden plover breeding failure, rather than the mis-match in timing. The phenology of *Daphnia galeta* (waterflea) in Lake Windermere has advanced by between 3.7 and 6.7 days per decade (period of study: 1934-2009), with warming spring water temperatures and earlier phytoplankton bloom being the suggested drivers (Thackeray *et al.* 2012). The strong selection pressures resulting from asynchrony between an insect and its host plant can result in rapid adaptive responses from the insect. For example, there has been disruption in the synchronous timing of the winter moth *Operophtera brumata* egg hatching and the bud burst of oak *Quercus robur.* However, the egg hatching date has been genetically changed, resulting in closer synchrony with the oak bud burst (van Asch *et al.* 2013).

Native parasitoids have been shown to quickly colonise arriving species (Schönrogge *et al.* 2012), in some cases resulting in a major shift in host as novel species become the main host (Schönrogge & Crawley 2000). However, rapidly expanding species may experience reduced parasitism, despite colonising areas occupied by their parasitoid (Menéndez *et al.* 2008). Reduced parasitism could provide colonising species with competitive advantages, enhancing rates of range expansion and allowing species to exploit a wider range of environments (Menéndez & Gutiérrez 2004). The colonisation of new plant species may also lead to shifts in invertebrate host plants; this has been widely observed with the utilisation of cultivated plants in gardens.

The average first flowering date of over 350 British plant species has advanced during the past decade (Fitter & Fitter 2002). Phenological studies of plants and their pollinators (in Japan) have shown some mis-matches in timing following changes in climate (Ellwood *et al.* 2012). In the UK, with rising spring temperatures have advanced the flowering date of the Early-Spider Orchid *Ophrys sphegodes* but the flight date of its pollinator the solitary bee *Andrena nigroaenea* has advanced more, leading to asynchrony and likely resulting in reduced orchid pollination success (Robbirt *et al.* 2014). Asynchrony between plants and their pollinators may have significant negative effects on both species (contingent on the degree of specialisation or redundancy) and therefore may have consequences for agriculture. Insect pollinated crops have become increasingly important in UK agriculture; current honeybee hives may only be able to supply 34% of pollination service (Breeze *et al.* 2011). Wild pollinators are not as effective as honeybees, but can contribute to pollinator services (Rader *et al.* 2009; Rader *et al.* 2012). It is not clear how the proportion of insect-pollinated crops will change in the future, but changes pollinator abundance or emergence timing may have significant effects. A high proportion of bee species in the UK are southerly in their distribution and warmer temperatures may result in more suitable foraging conditions and future range expansions, and could lead to improved pollination services.

Summer drought has been observed to affect plant-mediated interactions between herbivorous insects. Root-chewing larvae (*Argiotes*) reduced the abundance of leaf-mining larvae feeding on a mutual host plant (Staley *et al.* 2007b). Drought has also been observed to alter interactions between earthworms and above-ground multi-trophic groups, and the effects were different between monoculture crop and more diverse plant communities (Johnson *et al.* 2011).

Species interactions and changes in community composition

Colonisations, changes in species ranges and phenology, and potential (albeit subtle) habitat shifts may alter local assemblage composition in unpredictable ways; the consequences of which cannot be predicted. Species will differ in the speed with which they colonise new areas following climate changes. However, the relative scarcity of ‘northern species’, which have southern range margins within the UK, suggests that assembly modification through climate change will see more additions than losses of species. However, colonising species may encounter similar species occupying the same niche and southerly species may have the competitive advantage over their northern counterparts in the absence of restricting cold temperatures (Moore *et al*. 2007). For example, *Coelopa pilipes*, a coastal strandline fly with a southern distribution, has expanded its UK range northwards and has become more abundant (Edward *et al.* 2007). Increasing temperatures have been demonstrated to provide *C. pilipes* with the competitive advantage over the similar, previously dominant, northern species *C. frigida*, which has reduced in abundance (Edward *et al.* 2007). Alterations at one tropic level may be reflected in others, and could lead to changes in community composition. For example, experimentally elevated temperature led to reductions the species richness of herbivores, detritivores and parasitoids, suggesting that temperature effects on one trophic levels can be observed in others; changes in CO_2 and water levels had no or limited effects (Villalpando, Williams & Norby 2009).

Northward shifts and expansions in range will result in new contact for formerly sympatric species that have undergone prolonged periods of separation. During this separation, species may have lost the ability to discriminate against other formerly sympatric species, leading to hetero-specific matings and hybridization. This has been demonstrated in two closely related damselfly species (Wellenreuther, Tynkkynen & Svensson 2010). There is little evidence for the long-term consequences of hetero-specific matings and hybridization, but could include production of sterile offspring and high offspring mortality, potentially leading to local extinctions, since populations tend to be smaller at the edges of ranges. In contrast, it could also lead to the introgression of beneficial genes, such adaptations to warmer conditions.

Our understanding of current ecosystem functioning and the role of individual invertebrate species is very poor; there is a need to better link understanding of species autoecology to ecological functions. The direction and magnitude of alterations in ecosystem functions due to climate-change induced changes in invertebrate communities cannot currently be predicted.

Pest species

Rising temperatures will make the climate in the UK suitable for an unknown number of invertebrate pests, potentially including some of the world’s most destructive pest species (Bellard *et al.* 2013). Whilst many species will be unable disperse to the UK, modern shipping and timber movement frequently transport exotic species to the UK. For example, western corn rootworm *Diabrotica virgifera virgifera*, a North America species of Chrysomelid that is a pest of maize crops, has spread widely in central Europe. The UK is currently at the northern edge of the climate suitable for the species, but by 2050 temperatures in SE England are likely to be suitable (Baker *et al.* 2003) and this species could become a serious pest if it reached the UK. Similarly, climate simulation models suggest that increases in temperature of 2.9 °C would provide suitable climatic conditions in the UK for three Asian longhorn beetles; whilst the species are not capable of long-range dispersal, human-aided transportation could introduce them into viable climate (Vanhanen, Veteli & Niemela 2008). In contrast, the status of some existing crop pests may decline as the climate becomes less suitable for them, for example Newman (2005) predicts aphids to become less of a pest in southern England by 2080. Climate change may disadvantage some existing pest species where changing conditions leads to asynchrony with the host plant, but longer growth periods may favour other species (Cannon 1998).

Vivax malaria (*Plasmodium vivax*) was endemic in the wetlands of England from the 16th century (Gowland & Western 2012). There are six Anophelines in current in Britain that are capable of transmitting vivax malaria (Lindsay *et al.* 2010). Climate suitability shows that in the future central and southern England could support vivax malaria, particularly close to salt marshes, but malaria returning to the UK is not thought to be a serious threat within the next 50 years (Lindsay *et al.* 2010). Unlike malaria, the majority of potentially emerging arthropod-borne diseases require the colonisation of the UK by the insect vector. Sandflies are not endemic in the UK, but climate warming may allow them to spread from southern Europe, potentially resulting in the emergence of sandfly fever/Toscana virus (Gould *et al.* 2006). The biting midge *Culicoides imicola* is the vector of bluetongue and African horse sickness viruses. *Culicoides imicola* is a southern European species and is currently spreading north, with climatic factors thought to be responsible (Guis *et al.* 2012).

Data quality and limitations of modelling approaches

The relationship between species distributions and environmental variables can be modelled using a variety of statistical and machine-learning techniques (e.g. Guisan & Zimmermann 2000; Pearson & Dawson 2003; Thuiller 2003; Chefaoui, Hortal & Lobo 2005; Araújo & Guisan 2006). These species distribution models (SDMs) project a species' distribution from geographic space into niche space. A species' distribution can then be projected back onto geographic space, perhaps under changed environmental conditions, to give the species' future distribution. Similar models can be produced by relating a time series of population data at a single site to changing environmental conditions (Goulson *et al.* 2005a). Despite their widespread application, there are a number of issues associated with modeling a species' relationship with its environment. While methods have been proposed to deal with situations where the assumptions of SDMs are violated, such as spatial autocorrelation (Dormann *et al.* 2007) and dispersal limitation (Sullivan *et al.* 2012), these have not been applied in many studies.

There are a number data quality issues that are particularly relevant when attempting to model the response of invertebrates to environmental change. Biological recording in the UK is biased with much higher recording effort in the south (Hassall & Thompson 2010), the lowlands and densely populated areas. This geographic bias in recording effort is likely to be extremely important in detecting northerly and altitudinal range shifts. Range shifts are usually analysed by comparing area of occupancy between two time periods separated by a third period. However, records are also biased towards later time periods (Hassall & Thompson 2010) and this can result in low numbers of records in the earlier data set and poor confidence (Hickling *et al.* 2006). The spatial variation in recorder effort may also have a negative impact on model performance, as the environmental variables that are correlated with recorder effort may be wrongly identified as influencing the distribution of a species (Kéry 2011). There may also be a bias in recorder effort to the listing of rarer, more 'notable' species. Occupancy models can take this selective recording into account (van Strien, van Swaay & Termaat 2013) but this method requires replicated visits, which may not be available for historic data or where data are being modelled at large numbers of sites across large spatial scales. Patchy recording effort and the genuine rarity of some species exacerbates the difficulties in detecting local extinctions of species; for example c.28% of species of conservation concern in the Broads have not been recorded since 1988, but a further 27% were not recorded prior to 1988 (Panter, Mossman & Dolman 2011).

Spatial scale is an important consideration when constructing species distribution models, with different factors operating on a species distribution at different spatial scales (Hortal *et* *al.* 2010). Different resolution models result in different predictions of the future distribution of species (Gillingham *et al.* 2012a). However, models are typically constrained to a fairly coarse spatial scale due to the challenges of interpolating climate data, for instance UK climate data is available at a 5 x 5 km resolution (Met Office 2009). This may be an appropriate scale for wide-ranging bird species because they are likely to utilize the whole of the grid square. Such spatial scales may be particularly coarse when considering the responses of invertebrates that operate at scales of <100 m. High resolution analyses are likely to provide more accurate predictions of future distributions (Gillingham *et al.* 2012a), particularly at local scales (Gillingham *et al.* 2012b), because microclimatic variation within a grid cell can be considerable and invertebrate species may only experience a small number of microclimates in that square (McInerny & Purves 2011). However, at coarse scales (100 km^2) habitat is a better predictor of species distributions than temperature (Gillingham *et al.* 2012b).

Models frequently include temperature and rainfall variables, but frequency and duration of sunny periods are very important for many invertebrate species (Graham-Taylor, Stubbs & Brooke 2009). Despite the recognition that climate is not the only constraint on species distributions; biotic factors are rarely included in models (Araújo & Luoto 2007). Land-use is an important constraint on insect distributions (Dormann *et al.* 2008), but understanding how land-use may change in the future is complex and rarely incorporated in SDMs (Stanton *et al.* 2012). Other important environmental variables, such as water budgets (Dawson, Berry & Kampa 2003), are also rarely included.

Concern has been expressed about the ability of SDMs to predict distributions in new environments (Elith & Leathwick 2009). For example, Rapacciuolo *et al.* (2012) tested the ability of SDMs constructed using the past distribution of species to predict their current distributions, and found that SDMs were poor at predicting changes in occupancy status of grid cells. This problem affects SDMs of UK invertebrates. Anderson *et al.* (2009) modelled the distribution of two spider species using data from central Britain, but found that these models performed no better than random when used to predict the distribution in northern England; however, hybridisation between the two species complicates this example.

As well as being able to predict which areas will be suitable in the future, it is important to have information on species' dispersal capacity in order to generate realistic predictions of their future distribution, and to assess whether they can keep up with a moving window of suitable environmental conditions (Engler *et al.* 2009). However, accurate data regarding the dispersal distances of most invertebrate species are scant. Models assume that a species is in equilibrium with its environment (Guisan & Thuiller 2005), so assume that unoccupied areas are unsuitable. Range-shifting species may violate this assumption, as they may be absent from some locations due to dispersal limitation alone. Methods such as dispersal weighting (Sullivan *et al.* 2012) can account for this, but require distribution data at multiple time periods to construct dispersal models. Since dispersal distances are generally thought to be <1 km for many species, small-scale connectivity and landscape permeability are likely to be extremely important to a species ability to disperse, but these are poorly characterized and rarely included in models, particularly at appropriate scales. The adaptive capacity of species is also ignored by correlative SDMs, and can allow them to persist in areas that are predicted to be unsuitable for them (Arribas *et al.* 2012).

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Appendix 1. *Species for which the UK has an international responsibility, defined as 1) global Red Data Book (RDB) species; 2) species listed in Annexes II and/or IV of the EU Habitats Directive; and Biodiversity Action Plan (BAP) species that were identified as endemic to the UK or that the UK holds significant portion of the global population, during BAP designation. Species include several that are now thought to be extinct in the UK.*
*† marine species; * species for which the Habitats Directive recognises that the UK has an particular international responsibility; ^ species thought to be extinct in England (Brown et al. 2010)*

Taxon group	Species	English name	Global RDB	Habitat Directive	Global status of BAP species in the UK
Cnidarian	*Nematostella vectensis*	Starlet Sea Anemone	gRDB		
Cnidarian	*Edwardsia ivelli*^	Ivell's Sea Anemone	gRDB		Endemic
Cnidarian	*Eunicella verrucosa*†	Pink Sea Fan	gRDB		
Mollusc	*Anisus vorticulus*	Ram's-horn Snail		Annex II & IV	
Mollusc	*Margaritifera auricularia* subsp. *auricularia*	Spengler's Freshwater Mussel	gRDB		
Mollusc	*Margaritifera margaritifera*	Freshwater Pearl Mussel	gRDB	Annex II *	
Mollusc	*Myxas glutinosa*	Glutinous Snail	gRDB		
Mollusc	*Pseudanodonta complanata*	Depressed River Mussel	gRDB		Significant population
Mollusc	*Quickella arenaria*	Sandbowl Snail	gRDB		
Mollusc	*Vertigo angustior*	Narrow-mouthed Whorl Snail	gRDB	Annex II	
Mollusc	*Vertigo genesii*	Round-mouthed Whorl Snail	gRDB	Annex II	
Mollusc	*Vertigo geyeri*	Whorl Snail	gRDB	Annex II	
Mollusc	*Vertigo moulinsiana*	Desmoulin's Whorl Snail	gRDB	Annex II *	
Annelid	*Hirudo medicinalis*	Medicinal Leech	gRDB		
Ribbon worm	*Prostoma jenningsi*	Jennings's Ribbon-worm			Endemic
Spider	*Nothophantes horridus*	Horrid Ground-weaver			Endemic
Spider	*Semljicola caliginosus*	Cloud-living Spider			Endemic
Crustacean	*Austropotamobius pallipes*	White-clawed Crayfish	gRDB	Annex II	
Crustacean	*Metatrichoniscoides celticus*	a woodlouse	gRDB		
Crustacean	*Niphargus glenniei*	British Cave Shrimp			Endemic
Centipede	*Nothogeophilus turki*	Turk's Earth-centipede			Endemic
Dragonfly	*Coenagrion mercuriale*	Southern Damselfly	gRDB	Annex II	
Dragonfly	*Oxygastra curtisii*^	Orange-spotted Emerald	gRDB		
Stonefly	*Brachyptera putata*	Northern February Red			Endemic
Beetle	*Psylliodes luridipennis*	Lundy Cabbage Flea Beetle			Endemic
Beetle	*Thinobius newberyi*	Newbery's Rove Beetle			Endemic
Beetle	*Meotica anglica*	Shingle Rove Beetle			Significant population
Beetle	*Ampedus cardinalis*	Cardinal Click Beetle	gRDB		
Beetle	*Carabus intricatus*	Blue Ground Beetle	gRDB		
Beetle	*Cerambyx cerdo*	Great Capricorn Beetle	gRDB		
Beetle	*Graphoderus bilineatus*	a predaceous diving beetle	gRDB		
Beetle	*Limoniscus violaceus*	Violet Click Beetle	gRDB	Annex II	
Beetle	*Lucanus cervus*	Stag Beetle		Annex II	
Beetle	*Pseudotriphyllus suturalis*	a hairy fungus beetle	gRDB		
Lepidoptera	*Euphydryas aurinia*	Marsh Fritillary		Annex II *	
Lepidoptera	*Lycaena dispar*^	Large Copper	gRDB		

Lepidoptera	*Maculinea arion*	Large Blue		Annex IV	
Lepidoptera	*Gortyna borelii lunata*	Fisher’s estuarine moth		Annex II & IV	
Lepidoptera	*Coleophora tricolor*	Basil-thyme Case-bearer			Endemic
Lepidoptera	*Eudarcia richardsoni*	Dorset Tineid Moth			Endemic
Lepidoptera	*Luperina nickerlii* subsp. *leechi*	Sandhill Rustic (Cornish subsp.)			Endemic subsp.
Lepidoptera	*Zygaena loti* subsp*. scotica*	Slender Scotch Burnet			Endemic subsp.
Lepidoptera	*Zygaena viciae* subsp*. argyllensis*	New Forest Burnet			Endemic subsp.
Lepidoptera	*Lycia zonaria* subsp*. Britannica*	Belted Beauty			Endemic subsp.
True fly	*Gnophomyia elsneri*	Royal Splinter Cranefly			Significant population
True fly	*Idiocera sexguttata*	Six-spotted Cranefly			Significant population
True fly	*Lipsothrix nervosa*	Southern Yellow Splinter			Significant population
True fly	*Botanophila fonsecai*	Fonseca's Seed Fly			Endemic
True fly	*Dorylomorpha clavifemora*	Clubbed Big-headed Fly			Significant population
True fly	*Empis limata*	English Assassin Fly			Endemic
True fly	*Phaonia jaroschewskii*	Hairy Canary			Significant population
True fly	*Rhamphomyia hirtula*	Mountain dance-fly			Significant population
Hymenopteran	*Anergates atratulus*	an ant	gRDB		
Hymenopteran	*Formica aquilonia*	Scottish Wood Ant	gRDB		
Hymenopteran	*Formica lugubris*	Northern Wood Ant	gRDB		
Hymenopteran	*Formica pratensis*	Black-backed Meadow Ant	gRDB		
Hymenopteran	*Formica rufa*	Red Wood Ant	gRDB		
Hymenopteran	*Myrmica hirsute*	an ant	gRDB		
Echinoderm	*Echinus esculentus*[†]	Common Sea Urchin	gRDB		