Biodiversity climate change impacts report card technical paper

14. Mechanisms driving UK biodiversity responses to climate change: assessment and indicators

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EXECUTIVE SUMMARY

1. A mechanistic understanding of climate change impacts is important for anticipating future range shifts, species' vulnerability assessments and facilitating the design of effective conservation action. This paper uses the UK flora and avifauna as case studies, and describes and assesses the biological mechanisms through which climate change can influence assemblage structure. The evidence base is often limited, and much more empirical testing is required, but the relative importance of different mechanisms can be assessed.

2. Climate change-induced reductions in reproductive success and mortality and changes in competitive interactions are likely to alter plant abundance, with some species increasing whilst others decline. Such changes may already be occurring, although the longevity of many plant species will provide a temporary buffer to population change. Shifts in community composition arising from competitive interactions may be amenable to conservation management that adapts traditional practices (e.g. grazing, mowing) which are routinely used to reduce the intensity of inter-specific competition.

3. Mechanisms that are likely to drive plant population trends include the effects of drought stress, frost damage, and insufficient winter chill (preventing normal bud development). These mechanisms can have direct effects and contribute to shifts in competitive balance as the climate changes, and could impact plants across most habitat types. Some UK grasslands currently appear relatively resilient to climate change impacts, but this resilience may not last, and heath/moorland habitats are susceptible to additional pressures due to climate change related increases in wildfire risk.

4. Climate change is most likely to drive population trends in the UK breeding bird assemblage through altered over-winter survival, changes in spring conditions affecting breeding success and summer drought reducing food supplies for some species, such as some upland birds. Increased intensity of spring rainfall will periodically reduce reproductive success, with long-term impacts dependent on the change in frequency of such events.

5. Milder winters have driven increases in the abundance of many common and widespread resident species during the 1990s and 2000s, with effects typically stronger in small bodied species, although they can reduce the breeding success of some owls and raptors that predate small rodents. Populations of many winter migrants are very likely to decline due to shifts in wintering locations, and for some species these declines are also likely to reflect changes in global population size due to reduced quality of Arctic breeding environments.

6. Some summer migrants will be sensitive to changes in the frequency of Sahel drought, which climate models typically, but not universally, predict will increase in severity. There is so far limited evidence that populations of summer migrants have been adversely influenced by observed trophic mismatches between timing of breeding and peak food availability, but vulnerability to such mismatches may increase in the future in some long-distance migrant woodland species that rely on highly seasonal synchronous food sources.

7. Climatic variables affect growth and reproductive parameters in a wide range of plant and bird species. As such, the mechanisms underpinning population changes are linked to the variables that are known to be changing as a consequence of climatic changes.

What is frequently lacking is direct evidence of the relative importance of these different mechanisms in driving the observed abundance and range shifts, but the evidence base will expand with current research activity. There is considerable potential to develop novel mechanistic indicators of climate change impacts that could track the importance of each mechanism, and would complement empirical testing of mechanistic drivers.

1. WHY MECHANISMS MATTER

There is good evidence that changes in climate are associated with distributional shifts and population trends in some UK fauna (see below and other report card papers). A complete assessment of climate change impacts requires understanding the mechanisms driving these changes. This is essential for two fundamental reasons. First it better allows us to anticipate future changes (Buckley *et al.* 2010; Midgley *et al.* 2010; Bykova *et al.* 2012). Second, a core principle of conservation biology is that understanding the mechanisms driving population decline greatly facilitates the design of conservation management plans (Caughley & Gunn 1995; Green 1995). It becomes even more important with an issue like climate change where past experience may be an unreliable guide to the future. Conservation responses to climate change sometimes focus on facilitating range shifts by enhancing dispersal, and this is certainly important to enable species' distributions to 'keep pace' with climate change (Hoegh-Guldberg *et al.* 2008; Heller & Zaveleta 2009; Hannah 2011). Conservation action may also be used to increase species' resilience to climate change and thus facilitating maintenance persistence within current distributions despite climate change (Pearce-Higgins *et al.* 2011; Morecroft *et al.* 2012); achieving this will be greatly facilitated if the mechanisms through which climate change drives population trends have been identified (Kleijn *et al.* 2010; Carroll *et al.* 2011). Increasing resilience of populations in situ may also facilitate range shifts by increasing the number of potential recruits that can colonise new areas. Good evidence of the key mechanisms driving biodiversity responses to climate change lags behind the evidence documenting changes in phenology and species distributions, or using bio-climatic envelope modelling to project future range shifts.

2. OBJECTIVES

The primary objective of this technical paper is to describe, and assess the evidence for, biological mechanisms through which climate change can drive trends in species abundance of the UK's terrestrial flora and avifauna. Occasionally, examples are provided for coastal or marine species but only when the driving mechanism could apply to terrestrial systems. The paper focuses on the climatic drivers of population trends. Rising UK temperatures are well documented in recent decades and consistently projected for the future (UK Climate Projections 2009). Increased winter rainfall is consistently projected, but there is much more uncertainty in summer rainfall projections. Despite increased summer rainfall in recent years a trend towards lower summer rainfall, on average, is consistently projected, especially in the south-east (UK Climate Projections 2009; Figs 1&2). Given the major consequences of changes in precipitation for biodiversity, mechanisms relating to shifts in both temperature and precipitation are included in this paper. As carbon dioxide (CO_2) concentrations are such an integral part of climate change their impacts are also considered. Interactions between climatic drivers and other environmental change drivers do not form part of this assessment, though they have the potential to both exacerbate and mollify climate impacts. We do, however, look at impacts on birds and plants mediated by climate change-induced changes to other biodiversity. The consequences of human responses to climate change (adaptation and mitigation), such as changes in the timing and nature of agricultural activities and increased water abstraction, are beyond the scope of this review, but they will have major impacts on biodiversity.

Dispersal limitation, partly generated by habitat fragmentation, appears to be preventing many species from occupying areas that have recently become climatically suitable (although they may be colonised given more time); UK examples include plants (Buckland *et al.* 2001; Moser *et al.* 2011), Odonata (Hassal & Thompson 2010), and Lepidoptera (Menéndez *et al.* 2006; Willis *et al.* 2009). Given the relatively rapid, putatively climate-linked, range-expansion of some bird species previously regarded as habitat specialists with limited dispersal ability, such as the Dartford warbler *Sylvia undata* (Bradbury *et al.* 2011) and nuthatch *Sitta europaea* (Forrester *et al.* 2007), such fragmentation may be less important for avian taxa. However, habitat fragmentation can affect the population response of woodland bird populations to severe winter weather, and their subsequent recovery (Newson *et al.* 2014). Deterioration in environmental conditions can also promote dispersal (Hui *et al.* 2012). Dispersal limitation will result in an accumulating deficit between species' potential and actual ranges that, in combination with potential extinctions at trailing range edges, is likely to contribute to population decline. Dispersal limitation does not explain why local extinctions arise at trailing range edges, or why current population sizes cannot be maintained elsewhere in the species' range. It thus only provides a proximate mechanism for population decline and is not considered further.

The paper discusses a very wide range of mechanisms through which climatic drivers determine population trends. Given the complexities of ecological systems it is not possible to cover every single mechanism, indeed it is likely that some have not yet been identified in the literature. The paper thus focuses on the most plausible and/or widely reported mechanisms. Many papers that document population trends associated with climatic change suggest a driving mechanism based on informed opinion without presenting direct evidence for the focal mechanism. Even in those papers in which hypotheses receive empirical tests, alternative mechanisms are rarely considered. Consequently, an important part of the evidence base underpinning this paper is a consideration of the validity of the assumptions under-lying the proposed driver. IPCC's standard confidence and likelihood scales are used when assessing the evidence base for each mechanism.

3. GENERAL PRINCIPLES
Recent reviews (Cahill *et al.* 2012; Ockendon *et al.* 2014a) of the impacts of climate change on species' extinction and population changes have provided considerable insight into the ecological mechanisms involved. Although these reviews highlight a relatively limited evidence base, geographical bias towards northern latitudes of North America and Europe, and taxonomic bias towards birds, both studies provide a strong message that changes in species interactions are likely to be more important than direct effects, whilst the Ockendon study suggests this is most apparent at higher trophic levels. Thus it is not physiological intolerance to warmer temperatures or to changes in water availability that appear most important, but instead the effects of climate change on other interacting species, such as prey, predators or pathogens. Particular examples of this include changes in the timing of species' interactions (Yang & Rudolf 2010) and changes in plant-pollinator interactions (Memmott *et al.* 2007), but it is clear that such impacts can be complex, with multiple drivers impacting simultaneously on particular species, potentially leading to substantial variability in species and community response to particular climatic drivers (Tylianakis *et al.* 2008). This is illustrated by the differences in the importance of biotic and abiotic mechanisms between trophic levels; both appear similarly important in driving population changes in primary consumers, but secondary or higher consumer populations appear much more sensitive to altered species interactions (Ockendon *et al.* 2014a). The same study also provides evidence that the importance of biotic mechanisms

is significantly greater in the context of studies which show significant trends in the climatic variables involved (i.e. in the context of climate change), although could not discount that this finding may result, at least partly, from publication bias. Both the Cahill and Ockendon studies make reference to a range of studies from the UK, and many more from similar systems across temperate northern latitudes, and so their broad conclusions regarding the greater importance of climate change impacts on biotic interactions for determining shifts in species' distributions and population sizes are likely to be highly relevant to this paper's focus on the UK. Typically, temperate endotherms (Khaliq *et al.* 2014) and ectotherms (Hoffmann *et al.* 2013) also have considerable thermal safety margins, the gap between ambient temperature and thermal tolerance limits, further suggesting that direct physiological impacts on most UK species will be limited.

4. PLANTS
Reproduction and recruitment

Plant-pollinator interactions and trophic mismatches
Warmer springs have resulted in advances in the phenology of many key life cycle events, including timing of flowering and insect emergence. A meta-analysis of UK phenological data demonstrate that flowering dates have advanced more rapidly than invertebrate phenology, with the gap increasing more recently (Thackeray *et al.* 2010). Climatic models of flowering time and bee emergence in the Rocky Mountains, USA, also indicate that plants are likely to exhibit more advanced phenology than their pollinators (Forrest & Thomson 2011). Whilst Ignasi et al. (2011) report similar rates of phenological advances in the timing of bee emergence and flowering of bee pollinated plants across North America there is potential for trophic mismatches between flower production and peak pollinator availability that reduce pollination rates and subsequent seed production. Computer simulations of phenological shifts in a plant-pollinator network from North America suggest that there will be a significant decline in the number of pollinator species that plants interact with, resulting in reduced reproductive success in many plants and associated extinctions (Memmott *et al.* 2007). This modelling approach does not, however, take into account plant population persistence due to vegetative reproduction, self-fertilisation, or the emergence of novel plant-pollinator interactions. It thus seems likely to over-estimate the risk of plant extinctions. Indeed, studies based on a space for time substitution approach indicate that there is often considerable flexibility in the species comprising plant-pollinator interactions which, at least in diverse communities, could buffer plants from mismatches (Benadi et al. 2014), and phenological disruptions to plant-pollinator interactions may be limited to specific pairs of interacting species (Forrest 2015). The few studies conducted to date on changes in reproductive success due to mismatches between flowering time and pollinator availability provide a contrasting evidence base with studies finding that seed set does and does not decline (Hegland *et al.* 2009; Thomson 2010; Forrest & Thompson 2011; Ives & Rafferty 2011, 2012; Forrest 2015). It is not yet possible to draw general conclusions as the number of studies is rather limited, and is probably biased towards those species that are more likely to experience mismatches. Selection experiments suggest that future avoidance of mismatches will require genetic adaptation (Anderson *et al.* 2012), which may increase the number of species exhibiting mismatches in the future. The only study of pollination mismatches in UK plant populations, albeit unpublished, indicates that warmer springs reduce seed set in early purple and common spotted orchids, but not pyramidal orchids (Waterman, Cameron & Evans in prep).

There is some suggestive evidence that mismatches could be generally important in the UK as native plant species whose phenology is tracking climate change tend to have

stable or increasing geographic range sizes, whilst those in which phenology is not tracking climate change have contracting ranges (Hulme *et al.* 2011). This pattern could, however, be driven through other mechanisms, such as increased competitive advantage arising from longer growing seasons in species with advancing phenology (see below). The pattern may also be unrelated to climate change as species with more rapidly advancing phenologies may be generalists that are more resilient to other forms of environmental change. It seems highly likely that climate change will alter the relative timing of flowering and availability of their current pollinators in some UK plant populations. It is unlikely, however, that this will typically result in reduced reproductive success and declining population size, although this may be the case in the future for some species.

Insufficient winter chill

There is virtual certainty that the majority of UK plant species are advancing flowering phenology, but there is marked inter-specific variation and not all species exhibit this pattern (Fitter & Fitter 2002; Thackeray *et al.* 2010). Flower production involves a complex series of biochemical pathways which are initiated once a threshold level of vernalisation, i.e. winter chilling, has been experienced. Winter warming can result in these chilling requirements not being met driving delayed phenology. An analysis of flower phenology of 384 species at Chinnor (Oxfordshire, UK) from 1954-2000 indicates that the phenology of approximately one fifth of species has been delayed by reduced winter chilling that limits, or in a few cases cancels out, opposing trends towards earlier flowering induced by spring warming (Cook *et al.* 2012). Insufficient winter chill could also reduce the ability of plants to shift flowering time to maintain synchrony with pollinators, potentially reducing reproductive success (see above). Winter warming can also reduce the number of flowers produced in some species and thus seed production (Saure 1985; Niu *et al.* 2002; Liu *et al.* 2012). Experimental winter warming reduced flowering and reproductive success of St John's Wort *Hypericum perforatum* in ex-arable grassland in Oxfordshire (Fox *et al.* 1999). More evidence is required, but it seems likely that future climate change will alter the composition of the UK flora due to insufficient vernalisation influencing growing seasons, flower development and reducing reproductive success.

Drought and heat stress

Drought and heat stress can reduce flower production, which seems likely to reduce reproductive success (Llorens & Penuelas 2005; Fang *et al.* 2010; Abeli *et al.* 2012). Such effects have been observed in musk orchid *Herminium monorchis* populations in eastern England (Wells *et al.* 1998), and Scandanavian populations of early purple orchid *Orchis mascula*, common twayblade *Neottia ovate*, and wood sanicle *Sanicula europaea* (Inghe & Tamm 1988), i.e. species which occur in similar climates in the UK. Impacts of drought and heat stress on flowering patterns probably arise from stress reducing leaf area and causing premature leaf death, reducing subsequent carbohydrate storage that limits initiation and growth of inflorescences the following year (Wells *et al.* 1998). Late flowering species will be more vulnerable as they will have increased exposure to the potential future reductions in summer rainfall, and will benefit the least from projected increases in winter rainfall (UK Climate Projections 2009). Plant populations are currently unlikely to experience sufficient drought stress to reduce flower abundance during multiple consecutive years. Resultant impacts on population size will be further limited, albeit for an unknown time period, by the longevity of many plant species or their maintenance of persistent seed banks (but see below for climate change impacts on seed banks). It seems very unlikely that drought and heat stress impacts on reproduction are currently major drivers of plant population trends in the UK. Whilst projections of summer precipitation are uncertain, it seems likely that reproductive success will change in any locations that do experience increased drought and heat stress in the future..

Gamete performance and temperature
Temperature can influence gamete development, but these effects are relatively small and are predicted to have negligible influence on reproductive output, primarily due to the large quantities of pollen produced (Hedhly *et al.* 2009; but see Bykova *et al.* 2012). The effects of temperature on gamete performance are likely to be more marked, with temperature influencing pollen viability, germination capacity, pollen tube growth rate and length, and thus fertilisation success; these relationships are, however, unimodal with pollen performance and fertilisation success being maximised at intermediate temperatures (Hedhly *et al.* 2009; Thakur *et al.* 2010; Zinn *et al.* 2010; Bykova *et al.* 2012). The magnitude of these effects can be large, for example in situ experimental warming of 5°C doubled acorn production in Japanesse populations of *Quercus crispula* populations (Nakamura *et al.* 2010), and future warming is predicted to increase seed production in a number of broad-leaved trees in the Netherlands (van der Meer *et al.* 2002). The extent to which improved gamete performance drives these changes has not been determined and the strongest evidence for this mechanism involves the small leaved lime *Tilia cordata*, whose northern range limit in England is determined by temperature during the August flowering period which controls pollen germination and pollen tube growth (Pigott & Huntley 1981; Pigott 1992). Seed viability across European *Juniperus communis* populations, including those in southern England, is also negatively influenced by temperatures during the pollination and embryo development periods (Gruwez *et al.* 2014). There is high agreement and a robust evidence base that temperature strongly affects all aspects of the reproduction niche of plants (Bykova *et al.* 2012), but there will be considerable spatial, i.e. intra-specific, and inter-specific variation in the nature of this impact. Its importance for determining plant range shifts and population trends is unknown and predictions are further hindered by daily climatic variation, as even a single hot or cold day can prevent successful fertilisation (Zinn *et al.* 2010).

Seed bank persistence
Many plants establish persistent soil seed banks, the survival of which can determine their population dynamics. Climate change can increase mortality of young and mature plants through a number of other mechanisms (see below), and populations that are sensitive to these impacts may increasingly rely on seed banks for continued survival. This is of concern as climate change can alter seed bank persistence by changing soil moisture and temperatures, cooler conditions increase persistence and drought can have both positive and negative impacts on persistence, although these effects are mediated by decomposer activity and exposure to pathogens (e.g. Walck *et al.* 2011; del Cacho *et al.* 2012; Mordecai 2012; Ooi 2012; Ooi *et al.* 2014). In open and sparsely vegetated habitats surface soils warm to a greater extent than the air, potentially increasing the vulnerability of the flora of these habitats, and explaining the stronger impacts of warming and drought on seed bank persistence documented in open areas relative to those under a shrub layer (del Cacho *et al.* 2012). The composition of the viable component of the seedbank can also be altered by soil warming reducing germination success in some species, but increasing it in others (Hoyle *et al.* 2013). Climate change impacts on the longevity of UK seed banks have received little assessment; survival of *Convolvulus arvensis*, *Lotus corniculatus*, *Medicago lupulina* and *Rubus fruticosus* seed over two years was not influenced by winter warming of 3°C and a 20% increase in summer rainfall (Leishman *et al.* 2000). The limited evidence base and low agreement currently prevents assessment of the impacts of climate change on seed bank persistence of the UK flora.

Mortality and plant competitive interactions

Climatic factors can affect plant mortality rates by determining exposure to stress, altering soil conditions and changing the nature of biotic interactions. Changes in these factors will almost invariably reduce the suitability of a location for one set of species, whilst simultaneously increasing suitability for other species. Consequently, whilst there is a perhaps a tendency for the mechanistic literature to focus on negative impacts of climate change the situation at local scales is often more nuanced with a dynamic balance of winners and losers. Indeed, increased mortality may directly promote invasion by species with more suitable climatic tolerances by providing gaps in vegetation cover which colonists can exploit. Equally, importantly the mechanisms through which climate change can alter mortality rates can also determine plant species' relative growth rates, especially when climate change is less extreme. These climate induced shifts in growth rates can determine the outcome of competitive interactions and thus assemblage structure. It is often impossible to track the life histories of individual plants, thus limiting the ability to determine of vegetation change arises from mortality or shifts in competitive dominance, but both are likely to be important. Regular long-term monitoring of vegetation communities in permanent plots is essential for establishing climatic impacts on the UK's vegetation, for example an increasingly warm and prevailingly wet climate is associated with the spread of graminoids and bryophytes in the dwarf-herb vegetation on Ben Lawers, in the Scottish Highlands (Geddes & Miller 2012).

Drought stress
Drought can reduce species growth rates and, in extreme cases, induce mortality through desiccation, over-heating, carbon starvation and hydraulic failure (Wang *et al.* 2012). The growth rates of a number of UK trees are widely considered to be susceptible to drought, with beech *Fagus sylvatica* and silver birch *Betula pendula* being particularly vulnerable (Peterken & Mountford 1996). There is much variation in the susceptibility of UK tree species to drought induced changes in growth rates, e.g. sycamore growth rates decline following drought to a much greater extent than either ash *Fraxinus excelsior* or pedunculate oak *Quercus robur* (Morecroft *et al.* 2008). This further suggests that drought could alter the nature of inter-specific competition leading to shifts in species composition, as demonstrated by competitive release of *Quercus petraea* following drought induced mortality and reduced growth rates of *Fagus sylvatica* in Gloucestershire (Cavin *et al.* 2013). Climatic modelling of future relative growth rates predicts that by 2080, under a high emissions scenario, drought will contribute significantly to reduced growth rates of many native broad-leafed trees in southern England, whilst in central Scotland growth rates will typically be increased (Broadmeadow *et al.* 2009). Modelling of species' distributions (rather than growth rates) also suggest that by the end of the century most native tree species in southern England will be challenged as they will occur at the edge of their climatic space, but are unlikely to become locally extinct in this region (Broadmeadow *et al.* 2009). These bioclimatic models are based on an earlier set of climate projections (UKCP02) which predicted larger reductions in summer rainfall than the most recent projections which encompass much more uncertainty in the magnitude and occurrence of future drought conditions (UK Climate Projections 2009; Figs 1 & 2), in which there is more uncertainty (Fig. 1 & Fig. 2). There is additional uncertainty as rising CO_2 concentrations can enable plants to save water by closing stomata without reducing photosynthetic rates, which in forest environments can increase soil moisture content (Medlyn *et al.* 2001; Holtum & Winter 2010), and reduce drought severity (Wang *et al.* 2012).

Plants in other systems are also likely to be adversely influenced by drought stress, e.g. experimental drought reduces heather growth in the UK (Wessell *et al.* 2004), and reduced precipitation appears to be contributing to the loss of dwarf-shrub, forb and lichen cover in the Scottish uplands (Ross *et al.* 2012). Other species can, however, benefit from dry

conditions. Tree mortality arising from drought stress can stimulate increased growth of shrubs that previously competed with trees for water, although this in turn reduces the diversity of the ground flora due to increased shading (Anderegg *et al.* 2012). In UK grasslands, ruderal species tend to increase following drought stress (Morecroft *et al.* 2009), probably due to their ability to rapidly colonise gaps in vegetation cover arising from mortality of drought sensitive species. In grasslands drought typically increases forb abundance at the expense of grasses (Johnson *et al.* 2012; Signarbieux & Feller 2012), although drought stress is likely to reduce the competitiveness of shallow rooted forbs, including important agricultural weeds such as *Alopecurus myosuroides* (Stratonovitch *et al.* 2012). Experimental studies suggest that there is a considerable degree of resilience to drought, at least in established and typically diverse, grasslands in continental Europe (Naudts *et al.* 2011; Brilli *et al.* 2012) and the UK (Grime *et al.* 2008; Fridley *et al.* 2011), but this may not continue on shallow soils (Fridley *et al.* 2011) and could be further limited if climate change increases the frequency of extreme events, e.g. drought killed all seedlings and adult *Primula farinosa* in a Swedish grassland (Torang *et al.* 2010). Moreover, a recent experimental treatment in a in a mesotrophic grassland ecosystem in southern England found that a 15% increase in winter rainfall and a 39% decrease in summer rainfall (cf. IPCC 4th Assessment projections for 2100 of +15 % winter rainfall and -30 % summer rainfall) found that by the third year there was a decline in vegetation biomass due primarily to reduced abundance of grass species that favoured moist soils (Lee *et al.* 2014). If drought increases it is likely that it will influence the structure and composition of UK plant assemblages, although habitats differ in their vulnerability and there is some uncertainty regarding the magnitude of future drought stress.

Frost damage
The earlier vegetation emergence in spring, driven by climate change (Thackeray *et al.* 2010) may increase the risk of exposure to frost damage if vegetation phenology is advancing more rapidly than that of last frost dates. Analysis of late spring frost impacts on forest trees in North America in 2007 (Gu *et al.* 2008; Augspurger 2009; Man *et al.* 2009) and 2010 (Hufkens *et al.* 2012), and Germany in 2011 (Kreyling *et al.* 2012a), demonstrate that a number of tree species can incur considerable damage from late frosts that reduce canopy cover and adversely impact growth rates. These studies propose that damage may be sufficient to alter relative growth rates and thus competitive interactions and population trends. Insufficient time has elapsed since these frosting events to test this hypothesis, although late frost damage to *Aesculus glabra*, a North American broadleaf tree, significantly increased mortality rates (Augspurger 2011). Of particular relevance to the UK is the finding that German populations of beech *Fagus sylvatica*, ash *Fraxinus excelsior* and oak *Quercus petraea* showed very high frequencies of frost damage following a late frost event in 2011 (Kreyling *et al.* 2012a). Local adaptation to frost damage can, however, be considerable in some species, including *Fagus sylvatica* (Kreyling *et al.* 2012b), which questions the relevance to the UK of studies conducted outside the region especially as the UK's Atlantic-type climate could generate a very different relationship between spring temperatures and last frost dates than that occurring in continental Europe. Frost damage is, however, enhanced at woodland edges and under sparse canopies (Kreyling *et al.* 2012a; Augspurger 2013), and the fragmented nature of much of the UK's woodland may thus increase damage risk.

Other vegetation types are also sensitive to frost damage, which can determine biomass accumulation in grass species (Malyshev & Henry 2012). More importantly inter-specific variation in tolerance to frost damage is considered to be sufficient to alter competitive interactions and population growth rates in European grasses (Kreyling *et al.* 2012c) and North American forbs (Lucas *et al.* 2008). Frost damage can also increase flower mortality

and reduce reproductive success (Inouye 2008; Forrest & Thomson 2010). Climate change reductions in snow cover, that insulates plants from cold temperatures, can also increase frost damage but this is probably not relevant to most of the UK's flora as prior to climate change frosts frequently occurred when snow cover was lacking, although snow cover can determine the nature of floral assemblages in montane regions of the UK (Trivedi *et al.* 2007).

Assessing trends in vegetation phenology in relation to last frost dates provides some indication of changes in the magnitude of frost damage. The number of years in which UK oaks experience frost damage is predicted to increase from 15% (during 1961-1990) to between 40% and 60% by 2080 under a low and high emissions scenario respectively (based on UKCIP02 predictions; Broadmeadow *et al.* 2009). Broad comparisons of the rate of phenological advance of the UK vegetation (0.57 days per annum; Thackeray *et al.* 2010) with advances in late frost dates (mean 0.55 days per annum at four Scottish sites; Barnett *et al.* 2006) suggest little current change in frost damage risk, but there is considerable spatial and inter-specific variation. A central European study found that risk of frost damage had decreased in recent decades in almost all the focal phenological events (Scheifinger *et al.* 2003), and projections of the risk of future frost damage in downy birch *Betula pubescens* suggest that risk will decrease across most of Finland by the end of the century, although it will increase in high altitude maritime regions (Bennie *et al.* 2010). Caution is needed, however, when assessing the risk of frost damage from the temporal overlap between frosts and vegetation phenology as increased CO_2 concentrations induce physiological changes that increased the sensitivity of plant tissue to frost damage (Martin *et al.* 2010; Rixen *et al.* 2012). Assessment of current, and projected future, changes in the risk of spring frost damage due to climate change provide a conflicting evidence base, partly due to considerable inter-specific variation in the direction and magnitude of impact (Rixen *et al.* 2012; Augspurger 2013; Pagter & Arora, 2013; Vitasse *et al.* 2014; Xavier & Isabelle 2014). It thus seems likely that in some locations species will vary in the magnitude of frost damage that they experience, which has the capacity to alter relative growth rates and competitive interactions. The extent to which such changes will be sufficient to drive population trends is, however, highly uncertain.

Shading effects
It has been suggested that earlier emergence of woodland canopies could result in increasing shading of ground flora, contributing to population declines. It is certainly true that a number of woodland ground flora species are declining, e.g. spreading bellflower *Campanula patula* and bastard balm *Melittis melissophyllum* have declined in a number of woodland sites and favour open woodland (Preston *et al.* 2002). It is difficult to assess if such trends are driven by climate change promoting earlier canopy closure or by reduced woodland management, but the latter seems likely to be more important. The rates of phenological responses of more widely distributed woodland ground flora species, bluebell *Hyacinthoides non-scripta* and wood sorrel *Oxalis acetosella*, appears similar to that of a number of canopy forming tree species (data from Cook *et al.* 2012) further suggesting that it is unlikely that climate change will adversely influence woodland ground flora through this mechanism.

Lack of winter chill
Vernalisation (i.e. winter chill) is required for vegetative bud development as well as flower development (see section on reproduction) although there is much variation between species in their requirements. There is increasing evidence from northern temperate woodlands, including parts of Europe with similar climates to the UK, that winter warming

will reduce rates of advance in spring green-up as winter chill requirements fail to be met (Morin *et al.* 2009; Vitassse *et al.* 2011; Kaduk & Loss 2012). These impacts have not yet been demonstrated in the UK, but the potential is demonstrated by crowberry *Empetrum nigrum*; experimental warming of just 0.5°C delayed its vegetative phenology in a Welsh heathland in a year that followed unusually high ambient temperatures (Prieto *et al.* 2009). In North America, there is a trends towards delayed spring green-up at low latitudes (approximately 35°N), and the latitude at which this trend occurs is moving northwards by 1° latitude per decade (Zhang *et al.* 2007). Inter-annual variation in the magnitude of winter chill also determines vegetation phenology in some European tree populations (Luedeling *et al.* 2013), and insufficient winter chill has delayed or reduced leaf emergence in beech *Fagus sylvatica* and *Quercus petraea* at low elevations in the Pyrenees (Dantec et al. 2014). Lack of sufficient vernalisation could thus reduce the duration of plant growing seasons, which may have implications for competitive interactions, e.g. exotic shrubs that are invading some North American woodlands have longer growing seasons than natives due to divergent phenological responses to climate change (Fridley *et al.* 2012; Polgar *et al.* 2014). Despite the limited evidence base there is high agreement that lack of vernalisation will influence the vegetative phenology of UK plant species and such impacts seem likely to arise, not least because equivalent impacts on flower phenology has been demonstrated in the UK (Cook *et al.* 2012). There is insufficient evidence, however, to assess the magnitude of these impacts on altered relative growth rates and thus interspecific competition within UK plant communities.

Changes in soil biochemistry
Climate change can induce numerous alterations in soil biology (de Vries & Bardgett, 2014) ,chemistry and physical properties, and the interactions between the three, that may influence plants. Those shifts that appear to have the largest potential are discussed here. Extreme summer droughts can increase soil acidity by oxidising reduced sulphur held in organic soils (Evans *et al.* 2008). The consequences of this for vegetation in the UK have not been assessed in detail. Even if such extreme droughts increase in frequency the consequences for acidity of UK soils seems likely to be limited as many retain significant capacity to buffer acidification, despite reductions that have occurred due to nitrogen deposition and other forms of pollution (McGrath & Loveland 1992; Neal 2002; Phoenix *et al.* 2012). In addition, drought can reduce the magnitude of soil acidification arising from ambient nitrogen deposition in *Calluna vulgaris* heathlands (Kopittke *et al.* 2012).

The availability of nitrogen and phosphorous are important determinants of the structure of plant assemblages. In the UK, the availability of these nutrients drives reduced species richness, as grass dominated assemblages replace more diverse assemblages of forbs, lichens and bryophytes (Stevens *et al.* 2004; Ceulemans *et al.* 2012; Phoenix *et al.* 2012). Experimental warming can increase mineralisation rates, thus increasing nitrogen availability and invasion by grasses (e.g. European dry lowland heaths; Wessel *et al.* 2004). It is uncertain though whether climate change will promote similar patterns at other sites and habitat as many other factors influence soil nitrogen pools. These include (i) the soil microbial community, which can uptake large quantities of nutrients released by warming (Weedon *et al.* 2012); (ii) drought, which reduces mineralisation rates and can be a stronger determinant of these rates than temperature, but is often followed by a significant release of nitrogen when soil moisture levels subsequently rise (Wessel *et al.* 2004; Beiera *et al.* 2008; Hueso *et al.* 2012); (iii) soil carbon, as plants also respond to the ratio of carbon to nitrogen, rather than just nitrogen *per se*, and soil carbon is likely to be reduced because warming promotes soil respiration, although the nature of this trend is mediated by water availability (Sowerby *et al.* 2008; Beiera *et al.* 2008). The Harvard soil warming experiment found that soil warming resulted in increased carbon storage in a

temperate mixed *Quercus* and *Acer* woodland due to mineralisation releasing addition nitrogen that fuelled additional plant growth (Grant 2014). This pattern appears to be general in boreal and temperate forests (Chung *et al.* 2013), but it is unclear if there is inter-specific variation in growth rates that could influence competitive interactions. Inter-specific variation in growth rates following soil warming has been demonstrated in dwarf shrub communities in the Swiss Alps (Anadon-Rosel *et al.* 2014), but such changes in growth rates can be driven by direct effects of temperature rather than increased nitrogen availability (Thakur *et al.* 2014). Therefore, whilst it is virtually certain that climate change will alter soil biochemistry, the consequences for the composition of plant assemblages are highly uncertain.

Increased wildfires
In the UK large wildfires occur most frequently in moorland and lowland heath. Statistical modelling strongly indicates that climate change will increase the incidence of wildfires in the Peak District. Under the UKCP02 climate scenarios it is predicted that this region will have five wildfires each week in the summer by 2070, under a high emissions scenario, and approximately one per fortnight under the low emissions scenario (Albertson *et al.* 2010). Equivalent exercises have not been conducted for lowland heathland, but it seems likely that climate change will also increase the frequency of wildfires in this habitat. Indeed, in Dorset, the two largest recorded heathland fires in recent decades both occurred in warm and dry years (1976 and 2011). Even managed moorland burning, which is regularly used successfully to enhance, floral composition and biodiversity , but can induce negative impacts on moorland vegetation, biodiversity and carbon stocks when the frequency or intensity of burning is too high (DEFRA 2001; Harris *et al.* 2011; Glaves *et al.* 2013). It thus seems likely that increased risk of wildfires induced by climate change will negatively influence moorland and heathland flora. Impacts on other habitat types are unlikely to occur in the UK; in the Mediterranean regions of Europe wildfires are largely confined to habitats dominated by dwarf shrubs (which also dominate UK moorlands and heathlands) and this is predicted to remain the case in the future even under high emission scenarios (Mouillot *et al.* 2002). Pine forests are also at risk from wildfires, and whilst they are between two and five times less susceptible than shrublands (Marques *et al.* 2011, Verdu et al 2012), it is plausible that climate change will increase the wildfire risk in UK pine forests, especially those occurring in relatively warm and dry regions.

Increased competition with invasive plants
Over 26,000 non-native plant species have become established in the UK and can survive in current climatic conditions (Lack 2010). Less than 1% of these have spread far from their original introduction site, and even fewer are considered to have become conservation problems because they compete (eg Hottentot Fig *Carpobrotus edulis*) or hybridise (eg Spanish bluebell *Hyacinthoides hispanicus*) with native fauna (Kohn *et al.* 2009; Lack 2010). A species' ability to tolerate cold temperatures is a good predictor of its ability to escape from cultivation (Dehnen-Schmutz *et al.* 2007), and thus climate change could increase the proportion of species able to do so (eg tree mallow *Lavatera arborea* on islands in the Firth of Forth; van der Wal *et al.* 2008). Cold tolerance does not, however, determine whether a species becomes invasive in the UK following escape from cultivation, and trade intensity is likely to play a much more important role in determining invasion success (Dehnen-Schmutz *et al.* 2007; Bradley *et al.* 2012). Trade intensity could interact with climate change due to horticultural demand for novel plant species that are better adapted to new climatic conditions but it currently seems unlikely that climate change will directly increase considerably the number of invasive exotic plants in the UK. There is potential for climate change to increase the abundance and distribution of established invasive plants, as predicted for Irish populations of *Gunnera tinctoria*, which is

one of the most invasive plants in Ireland and outcompetes native flora along streams (Fennell *et al.* 2013). Climate change can, however, also decrease the potential invasive range of exotic plant species (Xu *et al.* 2013). Concern regarding the impacts of any new exotic plants species in the UK, and those that are currently established should be further tempered by the limited evidence for large adverse effects of invasive plants on the UK flora (Hulme, 2015).

Disease
It is widely suggested that climate change will increase the risk of plant diseases due to northwards range expansion of pathogenic organisms and their vectors. Disease has had a major impact on some UK tree species (e.g. Dutch elm disease) and numerous bacterial and fungal pathogens have emerged in the last decade that could have major impacts on UK woodland (e.g. *Phytophthora*, acute oak decline, and ash dieback). Climate change appears to have had a limited role in the emergence of these diseases, as they are non-native and spread primarily through trade in timber or horticultural products and, in some cases, non-native vectors (Anderson *et al.* 2004). Climate change could, however, increase the suitability of the UK's climate for a number of non-native forest pathogens (Broadmeadow 2009; Tubby & Webber 2010), and outbreaks of tree diseases caused by native and alien pathogens have been predicted to become more frequent and intense due to climate change (Sturrock 2012). On the other hand climate induced range shifts could lead to the local extinction of some plant diseases (Rohr *et al.* 2011), and warm summer temperatures reduce the impact of *Phytophthora* induced alder decline (Aguayo *et al.* 2014). Even in compatively well studied agricultural systems, such as wheat diseases, there are major gaps in knowledge which limit predictive capacity although it seems likely that climate change will not consistently worsen the incidence or severity of wheat disease (Juroszek & von Tiedemann 2013). This uncertainty arises because different elements of climate change (altered temperature, moisture and CO_2 concentrations) have divergent impacts on disease risk (Gouache *et al.* 2011) and different types of pathogens vary markedly in their response to climate change (Broadmeadow 2009; Luck *et al.* 2011; Ghini *et al.* 2012). Moreover, interactions between different elements of climate change alter the nature of these impacts, e.g. moisture determines infection rates of the pathogen *Colletotrichum gloeosporioides* in the seed cropping plant *Stylosanthes scabra* at ambient CO_2 but not enriched CO_2 (Panga *et al.* 2011). The abundance of plant disease vectors, typically invertebrates such as aphids and some beetles, is also influenced by climate change (Pearce-Higgins, 2015). Soil biota, such as mycorrhiza, can reduce disease impacts and many elements of climate change seem to have a beneficial influence on the ability of multitrophic interactions in the soil to suppress pathogens (Chakraborty *et al.* 2012). Despite these caveats it is notable that the 1976 UK drought increased the frequency or severity of fungal infections on wild UK plant species in 75% of studies (n = 19; Morley & Lewis 2014). The complexity of climate impacts on plant-pathogen interactions makes it difficult to form general statements regarding how climate change influences plant disease risk, other than some are likely to increase in intensity and frequency, whilst others decline (West *et al.* 2012; Chakraborty 2013).

Altered herbivory - vertebrates
Grazing is essential for the maintenance and diversity of many botanically important UK grasslands;increases and decreases in grazing pressure can reduce the conservation value of these sites. This grazing is delivered by a combination of livestock (sheep, cattle, horses), rabbits *Oryctolagus cuniculus* and wild deer. Previous reductions in rabbit populations, as a consequence of myxomatosis, drove declines in botanical diversity in many grasslands due to increased competition between plant species (Sumption & Flowerdew 1985). Deer browsing has a large influence on UK woodland flora, with intense

browsing limiting woodland regeneration and significantly reducing the occurrence and diversity of herb and shrubs layers, although some grasses benefit from increased deer numbers (Fuller & Gill 2001; Corney *et al.* 2008). It is thus important to assess if climate change is likely to alter the botanical diversity of grasslands and woodlands by altering rabbit and deer population sizes.

Data on climatic effects on UK rabbit populations are not available, but the demography of continental populations are influenced by numerous climatic factors. Wet springs reduce reproductive success by flooding burrows, and chilling offspring (Palomares 2003; Rödel & Dekker 2012). Harsh winters increase mortality and limit the onset of reproduction (Rodel & von Holst 2008), and are associated with reduced population size (Bijlsma 2004); these impacts may be particularly strong when a harsh winter follows a wet spring (Rödel & Dekker 2012). Dry summers can promote earlier termination of the breeding season (Rödel & Dekker 2012), and are associated with negative population trends in Spain (Delibes-Mateos *et al.* 2009) and Greece (Kontsiotis *et al.* 2013). It is not currently possible, however, to assess how UK rabbit populations will respond to climate change (see report card paper by Newman & MacDonald), and other factors, such as the spread and intensity of rabbit haemorrhagic disease, may ultimately control rabbit population size.

Many deer populations are increasing in the UK, whilst much of this increase is likely to be due to reasons other than climate change (Ward 2005, Newson *et al.* 2012) warmer winters have possibly contributed through increased survival (see report card paper by Newman & MacDonald). In temperate regions juvenile deer mortality is reduced by higher winter temperatures, and increased by higher winter rainfall and spring and summer drought (Putman *et al.* 1996; Gaillard *et al.* 1997). Demographic shifts arising from one climatic change (warmer winters), may thus be cancelled out by changes in other climate variables (precipitation), and the uncertainty in future precipitation trends further hinders projection of demographic change. The best UK data on climatic impacts on deer demography concern the red deer *Cervus elaphus* population on Rhum, in which wet winters are associated with reduced survival and population growth (Clutton-Brock & Albon 1989; Hone & Clutton-Brock 2007), high March rainfall with increased population growth (Hone & Clutton-Brock 2007), and warm spring temperatures with higher calf condition at birth (Sims *et al.* 2007). There is not, however, evidence for climate change induced shifts in either male or female reproductive success (Moyes et al. 2011). These climatic effects largely concur with those reported for other temperate regions, but appear to have little overall influence on some red deer demographic traits or their population size due to the antagonistic effects of different climatic variables through both direct and indirect pathways (Moyes *et al.* 2011; Stopher et al. 2014). In two French roe deer populations earlier springs are associated with lower population growth rates due to reduced recruitment of offspring into the breeding population, potentially through trophic mismatches (Gaillard *et al.* 2013). This study was, however, conducted in different climatic regions to those that occur in the UK and its applicability to UK deer population is unclear. It is thus uncertain if climate change will facilitate further growth in deer populations, but if the overall impact of milder yet wetter winters is increased survival, then deer impacts on woodland flora seem likely to increase.

Altered herbivory - insects
Grazing by insect herbivores, due to their diversity and population size, can sometimes have similar effects on plant species richness in UK grasslands to those induced by vertebrate grazing (Allan & Crawley 2011), and the effects of climate change on insect herbivory must thus be considered when predicting climate change impacts on UK vegetation. Higher temperatures are frequently associated with increased insect

abundance (reviewed in Cannon 1998; Bale *et al.* 2002).In temperate regions, such as the UK, temperature has been claimed to be the most important climatic factor that influences insect herbivores (Bale *et al.* 2002). Climate change has thus been predicted to increase the intensity of herbivore pressure on plants (Cannon, 1998; Coley 1998; Wilf & Labandeira 1999; Bale *et al.* 2002).

Scale insect abundance increases with temperature across a wide range of habitat types (Youngsteadt et al. 2015), which in some cases is primarily driven by increased egg production (Dale & Frank 2014). Similarly warming has been associated with larger UK aphid populations, probably due to increased numbers of generations within a year (Harrington *et al.* 1995), and increased growth of heather beetle populations, which is associated with increased intensity of their attacks (Rosenburgh & Marrs 2010). Increases in herbivore populations mediated by climate change can also arise through altered precipitation regimes, and through complex chains of inter-specific interactions involving other insect herbivores and their predators (Barton & Ives 2014). Climate change can also result in insect herbivores expanding their range of host plants (Lu *et al.* 2015), although opposing patterns have also been found (Lemoine *et al.* 2013). These shifts in dietary preference may arise because the production of secondary metabolites that deter herbivores is sensitive to CO_2 concentrations, heat and drought (Gutbrodt *et al.* 2011; Robinson *et al.* 2012).

It must also be considered that some changes in abiotic conditions associated with climate change can reduce the abundance of insect herbivores, as increased CO_2 concentrations can alter the direction of the effect of temperature on insect population growth rates (Robinson *et al.* 2012). Similarly, although warming per se increases heather beetle abundance (Rosenburgh & Marrs 2010) when warming is combined with drought and higher CO_2 concetrations heather beetle survival and abundance is reduced (Scherber *et al.* 2013). Drought can also reduce the abundance of aphids (Johnson *et al.* 2011) and tipulid larvae, which consume roots and can cause major economic damage (Milne *et al.* 1965; Blackshaw & Coll 1999). Insect herbivory rates also depend on the relative timing of insect emergence and the start of vegetation growth, especially when plants rapidly increase investment in defence through the production of secondary metabolites after initial leaf emergence. In such systems herbivory will tend to decrease if plant phenology advances at a faster rate than insect emergence, this does not seem to be occurring in the well studied oak *Quercus* and winter moth *Operophtera brumata* system, but such shifts have been sufficient to cause local population extinctions of other insect herbivores (Buse *et al.* 1999; Singer and Parmesan 2010).

Climate change can thus clearly have a diversity of outcomes for insect herbivore population size, and even if herbivore populations increase this may be compensated by similar rates of increase in plant growth rates, for example observed growth in oak aphid *Tuberculatus annulatus* populations, due to wetter winters, is matched by increased oak *Quercus* growth rates (Estay 2008). Consequently data-sets are required that assess long-term changes in herbivory rates in response to climate change, or equivalent experimental manipulations. The best such evidence from the UK concerns increased herbivory of St. John's Wort *Hypericum perforatum* in response to simulated summer drought, which over-rides the reduced pressure from gall-forming and sucking insects in spring in response to winter warming (Fox *et al.* 1999). More generally, in European southern boreal and sub-Arctic forests the load of sap feeding insects (i.e. insect biomass per unit leaf area) will increase, potentially substantially, with even moderate increases in summer temperatures of just 1°C (Kozlov *et al.* 2015), herbivory rates increase in forest and grassland plants in North America, although patterns vary substantially between individual pairs of plant-

herbivore interactions (Lemoine *et al.* 2013, 2014), and observed warming from the 1960s to 2009 is associated with increased Lepidopteran damage in Hungarian forests (Klapwijk *et al.* 2013). In contrast, experimental warming of *Quercus alba* seedlings in North America did not increase their herbivory rates (Burt *et al.* 2013).

The diverse array of interacting pathways combines with the limited evidence base to hinder predictions of how climate change will alter the composition of UK plant communities by altering insect herbivory. It seems highly likely that the nature of some pairs of plant-insect herbivore interactions will be altered by climate change, but resultant impacts on overall rate of damage and its consequences are insufficiently understood.

Plant mechanisms - conclusions
Long-lived perennial plants dominate the UK flora (Preston *et al.* 2002). This longevity will generate a time lag between climate change-induced reductions in reproduction and recruitment and population declines, but when these occur they may be rather rapid. In the short-term, climate change-induced plant population trends are more likely to be driven by changes in mortality and competitive interactions; these will cause declines in some species, but inevitably favour other species (Table 1). Conservation of the UK flora has a long history of managing competitive interactions by manipulating disturbance and grazing regimes. These strategies may have some potential to limit some impacts of climate change arising from shifts in competitive interactions, although this is likely to require altering traditional management regimes. Empirical assessment of mechanistic drivers and species relative sensitivities to these mechanisms is required to improve the evidence base and reduce uncertainty, although the richness of the UK flora imposes a severe challenge in achieving this.

5. BIRDS
There is good evidence for widespread climate change impacts on bird populations and communities across Europe. Gregory *et al.* (2009) separate bird species into those projected to increase in range extent across Europe as a result of climate change from those likely to decline, and use the divergence in population trends between the two groups as an indicator of climate change impact. Devictor *et al.* (2008, 2012) tracks changes in the composition of ecological communities using the Community Temperature Index (CTI). This is the sum of species temperature indices (STI) present at any location, weighted by the abundance of that species. STI is calculated from the spatial distribution of a species as the average temperature across a species' geographical range. These studies tend to show an increase in CTI through time. Population trends of species associated with warmer temperatures are therefore typically more positive than those associated with cooler temperatures. Analyses of UK bird populations confirm that they are sensitive to variation in temperature and precipitation, and that changes in these parameters have had significant impacts on the long-term population trends of a range of bird species, and on the composition of bird communities in the UK (Pearce-Higgins *et al.* 2015). Here, we review the evidence for potential mechanisms linking these climatic changes to the observed responses in an attempt to outline those which are likely to have been most important, or may become so in the future.

Effects of habitat structure and composition
Vegetation structure is an important determinant of avian nest site availability, perception of predation risk, food abundance and the accessibility of that food (Götmark *et al.* 2005; Whittingham *et al.* 2006; Holmes 2011). Indeed, models of avian distribution, abundance and reproductive success are typically greatly improved when they incorporate the effects of vegetation structure (Bradbury *et al.* 2005; Tattoni 2012). The composition of the

vegetation can also impact birds by determining the abundance and quality of food sources provided by vegetation either directly, such as seeds, or indirectly, such as invertebrates (Koricheva *et al.* 2000; Holland *et al.* 2006). Climate change-induced changes to vegetation structure and composition may thus have major impacts on avian assemblages. We now assess the evidence for such effects in broadly defined UK habitats.

Woodlands
The combined impacts of drought and disease could result in major declines in abundance of some tree species, such as beech in south-east England due to drought and possibly ash and oak due to pathogens (see section 2). The seeds produced by these and other tree species form an important winter food source for many passerines and their abundance can determine subsequent reproductive success, over-winter survival and population demography (Tinbergen 1985; Reed *et al.* 2012), although it is currently unclear the extent to which such seed availability is important for woodland bird populations in the UK, or has been replaced by winter provision of seed in gardens. Climate change induced tree mortality may thus reduce seed abundance. This may be offset, however, by increased seed production in the remaining trees, e.g. climate change is predicted to increase beech and oak seed production in the Netherlands by one third by the end of the century (van der Meer *et al.* 2002). Masting tends to be promoted by a cool, wet summer followed by a drought (Koenig & Knops 2000, Piovesan & Adams 2001), and therefore may be promoted by increased climatic variability, or reduced by declines in the frequency of wet summers. Oaks support particularly numerous and diverse insect assemblages (Southwood *et al.* 1982) and any climate change induced reduction in oak abundance could reduce food availability for breeding birds. Similarly, the timing of the spring peak in caterpillar abundance appears to vary between different tree species and between trees of different ages (Both 2012, Burger *et al.* 2012). More diverse woodlands may exhibit less pronounced seasonal peaks in the abundance of caterpillars, a key component of chick diets. Thus if climate change reduces woodland tree diversity (see above) this may heighten the seasonality of caterpillar abundance and increase avian species sensitivity to trophic mismatches (see below).

If deer populations increase due to climate change, for example as milder winters reduce mortality, this could lead to more browsing in woodlands (although this is uncertain, see section 2) which could have implications for bird populations. Intensive deer browsing removes woodland shrub layers and changes the herb layer resulting in population declines of a number of woodland birds that use these layers for breeding or foraging; two species that seem particularly likely to be adversely influenced, nightingale *Luscinia megarhynchos* and willow tit *Poecile montanus* are of national conservation concern (Gill & Fuller 2007; Newson *et al.* 2012); commoner species that rely on the woodland understorey for nesting and foraging, such as blackcap *Sylvia atricapilla*, are also sensitive (Holt *et al.* 2013). The potential for climatic changes to alter deer browsing pressure, leading to changes in woodland structure which then impact on the breeding success and abundance of a range of migratory birds is illustrated by detailed studies from montane forests in Arizona, USA (Martin & Maron 2012). A similar situation has arisen in temperate parts of the USA, where climate change-driven increases in elk *Cervus canadensis* populations have altered woodland vegetation communities that shift nest site selection in three declining warbler species, itself resulting in increased nest predation rates and reduced reproductive success (Auer & Martin 2013). Additional impacts on woodland birds may arise through changes in tree species composition and diversity that influence food availability, but whilst the mechanisms appear plausible, the evidence base is insufficient to assess the probability of these impacts.

Semi-natural moorland and blanket bog
Vegetation structure is a key determinant of bird communities in upland semi-natural environments (e.g. Pearce-Higgins & Grant 2006), which may be influenced by the climate, through variation in plant growth rates, changes in herbivore populations and fire. The growth of many plant species is positively related to temperature and the length of the growing season. This is projected to increase, which may therefore favour species associated with taller, denser swards, such as some chats and other passerines. A heterogeneous vegetation structure, with areas of both tall and short vegetation supports a wider range of species than a more homogeneous structure (e.g. Pearce-Higgins *et al.* 2009a). In practice, however, it is likely that the main driver of vegetation sward in the UK uplands, which are largely below the tree-line, will be variation in grazing management and changes in wild herbivore populations, rather than direct climate effects, although the two drivers may interact to alter the vegetation structure and composition of semi-natural heathland communities, with potential implications for the bird communities present, either directly, or through changes in prey availability or predation rates (Benton *et al.* 2003).

In addition to grazing and browsing, climate change could significantly increase the risk of fire-associated disturbance, particularly if associated with increased frequency of summer drought (Albertson *et al.* 2010; see above), which could be detrimental for species associated with denser vegetation such as stonechats and raptors (Grant & Pearce-Higgins 2012). Habitat changes due to increased wildfires may, however, benefit other bird species associated with short and open swards, such as skylark and golden plover (Pearce-Higgins & Grant 2006). Climate change may therefore influence the future structure of moorland bird communities, although whether this will favour species associated with taller or shorter vegetation will probably depend upon the relative frequency of wildfire compared with the likely increased rates of vegetation growth, and interactions with the additional effects of fire and livestock management.

In addition to changes in temperature, variation in precipitation may also influence moorland and peatland vegetation plant communities and structure. Whilst rising temperatures and reduced water availability may promote dwarf shrub vegetation (such as heather) rather than sedges (such as cotton grass) wetter climatic conditions would certainly promote bog vegetation. Whilst the main consequences of this shift for birds will be in altering vegetation structure, for herbivorous species such as grouse, climatic variation in dwarf shrub quality could have a significant impact on their populations (Pearce-Higgins & Green 2014), whilst a shift from dwarf shrub to sedge cover may also influence invertebrate availability, with implications for avian breeding success (Pearce-Higgins & Yalden 2004).

Semi-natural heaths
As with moorland and blanket bog, vegetation structure is also a key driver of lowland heathland bird communities, and therefore sensitive to similar climatic processes and non-climatic drivers, particularly again associated with grazing and fire. On lowland heathlands changes in soil fertility are also likely to be important. Increasing temperature can increase the availability of nitrogen to plants on heathlands in some circumstances (Jensen *et al.* 2003; Andresen *et al.* 2010a & 2010b), exacerbated by anthropogenic nitrogen deposition and fertilisation by grazing livestock. Through time, this will increase the expansion of competitive grasses at the expense of dwarf-shrubs (Heil & Diemont, 1983), reducing the extent of suitable habitat for dwarf-shrub associated species such as Dartford warblers and stonechat (Bibby & Tubbs 1975; Pearce-Higgins & Grant 2006; Murison *et al.* 2007).

Associated increases in grass sward densities could reduce habitat quality for a range of open-vegetation specialists such as nightjar and woodlark (Mallord *et al.* 2007).

Depending on management responses, climate change could significantly increase the fire risk on lowland heaths, particularly if associated with increased frequency of summer drought (Albertson *et al.* 2010; see above). Wildfires in the Mediterranean are associated with marked changes in bird communities, and reductions in population size for species associated with taller vegetation, e.g. a 44% decline in Dartford warbler densities due to changes in habitat structure, and reduced survival and recruitment (Pons 1998; Pons *et al.* 2003). Increased wildfires may thus reduce the rate at which UK Dartford warbler populations increase due to range expansions into higher elevation moorland sites (Huntley *et al.* 2007; Bradbury *et al.* 2011), and impact other species associated with denser vegetation such as stonechats and raptors (Grant & Pearce-Higgins 2012). Habitat changes due to increased wildfires may, however, benefit other bird species associated with short and open swards. More generally, Mediterranean wildfires reduced passerine survival rates by approximately 70% across five passerine species (Pons *et al.* 2003). Climate change may therefore influence the future structure of heathland bird communities, although whether this will favour species associated with taller or shorter vegetation will probably depend upon the relative frequency of wildfire compared with the likely increased rates of vegetation growth, and interactions with the additional effects of fire and livestock management.

Pastoral and arable farmland
Human responses to climate change, such as alterations in the timing of agricultural activities and crop selection, will be a strong determinant of vegetation structure in these habitats, but climate change will also have a direct influence. Warming is likely to promote earlier and more prolonged vegetation growth in a wide diversity of habitats including grasslands (Sparks *et al.* 2005; Kleijn *et al.* 2010). The projected increase in UK winter rainfall (UK Climate Projections 2009) strongly suggests that earlier onset of spring growth will not be limited by soil moisture content, suggesting that climate change will promote earlier development of tall and dense swards in grasslands and arable crops. Extension of the growing season into early winter also seems likely to increase the density and height of swards present during the winter. Such swards restrict avian access to food and limit intake rates in a wide range of species (Devereaux *et al.* 2004; Whittingham *et al.* 2004; Butler *et al.* 2005; Wilson *et al.* 2005). The availability of short swards can predict the distribution and density of numerous species at a landscape scale (Perkins *et al.* 2000; Whittingham *et al.* 2006). Climate change thus has the potential to influence avian populations by altering food availability mediated by sward development and structure. Indeed, this mechanism contributes to the decline in breeding success of Black-tailed godwits *Limosa limosa* in the Netherlands because advances in breeding dates have been less rapid that advances in the onset of the growing season (Kleijn *et al.* 2010). Denser swards during the winter may also limit food intake rates during the season when the majority of starvation related mortality occurs. Ground-nesting species can be grouped into those that select relatively open sites to increase predator detection (e.g. skylark *Alauda arvensis* and lapwing *Vanellus vanellus*) and those that select concealed sites to aid nest crypsis (e.g. grey partridge *Perdix perdix* and corncrake *Crex crex*; Whittingham & Evans 2004). Climate change induced increases in vegetation growth are likely to reduce habitat suitability for the first group, but increase it for the latter. In the UK most grassland birds use agricultural grasslands, the intensification of which has promoted earlier development of dense swards potentially increasing the sensitivity of grassland birds to climate change impacts. In general, however, it seems likely that farmland bird population size will be

regulated by farming regimes and how these alter in response to climate change, rather than direct consequences of climate change (Eglington & Pearce-Higgins 2012).

Reed-beds
The timing and vigour of vegetation growth seems likely to influence birds in other habitat types, with ground-nesting birds that use open woodland and scrub habitats potentially also influenced by shifts in vegetation growing seasons that influence the availability of suitable nest sites. The best evidence for this mechanism, however, probably concerns *Phragmites* reed-beds. These grow earlier following warmer winters (Dykyjova *et al.* 1970), and appear to increase breeding season length in Polish reed warbler *Acrocephalus scirpaceus* and bearded tit *Panurus biarmicus* populations, enabling more breeding attempts per season and reducing predation rates, and increasing population size (Surmacki & Stepniewski 2007; Halupka *et al.* 2008). These effects have not been documented in the UK. The bearded tit is poorly covered by population monitoring schemes, but reed warblers have increased markedly and are expanding their range northwards (Baillie *et al.* 2014) and thus their distribution and population size is changing in the manner predicted by this mechanism.

High alpine environments
The British breeding distributions of ptarmigan *Lagopus muta*, dotterel *Charadrius morinellus* and snow bunting *Plectrophenax nivalis* are almost entirely restricted to the summits of the highest Scottish mountains; the first two species are projected to lose most of their suitable climatic space in the UK by the end of the century, and snow buntings are predicted to lose all suitable climatic space (Huntley *et al.* 2007). The precise breeding habitat requirements for these species are not fully understood, but all species (especially ptarmigan) seem to prefer areas with a mix of dwarf-shrub, forb and lichen cover (Cramp *et al.* 1977-1994). The apparent climate change-associated loss of this floral assemblage (Ross *et al.* 2012; see section 2) may thus contribute to these declines, although other mechanisms could also contribute (see below). Globally, there is limited evidence of altitudinal shifts in birds in response to recent warming (Chen *et al.* 2011, Pearce-Higgins & Green 2014), in part because when upwards shifts have been documented it is difficult to distinguish between climate induced shifts and those arising from degradation of lowland habitats (e.g. the Swiss avifauna; Maggini et al. 2011). It is notable, however, that sample surveys suggest that the UK dotterel population has declined by 50% between the late 1980s and 2011 (Galbraith *et al.* 1993; Whitfield 2002; Holling *et al.* 2013). Warmer and wetter summers are also associated with a long-term decline in ptarmigan populations in Fenno-Scandanavia (Lehikoinen *et al.* 2014), suggesting that similar changes may arise in the UK population. Whilst the evidence base is limited it seems more likely than not that climate change will contribute to population declines of British bird species whose breeding habitats are restricted to high alpine environments, although whether such trends will primarily be driven by habitat loss or other factors is unclear.

Phenological mismatches
There is considerable evidence that the rate of change in the timing of biological events in response to climate change differs between species, and indeed, between different trophic levels. This creates the potential for climate change to result in mismatches between periods of peak food demands and periods of peak food availability or optimum environmental conditions, which could have significant impacts on species' demographic parameters. For example, in the UK, terrestrial plants have shown more rapid phenological advances than their primary consumers, whilst the magnitude of advance is least in secondary consumers (Thackeray *et al.* 2010).

This phenomenon has been best studied in deciduous woodlands, where Lepidoptera larvae exhibit a strong seasonal peak in their abundance, and many woodland passerines select these larvae to feed their nestlings. Differences in the rate of advance in caterpillar availability and the timing of nesting of their avian predators could generate mismatches that are sufficient to reduce reproductive success, or adult survival rates (Pearce-Higgins & Green 2014). Moreover, it appears that not all caterpillars are equal, with some woodland birds selecting caterpillar larvae from particular moth families, further increasing sensitivity to mismatches (Garcia-Navas & Sanz 2011). The magnitude of these mismatches can account for variation in pied flycatcher *Ficedula hypoleuca* productivity and population trends at a number of sites across continental Europe (Sanz *et al.* 2003; Both *et al.* 2006). Blue tit *Cyanistes caeruleus* populations exposed to mismatches have lower reproductive success (Potti 2009), and reduced adult survival rates due to increased parental effort whilst provisioning nestlings (Thomas *et al.* 2001) but the extent to which such mismatches then influence population trends is unknown. Indeed, whilst mismatches determine reproductive success in some great tit *Parus major* populations, they do not generally drive population trends as these are mediated by density dependence and determined by other environmental factors, including winter food abundance (Visser *et al.* 1998; Grøtan *et al.* 2009; Reed *et al.* 2013).

It has been suggested that migrant birds may be most vulnerable to such mismatch effects, because of their more limited potential to respond to changing phenological conditions on the breeding grounds when they winter thousands of miles away (Both & Visser 2001). Matching this, European migrants that have failed to advance their arrival phenology are more likely to have declined in abundance (Møller *et al.* 2008), whilst populations of long-distance migrants in the Netherlands have tended to decline in highly seasonal deciduous woodland habitats but not in less-seasonal wetland habitats, whilst resident and short-distance migrant populations have remained stable (Both *et al.* 2010). These correlations do not, however, prove causation, as generalist bird species are more likely to advance their phenology than specialists (Moussus *et al.* 2011) and are also more resistant to other forms of environmental change (Shultz *et al.* 2005). It is also noteworthy that few detailed studies of long-distance migrant populations have found strong evidence for mismatch being an important limit to breeding success (Pearce-Higgins & Green 2014). The importance of phenological mismatch in driving long-term population trends of long-distance migrants remains unclear (Knudson *et al.* 2011), particularly as any apparent link between the rate of phenological change and population trend could result from joint responses to a decline in the quality of wintering habitats (Zwarts *et al.* 2009).

Much of the above evidence for trophic mismatches influencing woodland birds focuses on European populations outside the UK. British blue tit and great tit populations are increasing (Baillie *et al.* 2014) suggesting that if mismatches influence these populations the adverse impacts are over-ridden by other factors, supporting findings from continental Europe (Reed *et al.* 2013). In the UK long-distance migrants are declining more than short distance migrants and residents (Vickery et al. 2014). Of potentially vulnerable long-distance migrants that breed in deciduous woodland, pied flycatcher populations have declined by 53% and wood warblers by 66% from 1995 and 2012 (Baillie *et al.* 2014). Annual changes in long-distant migrant population trends in England are negatively correlated with May temperature in contrast to positive effects of April and June temperatures, and positive effects of May temperature on resident and short-distance migrants that breed earlier (Pearce-Higgins *et al.* 2015). Similarly, the probability of local extinction of garden warbler *Sylvia borin* populations across Britain is higher at sites with greater increases in May temperature (Mustin *et al.* 2014), whilst the breeding productivity of European warbler populations in some woodland species, including garden warbler, is

negatively affected by anomalous warm temperatures, but this is not the case for all long-distance migrants (Eglington *et al.* 2015). These relationships could potentially result from the sensitivity of migrants to mismatch. Negative effects of May temperature could occur because migrants nest later than resident species and would therefore be less likely to adapt to May than April warming, although the timing and duration of the spring peak in caterpillar abundance is influenced by April temperatures as well as those in May, particularly in warm years (Smith *et al.* 2011; Gullett 2014). However, despite this somewhat circumstantial evidence potentially linking migrant population declines with mismatch, detailed studies at specific sites fail to find strong evidence for this, and suggest that other factors may be more important (Goodenough *et al.* 2011, Mallord *et al.* 2012). National-scale analyses of nest record data also suggest that warm springs do not generate marked reductions in breeding success in UK redstart *Phoenicurus phoenicurus,* wood warbler *Phylloscopus sibilatrix* and spotted flycatcher *Muscicapa striata* populations, all rapidly declining species, as would be expected were they sensitive to mismatch (Finch *et al.* 2014).

Phenological mismatch is most likely to be an important mechanism for climate change impacts in highly seasonal habitats with a synchronised food peak (Both *et al.* 2010) and where there are divergent phenological trends between predator and prey (Visser *et al.* 2012). Although deciduous woodland, particularly in continental Europe, is highly seasonal, other habitats are not, and exhibit less marked seasonal pulses in food availability (Dyrcz & Zdunek 1996; Both *et al.* 2010). As a result, the relative numbers of woodland species studied for which there is evidence of seasonality in resource availability influencing demographic processes, and evidence for differential fluctuations in the timing of predator food demand and food availability (5 of 16 species) is greater than for freshwater wetland (2 of 12 species) or open terrestrial habitats (none of 6 species; Pearce-Higgins & Green 2014). In the majority of these cases there is no evidence that the mismatches have resulted in declining reproductive success through time. Away from woodlands, in the UK, there is also little evidence for mismatches affecting populations of common sandpiper *Actitis hypoleucos* along upland streams (Pearce-Higgins *et al.* 2009) and ring ouzel populations breeding on moorland (Beale *et al.* 2006). Golden plovers *Pluvialis apricaria* also occupy highly seasonal peatland environments, with their chicks relying on the peak emergence of adult tipulids, but while a phenological mismatch has been observed there is little evidence that it has caused recent population declines in this species (Pearce-Higgins *et al.* 2010).

To conclude, the evidence base for assessing trophic mismatch impacts on UK bird populations remains limited by a lack of detailed population-level studies. Despite some correlative large-scale evidence which could be interpreted as consistent with mismatch effects, there is a lack of supporting evidence from detailed studies from individual populations. It is therefore possible that the lack of advancement of the phenology of long-distance migrants, and their declining population trends, are symptoms of the same deterioration in environmental quality, rather than being cause and effect (Pearce-Higgins & Green 2014). Certainly population trends of long-distance migrants to the UK are more closely associated with wintering location than phenological trends (Thaxter *et al.* 2010; Ockendon *et al.* 2012). Evidence for spatial variation in these trends, which tend to be more positive in northern Britain than the south, where they tend to be strongly negative, could suggest an effect of breeding habitat, but this may be due to spatial variation in rates of habitat degradation and loss rather than climatic influences (Ockendon *et al.* 2012, Morrison *et al.* 2013).

Rapid phenological shifts, unfavourable weather and reproductive success

Earlier breeding in years with warm springs is generally considered advantageous because it reduces potential impacts of trophic mismatches (Møller *et al.* 2008), but it can be disadvantageous. In northern Europe springs have warmed more rapidly than summer and this trend is projected to continue (Elguindi *et al.* 2013). Consequently, in species with long incubation periods, marked phenological shifts in egg-laying dates can result in chicks being raised during cooler and wetter conditions than would be the case if egg laying dates advanced less rapidly, leading to reduced reproductive success and population declines. This mechanism contributes to declines in Finnish black grouse *Tetrao tetrix* (Ludwig *et al.* 2003) and buzzard *Buteo buteo* populations (Lehikoinen *et al.* 2009); its influence on UK populations of these species is unknown, although UK grouse and raptor populations are adversely influenced by wet weather during the breeding season (Summers *et al.* 2004; Haworth *et al.* 2009; Fielding & Haworth 2009).

Direct weather effects
Breeding season conditions
In addition to effects related to mismatch, temperature can have a direct effect on the survival of chicks by influencing their energetic requirements and food availability. Such effects are widespread across species, but most apparent in insectivorous precocial species such as waders and grouse due to their exposure to ambient conditions, sensitivity to changes in prey abundance and the lack of parental compensation (Pearce-Higgins & Green 2014). Examples of this from the UK include common sandpipers (Pearce-Higgins *et al.* 2009b), capercaillie (Moss *et al.* 2001) and ptarmigan (Watson *et al.* 1998). That these effects are general across most species is illustrated by a generally positive relationship between spring (April to June) temperature across population growth rates of common and widespread resident species (Pearce-Higgins *et al.* 2015). This means that spring warming is likely to have contributed to increases in the breeding success of a range of resident species, especially those with short incubation periods, and may have contributed to the potentially positive effects of climate change on their long-term population trends.

Increased rainfall during the breeding season reduces reproductive success and chick condition in a number of British species of conservation concern (e.g. corncrake, Tyler & Green 2004; black grouse, Summers *et al.* 2004; capercaillie, Summers *et al.* 2004; lapwing, Bolton *et al.* 2010). Eight of twelve studies across seven UK upland bird species have shown that increasing summer precipitation has a negative effect on populations (Pearce-Higgins 2011). Such effects appear to be most apparent in gamebirds and raptors (Pearce-Higgins & Green 2014). For example, the strongest evidence that climate change induced changes in breeding season precipitation may have adversely affected populations, concerns golden eagles *Aquila chrysaetos* breeding in the west of Scotland. Reproductive success, in some monitored regions, has fallen by 25% between 1988 and 2006 during a period in which there was a significant increase in May rainfall; this reduction could be sufficient to drive a future population decline (Haworth *et al.* 2009; Fielding & Haworth 2009). These effects are likely to result from a combination of direct chilling, reduced foraging efficiency (as hunting time is reduced and prey are harder to locate) and potentially reduced prey activity. There is also evidence that cool and wet summers reduce adult survival rates in long-tailed tits *Aegithalos caudatus*, which is likely to be because provisioning a brood is more difficult in such conditions and parents trade-off their own survival against reproductive investment (Gullett *et al.* 2014).

High rainfall during the pre-breeding period can also reduce parental foraging opportunities, thus reducing body condition and subsequent reproductive success. This is probably the mechanism generating declines of 50% in the number of fledglings produced

by Scottish choughs in years with high late winter rainfall compared to the driest years (Reid *et al.* 2003; Fig 4). Projected increases in winter rainfall (UK Climate Projections 2009) seem likely to increase these negative impacts.

Winter survival

There is strong evidence that severe winter weather reduces the survival rates and population size of many resident British birds, especially small bodied passerines (Greenwood & Baillie 1991; Peach *et al.* 1995, Catchpole *et al.* 1999). Further, extended snow and ice cover can be detrimental to species feeding on the ground, such as raptors and waders, and some wetland species (Saether *et al.* 2004). Such effects appear to occur through a combination of direct effects of cold combined with reductions in food availability. Detrimental effects of cold weather are most apparent in March and April, when birds are most likely to be resource-stressed as they invest in the forthcoming breeding season and when food resources may be most depleted, rather than in January and February, when temperatures are coldest (Pearce-Higgins & Green 2014).

As a result of these effects, higher winter temperature has a positive influence on the population growth of many common and widespread resident species, suggesting that they are likely to have benefitted from recent climate warming (Pearce-Higgins *et al.* 2015). Specific analysis on woodland birds suggests, perhaps not surprisingly, that it is small-bodied species for which winter temperature is most important (Newson *et al.* 2014). Similar responses are apparent in short-distance migrants that winter elsewhere in Europe, but not in long-distance migrants that winter in Africa (Pearce-Higgins *et al.* 2015). The extent to which these trends will continue in the future is more uncertain. Indeed, a long-term study of long-tailed tits from the mid-1990s to 2011 found that winter temperatures had little impact on adult survival rates or recruitment rates of male chicks, the least dispersive sex (Gullett 2014; Gullett *et al.* 2014), potentially due to a relative lack of severe winters during this period. A general rule of population demography is that following a beneficial change in one environmental factor that increases population size there is a change in the environmental factor that regulates population size (Newton 1998). Consequently, whilst recent increases in winter temperature may increase avian population size, this trend may not continue if other factors such as winter food availability or breeding success then limit population growth. An example of this is the golden plover population breeding in the Peak District, which winters locally. During the 1970s to 1990s the population was limited by winter severity (Yalden & Pearce-Higgins 1997), but more recent analysis following a reduction in winter weather severity indicates that winter temperature no longer limits the population, and had been replaced by summer climatic conditions as the main driver of population change (Pearce-Higgins *et al.* 2010). Moreover, high winter rainfall can reduce survival of small passerines in both relatively warm (blue tit in the Mediterranean, Grosbois *et al.* 2006) and cool environments (long-tailed tit *Aegithalos caudatus* in the UK, Mead *et al.* 2010; Gullett *et al.* 2014). If winter rainfall increases in the UK (UK Climate Projections 2009) future climate change could reduce overwinter survival of some small bird populations.

Extreme events

Aside from these general effects of temperature and precipitation, it is possible that the impact of extreme climatic events, whether heat waves, extended cold-periods, drought or flood, may have greater impacts on populations than more gradual changes in mean conditions. For example, the summer heat wave event in France in 2003 that generated a maximum temperature anomaly of 6°C (relative to the 1971-2000 average temperature at this season) drove population declines in a large number of bird species, especially those with European distributions centred on relatively cool areas (Jiguet *et al.* 2006). Similar

impacts have been noted in North America (Albright *et al.* 2011). The mechanisms driving these declines are uncertain, but given the diversity of species influenced it seems likely that reduced survival due to heat stress may have contributed to population declines, although other factors, such as variation in prey abundance may have been important. Heat stress can also have unexpected consequences for avian population demography by altering biotic interactions. As an example, great skuas *Stercorarius skua* breeding on Shetland increased bathing time in response to heat stress and thus reduced nest attendance, which resulted in increased chick mortality due to intra-specific predation (Oswald *et al.* 2008). Future increases in extreme summer temperatures are more likely than not and could be as marked as 6-10°C across much of the UK (Fig 3).

The unusually wet breeding season of 2007 reduced productivity of blue tits by 35%, great tit productivity by 47% and that of a wide range of warbler species by approximately 25%; with many examples of nest loss due to intense rainfall over a short period of time flooding nests or chilling their contents (Grantham & Robinson 2008). This was repeated again in 2012, leading to significant reductions in the breeding success of a range of migrant and resident species, including a 42% reduction in warbler success compared to the previous five years (Kew & Leech 2013). The observed trend over the last 20 years has been an increase in summer precipitation. There is much uncertainty in projections of future changes in precipitation in the UK, but the mid-range estimates are that, despite reduced total summer precipitation (Fig 1; Burke & Brown 2010), the amount of rainfall on the wettest summer days will increase slightly across much of the UK (Fig. 2). If this projection is realised, the frequency of periodic large-scale reductions in breeding success is likely to increase, but consequences for longer term population trends are harder to predict.

There are significant challenges in generalising about the impacts of extreme events upon species' populations, because, due to their very nature, extreme events are rare. An attempt to examine variation in bird population responses to three winter cold and three drought extreme events showed that species' responses varied significantly between each (Oliver *et al.* 2013). As a result, it is difficult to characterise the species' most vulnerable to such extreme events, although there was some evidence that frugivores and granivores are less sensitive to extreme winter cold than other species.

Climate change and food abundance
Annual variation in food resources is a key driver of bird population trends (Arcese & Smith 1988, Marshall *et al.* 2002). Whilst this may vary with trophic mismatch (above), equally, or potentially more important, will be variation in prey abundance and population size driven by climate change (Durant *et al.* 2007). There is good evidence for the marine environment that this has been one of the main ways that recent warming has impacted seabirds (e.g. Frederiksen *et al.* 2006), but the impacts for terrestrial bird species are generally less certain. The clearest evidence concerns tawny owls in Kielder Forest, northern England. Dampening of the inter-annual cycle in vole population size reduces breeding success and is associated with warmer and wetter winters. Stochastic population models indicate that this dampening will eventually drive the local owl population towards extinction (Millon *et al.* 2014). There is also evidence from outside the UK that increased temperature is reducing food abundance sufficiently to drive some avian population declines. Gray jay *Perisoreus canadensis* populations at the southern edge of the species range are declining because the food caches the species rely on during the winter are decaying more rapidly during warmer autumns, leading to food shortages (Stickland *et al.* 2011). The south hills crossbill taxon *Loxia (curvirostra) sinesciuris* is declining due to higher summer temperatures that promote premature opening of conifer seed cones, leading to reduced seed availability (Santisteban *et al.* 2012). Whilst there is some evidence from

continental Europe that temperature is influencing the production of tree seeds (sometimes beneficially, see above), these changes have not yet been demonstrated in the UK or linked to avian population trends. Insect development rates and life cycles are expected to be highly responsive to temperature. Potentially negative impacts of climate change on moth populations and positive effects on aphids (see report card paper by Pearce-Higgins), may therefore have significant effects on populations of their avian predators. Linking these climatic impacts on important prey populations to bird demographies and populations should be an urgent priority, as this mechanism is regarded as being a key driver of impacts of climate change upon bird populations (Pearce-Higgins & Green 2014).

There is also strong evidence linking a trend towards drier and warmer summers to changes in food resources and bird populations, although the uncertainties regarding projected changes in summer precipitation (see above) must be acknowledged when interpreting this research. Drier conditions reduce the abundance of craneflies (tipulids) in upland environments, which are a key food source for many upland bird species (Pearce-Higgins *et al.* 2010), and other drought-sensitive invertebrates such as earthworms and chironomids (Pearce-Higgins 2010). Predicted annual fluctuations in cranefly abundance in response to summer temperature account for observed population fluctuations in a golden plover *Pluvialis apricaria* population in the Peak District (Pearce-Higgins *et al.* 2010), whilst upland birds that feed on invertebrates that are sensitive to drought conditions have declined more than species that use other food sources, suggestive of a climate change contribution to these declines (Pearce-Higgins 2010). More broadly, UK thrushes (blackbird, song thrush, and ring ouzel; Peach *et al.* 2004; Beale *et al.* 2006; Robinson *et al.* 2007), lowland waders (e.g. snipe *Gallinago gallinago*, Green 1988; lapwing *Vanellus vanellus*, Bolton *et al.* 2010) and yellow wagtail *Motacilla flava* (Gilroy *et al.* 2008) are also vulnerable to reduced breeding success in response to summer drought. A number of these species are of national conservation concern (Eaton *et al.* 2011). These effects partly arise from reduced breeding success per attempt, probably due to reduced abundance and accessibility of invertebrate prey. Summer drought also promotes earlier termination of the breeding season, reducing the number of broods raised, and limiting re-nesting opportunities following nest failure due to predation or other factors (Green 1988). It seems likely that increased summer drought will adversely influence a number of ground-feeding bird species, probably through such mechanisms. It is worth noting that climatic effects operating through such variation in prey abundance may be manifest through lagged relationships between populations and climate, and therefore will require careful analysis to detect (Pearce-Higgins *et al.* 2011). A consistent lagged effect of summer temperature and precipitation indicative of negative drought effects is apparent across population trends of migrants in England (Pearce-Higgins *et al.* 2015), although the precise mechanism associated with this is unclear.

Migrants and climate change outside the UK
Potential impacts of climate change on migratory behaviour and the consequences of this are discussed in the Morrison and Robinson report card paper on migration. The focus, here, is on the mechanisms through which climate change outside the UK can determine the population size of avian migrants wintering and breeding in the UK.

Winter migrants
A number of wildfowl and wader species that winter in the UK have declined significantly in their abundance in the UK. For example, between the 1997/98 and 2007/08 winters, Bewick's swan *Cygnus columbianus* declined by 44%, Greenland white fronted geese *Anser albifrons flavirostris* by 40%, pochard *Aythya farina* by 46% and dunlin *Calidris alpina* by 39% (Eaton *et al.* 2011). These declines are continuing (Eaton *et al.* 2013), and

in many cases may partly be due to birds now wintering in sites further north and east in response to winter warming, termed short-stopping. There is increasing evidence from across Europe that warming has delayed the autumn migration of a range of wildfowl and is associated with northwards shifts in their distributions (Gunnarsson *et al.* 2012; Lehikoinen & Jaatinen 2012; Elmberg *et al.* 2014). Other species are now wintering in the UK in larger numbers, perhaps because of the same process, as they shift their wintering grounds from more southern sites in the Mediterranean and west Africa (e.g. the wintering black-tailed godwit *Limosa limosa* population has increased by 53% between the 1997/98 and 2007/08 winters and by over 440% since 1982/83; Eaton *et al.* 2011; Eaton *et al.* 2013). For some species, such as Bewick's swan, the total numbers wintering in Europe have declined strongly suggesting that populations are really in decline. Moreover, two wildfowl species that winter around the UK coasts have recently been upgraded as globally threatened due to declining winter counts (long-tailed duck *Clangula hyemalis,* vulnerable, BirdLife International 2012b; velvet scoter *Melanitta fusca,* endangered; BirdLife International 2012c). All these species breed in the Arctic, which is the region that has experienced the largest temperature increases (IPCC 2007). Climate change is likely to be reducing the suitability of this region through a number of mechanisms, including increased spring precipitation (with recent increases reducing Greenland white fronted geese reproductive success; Boyd & Fox 2008), and increased nest predation due to climate change reducing the availability of the predators' preferred prey species leading to increased predation on birds' nests (known to reduce breeding success of some Arctic breeding auk and geese populations; Smith *et al.* 2010; Rockwell *et al.* 2011; Robinson *et al.* 2014). Finally, whilst the evidence that trophic mismatches have little impact on avian populations breeding in the UK, there is increasing evidence that goose populations breeding in the high Arctic and wintering in more temperate parts of Europe are adversely impacted by trophic mismatches due to faster rates of warming on the breeding grounds than spring staging areas (Clausen & Clausen 2013). Climate change thus seems likely to contribute to declining UK populations of wintering waterbirds, and increasing populations in a smaller number of such species; the declining species include some that are declining in total population size.

Summer migrants

In contrast to resident species, long-distance migrant populations are driven by changes in environmental conditions on their African wintering grounds. Specifically, a high percentage of species populations fluctuate in response to changes in rainfall in the Sahel, where species either spend the winter, or stop-over on migration (Ockendon *et al.* 2014b). For example, Sahel drought during the 1970s reduced the survival rates and abundance of UK sedge warbler *Acrocephalus schoenobaenus*, whitethroat *Sylvia communis* and redstart populations and other species may have been adversely affected (Peach *et al.* 1991; Baillie & Peach 1992). Reduced Sahel rainfall also limits red-backed shrike *Lanius collurio* fecundity through carry over effects (see below; Schaub *et al.* 2011), and UK redstart populations (Finch *et al.* 2014), but such effects were not detected in UK wood warbler or spotted flycatcher populations (Finch *et al.* 2014), and are typically weak across a wide-range of migratory passerines (Ockendon *et al.* 2013). Recent Sahel drought has been attributed to anthropogenic forcing, partly through the increased emission of greenhouse gases (Held *et al.* 2005). Subsequent increases in precipitation during the 2000s have led to a partial recovery in Sahel migrant populations in the UK (Pearce-Higgins & Green 2014). There is uncertainty regarding future precipitation trends in this region, and whilst drought has been projected to increase in the future (Held *et al.* 2005; Neupane & Look 2013), possibly to a much greater extent and duration than that experienced in the 1970s (Shanahan *et al.* 2009; James *et al.* 2014), other studies state that there is too much uncertainty regarding the direction of precipitation trends in this

region to make robust predictions (Solomon *et al.* 2009). Thus despite robust evidence, and a high level of agreement, that Sahel drought drives migratory bird population declines, there is uncertainty regarding future precipitation trends in the Sahel, although the long term outlook seems more likely to be increased drought than a continuation of the current amelioration.

Carry over effects
Not only may climatic changes on the wintering grounds affect populations directly through variation in overwinter survival, but they may also carry-over to affect breeding parameters. The complexities of carry-over effects have perhaps been best identified in black-tailed godwits *Limosa limosa* wintering in Iceland, where the individuals wintering in the best-quality areas return earliest to the breeding grounds conferring significant reproductive advantage, and resulting in fledglings which also exhibit an advanced phenology relative to their parents (Gunnarsson *et al.* 2006, Gill *et al.* 2014). However, they may also affect long-distance Afro-Palaearctic migrants. Whilst there is evidence that annual variation in Sahel rainfall does have a weak effect on the timing of breeding across 19 migrant passerine species, this effect is largely masked by the effects of breeding season temperature (Ockendon *et al.* 2013). This effect may result from a combination of warmer springs being associated with more food resources upon arrival to the breeding grounds speeding up egg-production, or covarying temperature effects between the UK and spring temperatures in Iberia which may speed migration. Further evidence for the latter comes from additional analyses on three of these species (redstart, spotted flycatcher and wood warbler) which identified strong effects of temperature in the Mediterranean during the spring passage period upon the subsequent timing of breeding (Finch *et al.* 2014). Although the evidence for carry-over effects upon clutch size and subsequent reproductive success is much weaker, increasing Sahel rainfall was found to increase sand martin and tree pipit clutch size (Ockendon *et al.* 2013), and increase redstart brood size (Finch *et al.* 2014).

Many UK migrants spend either very little or no time in the Sahel, and whilst these species are also likely to be influenced by climate change on their African wintering grounds it is currently impossible to assess the magnitude or direction of these trends given the lack of information regarding their winter distributions and ecology.

Disease and parasites
Pathogens can cause marked declines in avian populations, e.g. greenfinches *Carduelis chloris* recently declined by 35.5% between 2006 and 2007 in regions of the UK with severe outbreaks of *Trichomonas gallinae* but by just 11% in areas with limited outbreaks (Robinson *et al.* 2010). Climate change can alter the abundance, phenology and virulence of avian pathogens, parasites, and host susceptibility (Merino & Møller 2010). Empirical examples of such changes are rather scant, but this probably reflects limited research effort rather than the lack of effects. In northern England, red grouse *Lagopus lagopus scotica* population size is regulated by the gastro-intestinal nematode *Trichostrongylus tenuis* which reduces host reproductive success; wet Mays and warm Julys increased parasite transmission, raising parasite intensity and driving a population crash in the red grouse host (Cattadori *et al.* 2005). This provides a good example of how climate change could interact with pathogens and parasites to determine avian population size, but the uncertain nature of future trends in summer precipitation projections in northern England hinders development of projections of grouse population trends.

Some wildlife diseases, including avian ones, appear to be spreading and becoming more prevalent in the Arctic and subarctic due to climate change but the baseline data required

to verify these trends are typically lacking (Van Hemert *et al.* 2014). Warming has, however, increased the duration and magnitude of the seasonal peak in mosquito abundance in the Arctic and has been associated with increased avian reproductive failure and adult mortality (Gaston *et al.* 2002). Similar impacts could occur in the UK in areas with high numbers of mosquitoes, or other biting insects (such as midges in upland areas). Increased mosquito abundance is one factor that probably contributes to climate change induced increases in avian blood parasites (Garamszegi 2011), which can reduce blue tit survival rates, including those of British populations (Lachish *et al.* 2011). Pathogens and parasites do, however, exhibit divergent responses to climate change and increased risk from one parasite can be balanced by decreased risk from another (e.g barn swallow *Hirundo rustica* Møller 2010), and heterogeneity in the direction and magnitude of shifts in the distributions and abundance of parasites and their vectors creates a complex picture of climate change induced changes in avian disease frequency and prevalence (Møller *et al.* 2013; Perez-Rodriguez *et al.* 2014). Whilst there is no good evidence to date that climate change has affected populations of UK birds through adverse impacts of pathogens and parasites, there is potential for this to occur, but the magnitude of this risk cannot currently be reliably assessed for UK avian populations.

Changes in predation rates
There is increasing recognition that predation can limit bird populations, particularly of ground-nesting waders and gamebirds (Gibbons *et al.* 2007), although evidence for widespread impacts of predation on songbirds is less clear (Newson *et al.* 2010). Pienkowski (1994) suggested that predation was one of the main ecological factors that limits ringed plover *Charadrius hiaticula* populations towards the lower latitudinal limit of the species' range, i.e. the UK. Where that is the case, then climate change shifts in the abundance or behaviour of those predators may form the proximate mechanism behind range contraction at the trailing edge although evidence for such impacts is currently lacking. In central Europe, climate-driven changes in the phenology and abundance of edible dormice due to milder winters have led to an increase in predation rates on cavity nesting bird species (Adamik & Kral 2008), but there is no evidence that winter severity is linked with total nest predation rates in a UK long-tailed tit population (Gullett 2014). Expansions in the red fox range across the Arctic in response to increased plant productivity and vole densities driven by warmer temperatures demonstrates how such changes may occur (Hesteinsson & MacDonald 1992, Killengreen *et al.* 2007). Similarly, climate change induced reductions in the abundance of Arctic predators' preferred prey can result in dietary shifts that increase predation pressure on nesting birds (Smith *et al.* 2010; Rockwell *et al.* 2011). However, these effects may ultimately be short-lived as very large reductions in the population size of some avian Arctic predators, such as snowy owl *Nyctea scandiaca* and long-tailed skua *Stercorarius longicaudus*, are predicted to occur due to climate change induced crashes in their main prey species, e.g. collared lemming *Dicrostonyx groenlandicus* (Gilg *et al.* 2009).

The vulnerability of birds to predation may also be affected by the weather, and therefore climate change. As an example, wintering redshanks *Tringa totanus* are more likely to forage closer to woodland in cold conditions, where they are more vulnerable to sparrowhawk *Accipiter nisus* predation (Creswell & Whitfield 2008). When chicks are in poor condition, for example due to weather influences on food availability of provisioning rates, they can also be more vulnerable to predation due to changes in begging intensity (Evans *et al.* 1997; Evans 2004). Predation rates, particularly nest predation in ground nesting birds, are also influenced by vegetation height and condition (which is influenced by climate) but the effects are usually fairly weak (Rands 1988, Campbell *et al.* 2002; Wilson *et al.* 2005).

Avian population demography can also be influenced by sub-lethal effects of predation, as perception of predation risk alters prey behavior. Theory and empirical evidence indicate that these sub-lethal effects can influence prey population size to a greater extent than mortality due to predation (Cresswell 2011). Changes in predator population size induced by climate change could thus influence prey population size by altering perceived predation risk even if mortality rates are not altered. Despite the potential for climate change to influence avian populations in the UK by altering predation pressure and sensitivity, there is little evidence that this has been an important mechanism in driving changes to bird populations in the UK.

Changes in inter-specific competition

The role of competition between species in limiting bird populations is uncertain. Although predicted as important by much ecological theory, there is relatively little evidence for this in practice (e.g. Ricklefs 2012). It has been suggested that geographic range limits of closely-related species are maintained through competition (or via apparent competition when species share parasites or predators), and therefore latitudinal or altitudinal shifts in distribution in one species may drive contractions in the other, for example between the blackbird *Turdus merula* and ring ouzel *Turdus torquatus* (von dem Bussche *et al.* 2008). Such statements are, however, largely speculative and backed by little empirical evidence. The magnitude and outcomes of inter-specific competition between North American warblers on their wintering and breeding grounds is mediated by climatic conditions (Martin & Martin 2001; Dugger *et al.* 2004; Studds & Marra 2005). Equivalent evidence for European migrants is much lacking and there is little understanding of the role of competition on the wintering grounds (Salewski & Jones 2006). There is evidence from one study site in continental Europe that changes in the nesting phenology of European great tits and pied flycatchers alters the competitive balance between the two species as they vie for nesting holes but effects at the population level have not been established (Ahola *et al.* 2007). We are not aware of any UK studies showing how climate change alters the competitive interactions between bird species despite significant changes in avian assemblages. Investigating the role of inter-specific competition in structuring avian assemblages, and the influence of climate on these interactions is important, especially as climate induced changes in species' distributions and population size will alter the intensity of competition and the identity of potentially competing species.

Discussion of bird mechanisms

Climate change is likely to influence avian populations in the UK through a diverse suite of biological mechanisms (Table 2). These impacts will arise across all habitat types, although the precise driving mechanisms will vary across habitats and species. Perhaps the strongest evidence is for climatic impacts on overwinter survival rates of both resident and migrant species. Increasing winter temperatures have probably contributed to increases in the abundance of common and widespread resident species. Whilst these populations will then fluctuate in response to periodic severe winters (which could be described as extreme events) it is unclear if these populations are now generally limited by winter severity. A trend towards milder winters has also increased the rate of short-stopping of some winter migrants, reducing the abundance of some waterfowl and wader populations in the UK as they winter further east and north. Changes in the abundance of many long-distance Afro-Palaearctic migrants can also be strongly related to changes in precipitation on their wintering grounds, which are strongest for those species which utilise the semi-arid Sahel region. However, for these migrants, the extent to which it is changes in African climate, climate change on the breeding grounds reducing productivity, or other

non-climatic factors, which have caused the long-term declines in many of these species, remains uncertain.

If climate change induces increased summer drought the breeding success and survival of a number of ground-feeding species are likely to decline, in part due to reduced prey availability. Summer precipitation projections also include the potential for increased intensity of rainfall, which would result in periodic reductions in reproductive success of open-nesting and precocial species such as raptors and gamebirds in particular, and may also influence adult survival rates in passerines. General increases in breeding season temperatures are likely to boost productivity in a range of species. Some long-distance migrants breeding in highly seasonal environments, such as deciduous woodland, may experience increased phenological mismatch that adversely influences breeding success. The evidence for this, however, is surprisingly scant at the species-level. Whilst there has been much discussion about the occurrence of extreme events in the UK, there is little robust evidence to assess their potential impact on bird populations.

In the longer-term, the direct effects of climate change on habitat composition and structure are likely to alter avian assemblages, but these effects could be swamped by shifts in land management practices induced by human responses to climate change (although assessing these was outside the brief of this report card paper).

CONCLUSION
Numerous mechanisms have been identified through which climate change could drive population trends. The evidence base under-pinning assessment of many of these mechanistic drivers is currently rather limited, but is likely to grow rapidly due to continued analyses of long term datasets and more detailed shorter-term studies. As a consequence it seems likely that future assessments will make considerable progress in assessing the relative importance of each mechanism, and how divergent mechanisms interact to determine population size. Consideration of the relative importance of each mechanism must, however, take the full range of potential future climatic conditions into account. Despite the limitations in the current evidence base there is much variation between mechanisms in the probability that they will influence the UK's flora and avifauna. Identifying these will have important consequences for assessing species vulnerability to climate change, predicting future range and population changes and particularly to designing conservation action to increase resilience.

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Fig. 1 Change in total summer precipitation (June, July and August) by the 2050s under a low (a - c) and high (d – e) emissions scenario at 10% (a, d), 50% (b, e) and 90% (c, f) probability levels; maps drawn from UK Climate Projections (2009).
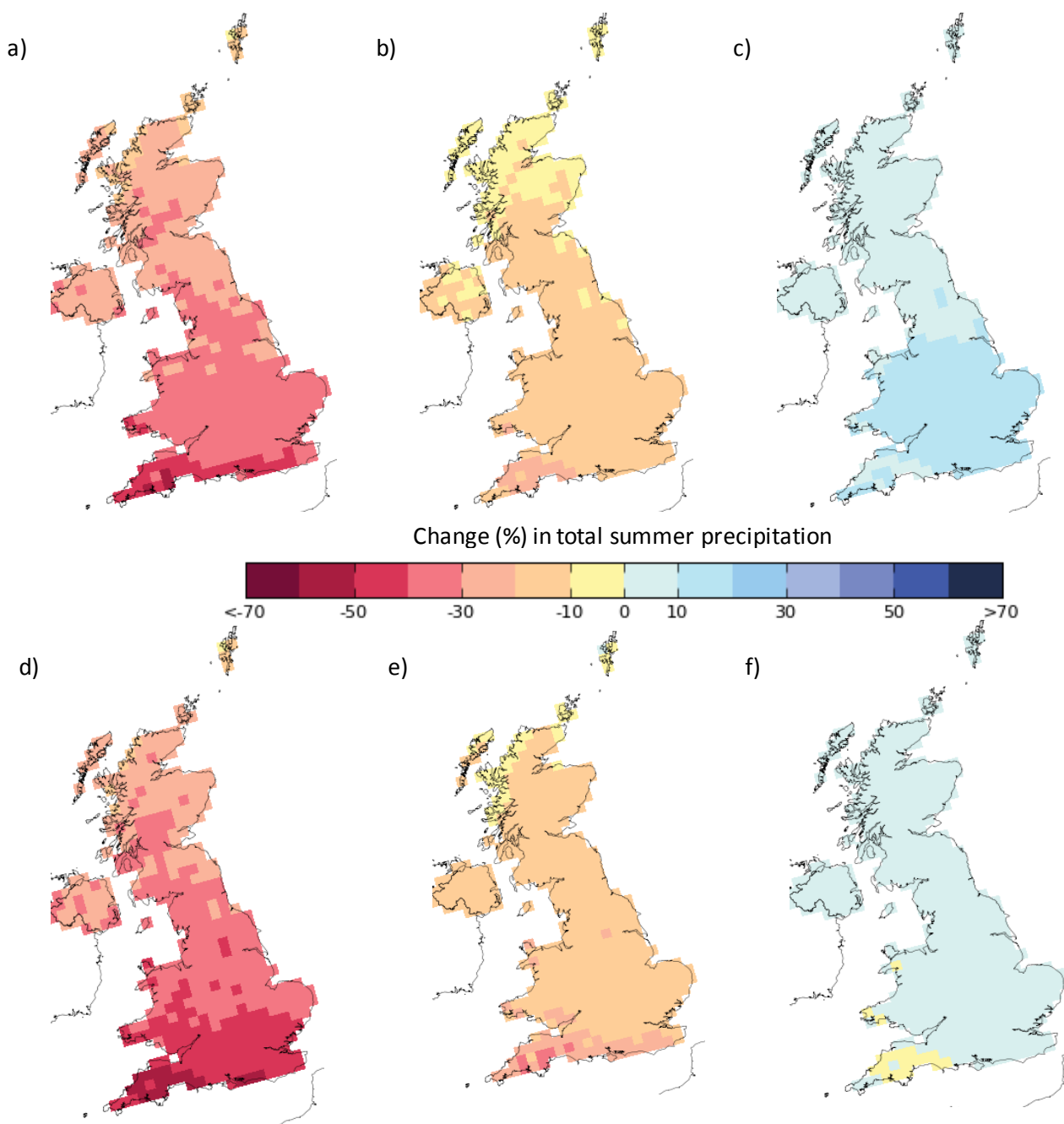
Fig. 2 Change in precipitation on the wettest summer day (June, July and August) by the 2050s under a low (a - c) and high (d – e) emissions scenario at 10% (a, d), 50% (b, e) and 90% (c, f) probability levels; maps drawn from UK Climate Projections (2009). Patterns are similar for the wettest spring day.
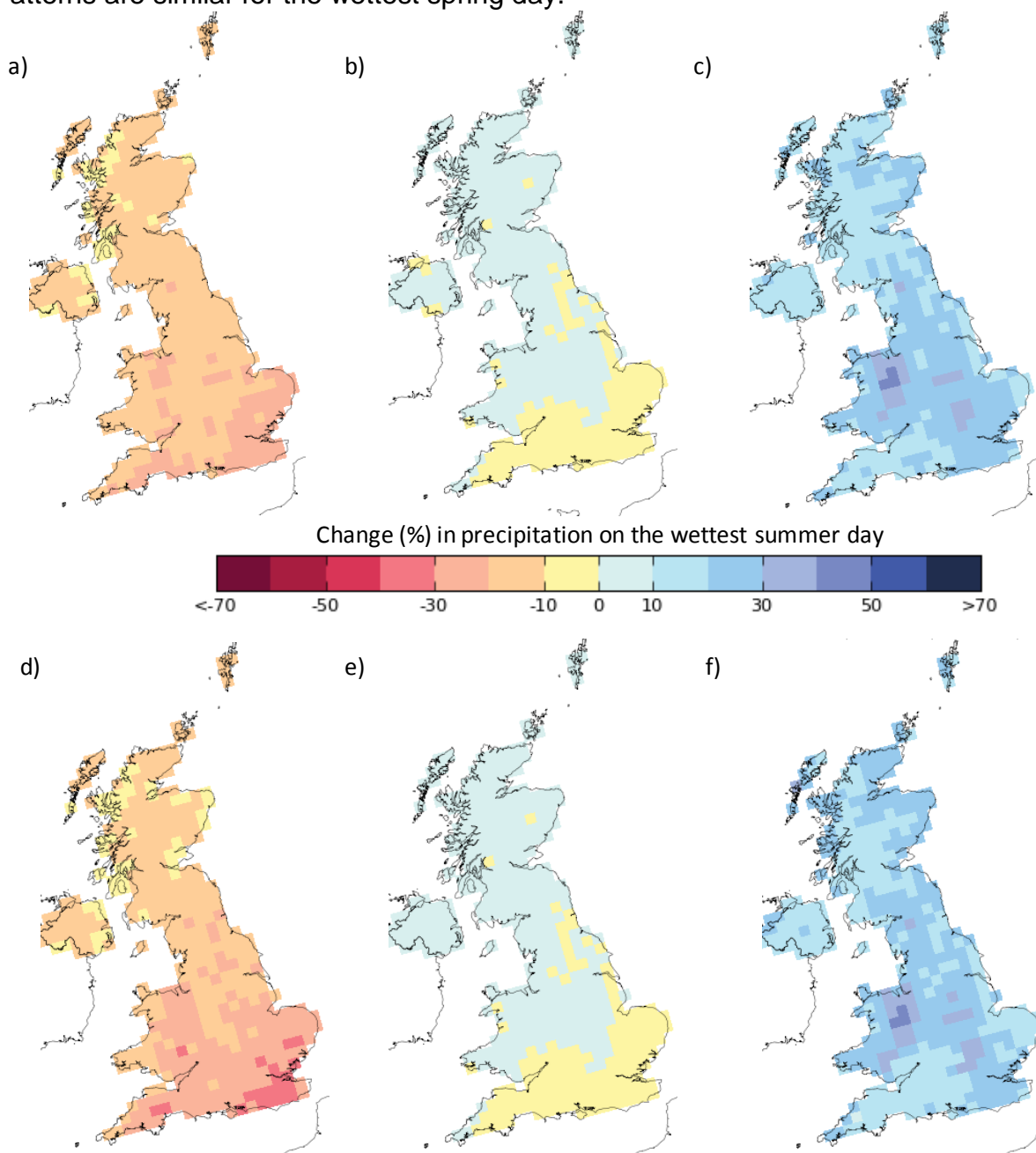
Fig. 3 Change in temperature of the warmest summer day (June, July and August) by the 2050s under a low (a - c) and high (d – e) emissions scenario with 10% (a, d), 50% (b, e) and 90% (c, f) probability levels; maps drawn from UK Climate Projections (2009).
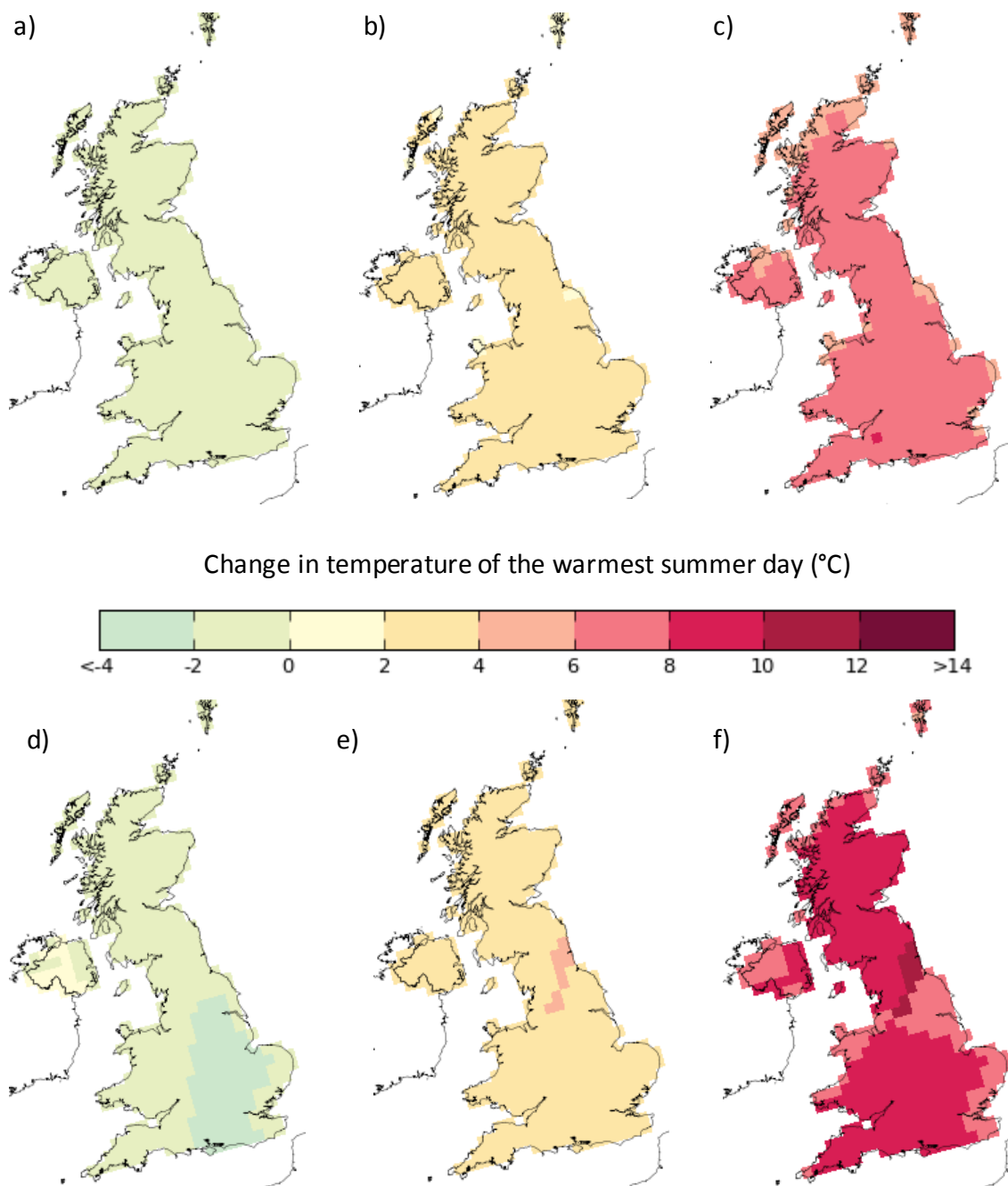
Fig. 4 Chough fecundity is reduced by precipitation during the late winter pre-breeding season (data from Reid *et al.* 2003), which is predicted to increase in the future within the species' current distribution UK Climate Projections (2009).
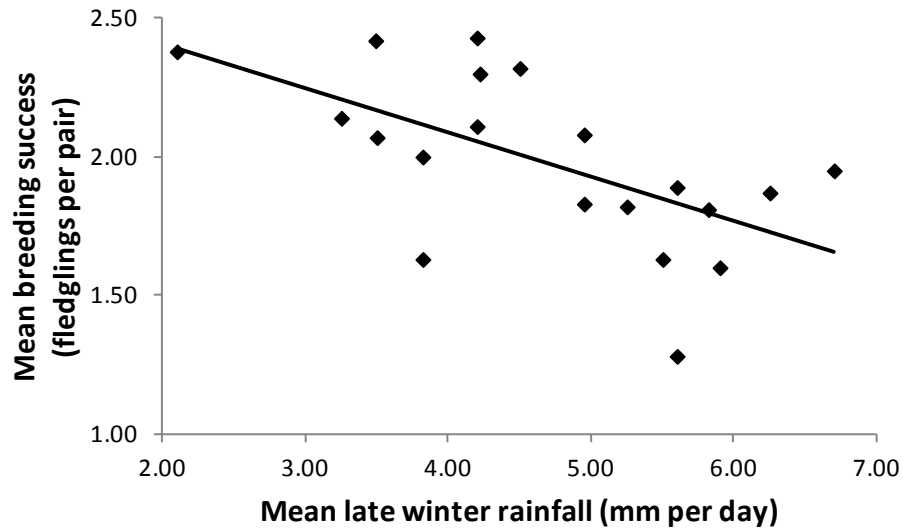
Table 1 Summary of the key biological mechanisms through which climate change may influence the community composition of the UK flora, by altering species' reproduction and recruitment, mortality or competitive interactions. Assessments of the evidence base, level of agreement and likelihood of change use standard IPCC confidence scales.

Mechanism	Demographic trait	Evidence base	Agreement	Likelihood of impact on community composition
Drought and heat stress	Reduced reproduction /recruitment	Medium	Medium	Likely: both winners and loosers
Phenological mismatches between flowering time and pollinator availabiity	"	Limited	Low	Unlikely: for generalists. About as likely as not: for specialists (which comprise a small proportion of the flora but are most likely to be negatively affected)
Insufficient winter chill	"	Medium	Medium	About as likely as not: most impacts that do arise will be negative
Gamete performance	"	Limited	Medium	Unlikely to influence most species: any change that does occur will incorporate winter and loosers
Seed bank performance	"	Limited	Low	Impossible to assess
Drought stress	Increased mortality/ altered competition	Medium	Medium	Likely: both winners and loosers
Frost damage	"	Limited	Medium	About as likely as not: both winners and loosers
Insufficient winter chill	"	Medium	Medium	Likely: both winners and loosers
Disease	"	Medium	Low	Likely: to influence incidence of specific diseases but currently impossible to assess typical impacts on total disease load.
Increased wildfires	"	Medium	Medium	Likely: primarily in moorland/heathland, a mix of winners and loosers with relative proportions depending on fire intensity and frequency.
Increased impact of currently established	"	Medium	Low	Likely: with native species declining, but probably only implies to a small number of

invasive plants				invasives
Altered herbivory: vertebrates	"	Limited	Low	About as likely as not (woodlands); impossible to assess (grasslands)
Altered herbivory: invertebrates	"	Limited	Low	Likely to influence specific plant-herbivore interactions with both winners and loosers; about as likely as not to influence total herbivore load to a sufficient extent to alter composition of floral assemblages
Changes in soil biochemistry	"	Limited	Medium	Soil biochemistry is likely to change, particularly with regard to increased nitrogen availability, but it is currently impossible to assess the impacts of this on floral assemblages
Establishment of new invasives	"	Limited	Low	Unlikely
Shading effect	"	Limited	Medium	Unlikely

Table 2 Summary of the key biological mechanisms through which climate change may influence the size of UK avian populations (excluding marine species). Mechanisms that are particularly likely to influence reproduction or survival are indicated with (R) and (S) respectively, but the majority of mechanisms can influence either of these traits. Assessments of the evidence base, level of agreement and likelihood of change use standard IPCC confidence scales.

Mechanism	Evidence base	Agreement	Likelihood of future impact
Direct effects of milder winters improves survival (S)	High	Medium	More likely than that: many small-bodied species have probably already benefited but populations may now be limited by other factors. For other species, effects of winter weather partly dependent upon changes in precipitation; very wet or snowy winters can reduce survival rates.
Sahel drought reduces Afro-Palaearctic migrant population size (S)	High	High	More likely than not due to uncertainty in aridity trends, but virtually certain if aridity increases
Changes in summer rainfall affect subsequent breeding success and survival (S & R)	Medium	Medium	Likely: both winners and losers, the identity of which is dependent on the nature of change in precipitation patterns
Increasing spring temperatures increase breeding success (R)	Medium	Medium	Likely: many resident species may benefit, but could have negative impacts on species confined to cooler upland areas or those sensitive to phenological mismatch (see below)
Phenological mismatch reduces reproductive success of UK breeding populations (R)	Medium	Low	Woodland: about as likely as not for long-distance migrants. Other habitats and species: unlikely
Rapid phenological shifts increase exposure to poor weather (R)	Limited	Low	About as likely as not: mainly losers
Climate change reduces prey abundance (S & R)	Medium	Low	Likely: for insectivorous upland birds reliant on drought-sensitive prey, and for owls and raptors predating small mammal populations with cyclic fluctuations in population size. As likely as not: for other species
Increased frequency of extreme events (S & R)	Limited	Low	About as likely as not: Possible periodic negative effects of severe winters, drought, heat stress, but the long-term consequences unclear.
Changing Arctic conditions influences global abundance of winter migrants	Medium	Medium	Likely: some species may benefit in the long-term if their predator populations collapse, but others are likely to

(R)			decline
Changed abundance of winter migrants due to short stopping	Medium	Medium	Very likely: both increases and decreases in UK population size
Increased fire risk	Limited	Medium	Moorland and lowland heath: likely. Other habitats: very unlikely
Increased deer browsing	Limited	Low	Woodland: impossible to assess due to uncertainty regarding climatic control of deer population size, but virtually certain if climatic control is strong. Other habitats: unlikely
Major loss of broad habitat type	Limited	Medium	Alpine vegetation: about as likely as not. Other habitats: exceptionally unlikely
Altered vegetation growth rates/structure	Limited	High	About as likely as not: winners and losers
Changes in tree species composition due to drought and disease	Limited	Low	Woodland: about as likely as not (assuming that climate change alters tree species composition). Other habitats: not applicable
Increased predation risk	Limited	Low	Impossible to assess
Increased disease	Limited	Low	Impossible to assess
Increased inter-specific competition	Limited	Low	Impossible to assess