
Newson, Stuart E.; Oliver, Tom H.; Gillings, Simon; Crick, Humphrey Q.P.; Morecroft, Michael D.; Duffield, Simon J.; Macgregor, Nicholas A.; Pearce-Higgins, James W. 2014. **Can site and landscape-scale environmental attributes buffer bird populations against weather events?** *Ecography*, 37 (9). 872-882. 10.1111/ecog.00575

Can site and landscape scale attributes buffer bird populations against weather events?

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Running title: Can site and landscape scale attributes buffer populations against weather impacts?

ABSTRACT

Projected impacts of climate change on species' populations and distributions pose a challenge for conservationists. In response, a number of adaptation strategies to enable species to persist in a changing climate have been proposed. Management to maximise the quality of existing sites may increase the resilience of populations in those sites to climate change and reduce or minimise climate-driven declines in population abundance. Alternatively large-scale management of landscapes could potentially improve the resilience of the metapopulations by facilitating inter-population movements, as well as reducing the obstacles to species' range expansion, allowing species to shift to new locations regionally or locally to track changing conditions. However, despite this theoretical base, there is limited empirical evidence in support of these management interventions. This makes it difficult for conservationists to decide which strategy to adopt under different circumstances. Here we used extensive long-term monitoring data for woodland birds at individual sites and look at the two-way interactions between habitat and both weather and count in the previous year, to test the extent to which certain site and landscape scale habitat attributes may buffer populations against variation in winter weather (a key driver of woodland bird populations) and facilitate subsequent population growth.

Our results provide some support for the idea that landscape scale attributes (patch isolation and area of woodland habitat) may influence the ability of some woodland bird species, which are known to be sensitive to habitat fragmentation, to withstand weather-mediated population declines. These effects were most apparent in generalist woodland species. There was also evidence that several woodland species, primarily woodland specialists, are more likely to increase following population decline where there is more woodland at the site and landscape scales. These results provide empirical support for the concept that landscape scale conservation may deliver climate change adaptation for some woodland bird species, although are unlikely to provide a universal benefit to all.

Keywords

habitat fragmentation, climate change adaptation, climate warming, population growth rate, temperature, woodland birds, weather

INTRODUCTION

Climate change is expected to have significant impacts upon global biodiversity through the course of this century, resulting in a significantly increased risk of extinction for many species (e.g. Thomas et al. 2004, Bellard et alet al. 2012, Warren et al. 2013). Given projected large-scale shifts in the distribution of suitable climate for species, it is anticipated that species' ranges will move polewards and to higher altitudes in response to climate change, driven by range expansion and colonisation at the leading edge, and population decline and extinction at the trailing edge (e.g. Huntley et al. 2008). Indeed, there is increasing evidence that species' ranges, populations and communities are responding as expected to recent warming (Hickling et al. 2006, Gregory et al. 2009, Both et al. 2010, Chen et al. 2011, Devictor et al. 2012,). In addition, there is the potential for climate change to increase local extinction from weather events, or increase the need for mobile species to move in response to such events. This would increase the importance of metapopulation dynamics to enable movement across a landscape and facilitate recolonisation. As a result, there is particular interest in the potential for management intervention to reduce or to negate the negative effects of climate change (adaptation).

Climate change adaptation may therefore focus on increasing the ability of species to respond to climate change, by either improving the resistance of populations to detrimental change at existing sites or to allow species to move away from sites undergoing detrimental climate change (Pearce-Higgins et al. 2011). These two options result in different adaptation strategies, and there is considerable debate as to which may be most effective (e.g. Opdam & Wascher 2004, Heller & Zavaleta 2009, Hodgson et al. 2009, Green & Pearce-Higgins 2010). To increase the resilience of populations to climate change on existing sites, site based adaptation should aim to maximise the size and quality of those sites, which may involve the prioritisation of large sites for protection, and restorative management to further increase the size and quality of such sites (e.g. Pearce-Higgins 2011, Morecroft et al. 2012). Alternatively or additionally, in order to reduce the obstacles to species' movement across the landscape, better connected landscapes should be developed in order to facilitate species' range-shifts in response to climate change (e.g. Hopkins et al. 2007, Hodgson et al. 2009, Oliver et al. 2012a). However, the evidence for the role of either site based or landscape scale adaptation in increasing the resilience of populations to climate change is largely theoretical and based upon limited empirical evidence. Given the long-term nature of climate change, collecting such evidence is difficult and is not readily amenable to experimentation, although a high conservation research priority, given the requirement to implement effective adaptation strategies now.

As a contribution to addressing this knowledge gap, we used detailed long-term monitoring data of variation in woodland bird populations at individual sites to appraise the relative importance of site and landscape scale attributes in influencing spatial variation in population growth. Whilst there is considerable literature on the relative importance of patch size and connectivity on the occurrence and abundance of birds (e.g. Lampila et al. 2005), we, uniquely, test the extent to which these attributes affect population sensitivity to weather events, and their ability to recover from them, as a means to inform land management adaptation responses to climate change. Specifically we firstly examine generic principles of site based adaptation by testing whether the sensitivity of populations to unfavourable weather is moderated by the size and configuration of the woodland patch they are in, assuming large sites with a low edge:area ratio are of higher quality for woodland specialists. Secondly, we examine whether the rate of population increase from a low count is enhanced by reduced patch isolation which is likely to facilitate dispersal between patches, as a test of landscape scale adaptation principles. This is achieved by using long-term population monitoring data of birds in British woodlands; a group of species, mainly small resident species, which are known to be sensitive to severe winter weather

(Greenwood & Baillie 1991, Robinson et al. 2007), and vulnerable to habitat fragmentation and isolation (van Dorp & Opdam 1987, Bellamy et al. 2003, Dolman 2007).

METHODS

Common Bird Census data

This study uses data from an extensive volunteer survey, the British Trust for Ornithology / Joint Nature Conservation Committee (JNCC) Common Birds Census (CBC). The CBC was introduced in 1962 to provide the first systematic monitoring of terrestrial bird abundance of the UK. Under the CBC, bird territories were mapped from observations made on between seven to ten site visits per year between April and July (Marchant et al. 1990). This territory mapping methodology provides robust estimates of the number of breeding territories present within each census plot so that observed changes in abundance closely reflect local population changes (Bibby et al. 1992). CBC plots were largely categorised as “woodland” or “farmland” and we concentrate on “woodland” CBC plots (plots where woodland is the predominant habitat) surveyed between 1965-2000, during which there were several extremely cold winters, and a sufficient number of plots monitored for change in relative abundance of woodland birds to be monitored over time. Plots with fewer than eight years of data or more than 25% missing values between the first and last year of the site’s coverage were omitted here. The mean number of years that plots included in the analyses were monitored for was 23 years (range 9-35 years). Whilst we do not expect the CBC to be biased in any particular way, the CBC is not a random sample or a stratified sample of sites with respect to woodland structure and tree species composition. We also assume that CBC plots are independent of one another (range of separation distances 6-47 km, mean 15.3 km). Whilst there may be some level of synchrony between sites, considering Bellamy et al. (2003), the magnitude of the effects are likely to be small at this separation distance.

The CBC has since been replaced by the UK Breeding Bird Survey, a transect-based system. The relevance of woodland to different bird species will vary with the extent to which each species' associates with woodland. We therefore ensured that the analysis was focussed on woodland birds (those of broad-leaved / mixed woodland). To establish which species could be treated as woodland birds, we used bird and habitat data recorded by Breeding Bird Survey (BBS) volunteers (Risely et al. 2013), which provides representative coverage of birds and habitats across the UK, to calculate a Jacobs' habitat preference index value (Jacobs 1974) for each species in broad-leaved / mixed woodland as:

$$J = (r - p) / [(r + p) - 2rp]$$

where r is the used proportion and p the available proportion of habitat in the BBS square, using BBS bird counts and habitat data from 1994-2009. It ranges between +1 for maximum preference and -1 for maximum avoidance. From this, we identified 21 resident species for which the CBC sample size has been sufficient in the past to produce trends in relative abundance (Marchant et al. 1990) and for which broad-leaved / mixed woodland was the preferred or second most preferred habitat. Ranking these species according to their Jacobs' index value, we further split these species into two groups, comprising woodland specialists (Jacobs index >0.35) and woodland generalists (Jacobs' index <0.30, Table 1). This list covers a large proportion of woodland bird species in Britain, although excludes some species which are too scarce, nocturnal or have territories that are too large to be surveyed adequately by the CBC.

Environmental attributes of sites and the wider landscape

To reduce the degree of multiple testing, we focussed on a small number of key habitat variables that describe site and landscape attributes, and a single weather variable. The availability and configuration of broad-leaved / mixed woodland, at the site level and within the wider landscape, was assessed using the 25-m resolution parcel data from the Land Cover Map 2000 which maps discrete patches to a minimum size of 0.5ha (LCM2000, Fuller et al. 2002). These data describe the location and size of contiguous patches of land of relatively uniform habitat or land use. Whilst these data have a high spatial precision and appear to be the most suitable large-scale dataset for this purpose, we accept that the habitat categorisation is fairly coarse, with limited ability to identify subtle biological differences in habitat quality for the species analysed. Whilst LCM2000 describes a number of habitat types, we focus here on broad-leaved / mixed woodland and extracted habitat measures at the site (radius 0.5 km around plot centres) and landscape (5 km radius) level. Two further landscape radii of 2 and 10 km were considered at the beginning of the study, but because habitat attributes were strongly correlated across landscape scales ($r > 0.90$), we chose to focus on the mid-distance 5 km landscape scale only. In particular, we calculated: total % cover of woodland habitat (W) at the site (0.5 km) and landscape (5 km) scales, patch isolation (mean edge to edge distance between patches, D) at the landscape scale and site 'edgeness' (E, calculated as the total perimeter of woodland patches within 0.5-km divided by the minimum possible perimeter given the area of woodland habitat present). The last two metrics were calculated using the package Fragstats (McGarigal & Marks 2002). Site level measures of woodland patch size (W0.5) and woodland edgeness (E0.5) are used to test the potential effectiveness of site based adaptation, whilst W5 and D5 relate to landscape attributes likely to describe the isolation of the site and test principles of landscape scale adaptation. CBC plots covered a wide range of woodland extent at the site level (W0.5) of 0.04 - 100% (mean = 25.4%) and at the landscape scale (W5) of 3.8 - 100% (mean = 27.4%). Patch isolation at the landscape scale (D5) defined as the distance between woodland patches, ranged from 100 - 640-m (mean = 180-m) and site 'edgeness' (E0.5) defined above, ranged from 0 - 3.27 (mean = 3.27).

Habitat variables are correlated and describe related components of the environment, making it difficult to disentangle the relative contribution of these different processes in driving bird populations. Large woodland sites tend to be in more wooded landscapes (correlation between

W0.5 and W5; $r = 0.46$, $n = 176$, $P < 0.0001$). Both site attributes (W0.5 and E0.5) and landscape attributes (W5 and D5) are also strongly correlated ($r = 0.48$, $n = 176$, $P < 0.0001$ and $r = -0.62$, $n = 176$, $P < 0.0001$ respectively). In order to prevent potential cross-correlations between variables reducing our ability to identify meaningful effects, the effects of each habitat variable were tested in isolation from the others. However, this does mean that species-relationships with different habitat measures may not be independent of each other.

To examine whether there is evidence that site and landscape scale habitat variables can moderate the effect of weather variation upon species' populations, we considered mean daily minimum winter temperature (MIN) from the winter period (December-February) between consecutive surveys, as this has been shown in several studies to be associated with changes in avian demography (e.g. Sæther et al. 2004, Robinson et al. 2007, Knape & de Valpine 2010). This was provided at a 5-km resolution by the Meteorological Office through the UK Climate Impacts Programme, and matched to the centre point of each CBC plot (UKCIP, http://www.ukcip.org.uk). To ensure that we modelled local population growth as a function of locally warm or cold weather, we used in our analysis minimum winter temperature anomalies (variation from the mean) from each site calculated across the CBC period, 1965-2000. Minimum temperature anomalies ranged between -4.29 and 3.46 ^{o}C.

Examining importance of site and landscape variables in mediating climate response

We used a repeated measures generalized linear model (GLM) with Poisson errors and log link, applied using the GENMOD procedure in SAS (SAS Institute 2001) to look at the relationship between species counts and various habitat variables and winter temperature and their interactions. Non-independence of successive counts in the same CBC plots was taken into account by applying a repeated statement using plots as the subject. We modelled between-year change in bird numbers by including the log of the count in the previous year as an offset, and including the count in the previous year as an additional covariate to account for density-dependence (Greenwood & Baillie 1991). Because the deviance divided by the degrees of freedom was close to one in all cases, it was not necessary to account for overdispersion. For these analyses, it was necessary to exclude all cases with zero counts in the previous year, a small number for most species (Table 1). Because the percent woodland cover of the removed counts at the site and landscape scales were almost identical to those included in the main analyses (W0.5 range 0.08-100% mean = 25.8%, W5 range 3.5-100% mean = 27.1%), their removal is unlikely to bias the current analyses towards larger woodland plots.As mentioned earlier, relationships with each habitat variable were modelled separately. For each, a structured approach to the analysis was used to produce models of increasing complexity as follows.

i) The direct effects of each site and landscape attribute were tested separately in a model that also included the effect of weather (MIN) and count in the previous year (C) to account for density-dependence. These models test the extent to which population growth is directly related to both site and landscape scale attributes, irrespective of weather, and to weather, irrespective of habitat. We therefore expect positive relationships between W0.5 and W5 and population growth, but negative relationships with D5 and E0.5. The relationship between MIN and population growth should identify the species most vulnerable to cold weather.

ii) Two-way interactions between habitat predictor variables and both weather and count in the previous year were then added to the model of (i) above. Interactions with weather tested whether site and landscape attributes moderate the response of populations to weather effects, a test of species' sensitivity. Interactions with count in the previous yeartested whether site and landscape attributes interact with the effects of density dependence; specifically, whether habitat attributes increase the rate of growth of very small populations and / or the rate of decline of very large populations. Again, habitat attributes were modelled separately, whilst the interaction between C and MIN was included in all models to cover potential effects of density-dependence on the response of populations to cold weather. In terms of sensitivity, negative interactions between both W0.5 and W5, and MIN, would indicate that the effects of cold winter weather were reduced at large patches (W0.5) or in a well-wooded landscape (W5). Positive interactions between both D5 and E0.5, and MIN, would indicate that population declines as a result of winter temperature were reduced in well connected patches and patches with little edge. If habitat was strongly related to the ability of populations to increase from a small count, we would expect statistically significant negative interactions between C and both W0.5 and W5 (effects more positive when count in the previous year was small) and interactions with both D5 (distance between woodland patches) and E0.5 (more edge habitat) to be positive (i.e. rate of increase from small populations slower in more isolated and edgey habitats).

For all analyses we calculate and present species-specific coefficients, but also use the SURVEYMEANS procedure in SAS (SAS Institute 2001) to calculate a weighted mean coefficient and standard error to summarise results across species, weighting by 1 / standard error, for woodland specialists and generalists separately as defined above. A t-test was subsequently used to test whether the weighted mean was significantly different from zero. A formal comparison of weighted means was not made, but non-overlapping 95% confidence intervals imply a significant difference at P = <0.05.

RESULTS

Direct effects of environmental variables on population growth rate

Growth rates of most species showed strong density-dependence, being consistently negatively correlated with the count in the previous year, C, indicating that populations were more likely to decline from a high count. There was no consistent cross-species positive effect of minimum winter temperature, MIN, upon population growth, although this was close to significant for habitat specialists (weighted mean) and populations of some species (goldcrests, long-tailed tits and coal tits) showed the expected significant increase following warmer winters (Table 2).

There was little consistent evidence that population growth rates of either habitat generalists or specialists were significantly affected by either of the site based attributes. Population growth of two species (lesser spotted woodpecker and bullfinch) was more positive at small woodland sites (W0.5). This proportion of significant tests is not different from that expected by chance across multiple tests, but is opposite to the direction expected (Table 2).

There was more evidence in support of population growth being influenced by landscape scale attributes, with more significant effects than expected by chance (11 / 42 tests), although, again, no consistent overall trend across species was apparent. Population growth rates of Nuthatch and Coal Tit were positively correlated with the extent of woodland habitat within the wider landscape (W5); this contrasted with negative relationships between W5 and population growth for Lesser Spotted Woodpeckers and Blue Tits. The growth of Nuthatch populations was also strongly negatively related to distance between woodland patches, being more positive at less-isolated sites (Table 2). The same negative associations, albeit less strong, were apparent for two habitat generalists, Blackbird and Chaffinch. In contrast the growth rates of Willow Tit, Blue Tit, Long-tailed Tit and Wren populations were each significantly more positive where there was reduced habitat connectivity, as measured by D5 (Table 2).

Species sensitivity to winter temperature in relation the habitat

Species' sensitivity to winter weather was not affected by site attributes for any species, but was significantly mediated by landscape attributes with 8/42 tests being statistically significant (Table 3). Five woodland species showed significant positive interactions between D5 and MIN, which was also significant when averaged across all generalists, suggesting that the positive effects of winter temperature (indicative of strong negative effects of cold weather) were greatest at more isolated sites.. At sites located in landscapes where woodland patches are close together (D = 100m), there was little effect of minimum temperature upon generalist population growth rate, whilst at isolated woodland (D > 400m), population growth in cold winters (MIN < 2.5 ˚C), tended to be negative (Figure 1). These relationshipswith isolation were mirrored by a significant negative interaction between woodland extent (W5) and MIN for Blue Tit, with relatively consistent effects among other generalist species.

However, the effects of woodland isolation were consistent across woodland specialists, with the effects of winter temperature on Willow Tits apparently reduced by isolation, whilst the effect of winter temperature on Great spotted Woodpecker appeared greatest at sites with high woodland cover in a 5 km radius, both contrary to expectation (Table 3).

Population increases from a lowcount as a function of habitat

The same models also showed that the ability of populations to increase from a previous low count was affected by the extent of woodland cover at sites (W05*C) and within landscapes (W5*C) more often than expected by chance (8/42 tests). In all but one case (willow tit), these results were for negative slopes, suggesting that growth from small population sizes was more rapid where woodland extent was greater (Table 4). A highly significant relationship in the expected direction was shown for habitat specialists as a whole (weighted mean), in relation to W0.5. Interestingly, at sites with very little woodland (W0.5 = 0%), population growth was stable irrespective of C, but at large sites there was a much stronger impact of density-dependence, with greater population declines following high counts, but positive population growth following years of small population size (Figure 2). At the site level, there was no evidence that species were less likely to increase from low numbers where there was more woodland-edge habitat;

conversely, edge habitat actually appeared to promote recovery of Chaffinch, Great Tit and Marsh Tit populations.

In relation to the influence of connectivity of woodland patches (D5*C), Lesser Spotted Woodpeckers showed more positive population growth from a low count at sites where the distance between woodland patches was lower (an association also bordering on significance for Nuthatch). This pattern was generally reflected across species (Table 4), but there were some notable exceptions, with the reverse pattern apparent for both Treecreeper and Willow Tit, suggesting recovery was faster within landscapes with more distant woodland patches.

DISCUSSION

Our analysis provides evidence in support of benefit being associated with both reducing the extent of habitat fragmentation in the wider landscape, and increasing the size of habitat patches; conservation principles which are being widely advocated in the scientific (Opdam & Wascher 2004, Heller & Zavaleta 2009, Hodgson et al. 2009) and policy-focussed (Hopkins et al. 2007, Lawton et al. 2010) literature. Importantly it was not the direct effects of site and landscape scale habitat attributes upon population growth rates which were apparent (these have been previously well-studied for the woodland species of interest; e.g. Hinsley et al. 1995, Bellamy et al. 1996b). Instead it was the role that they may play in influencing individual population responses to winter temperature, and the rate of population increase from small counts that appeared important. We detected more statistically significant correlations that influenced species' population responses to winter temperature and increases from small population sizes than we would have expected by chance. Although the directions of these relationships varied between species, we found two important general results across species. Firstly, populations of woodland generalists were most sensitive to detrimental effects of winter weather if they were located within fragmentated landscapes with large distances between patches (Figure 1). Secondly, populations of woodland specialists were more likely to increase from a small population size, such as following an extreme weather event, if they were at large woodland sites (Figure 2).

Our initial expectation was that site attributes would be more important for increasing the resilience of populations to detrimental weather (e.g. Hodgson et al. 2009, Pearce-Higgins 2011), with populations in large sites less likely to decline after a cold winter. There was no evidence for this. Instead, we found a beneficial effect of reduced fragmentation upon population responses to cold weather. The apparent stability of populations within structurally well-connected landscapes suggests that density-dependent processes may operate at a fine scale and buffer local population responses to weather (Kluijver & Tinbergen 1953, Clobert et al. 1988). There is a potential mechanism here, where in a well-connected woodland, individuals lost during a cold winter appear likely to be replaced by local immigrants from other nearby sites, whereas in response to a warm winter, additional potential recruits appear more likely to disperse to other sites. However, at an isolated site, apparent rates of immigration to replace individuals lost during a cold winter, or the emigration of individuals that survive during a warm winter, may be reduced, leading to geater fluctuation in the population. Whilst these processes have previously been documented for individual woodland bird species (e.g. Bulmer & Perrins 1973, Slagsvold 1975), and the broader effects of fragmentation upon these bird populations is well established (Bellamy et al. 1996b, Hinsley et al. 1996, Bennett et al. 2004), this is, to our knowledge, the first time the consequences of fragmentation upon local population responses to temperature have been established and generalized across species.

Similarly, population increases of habitat specialists from small counts were enhanced at sites containing a large amount of woodland (Figure 2), whilst small woodland sites tended to show more stable population trends. This suggests that large woodland sites, which also tend to be in more wooded landscapes, may again be associated with a greater source of individuals to repopulate an area following pertubation. Populations at large sites were more likely to recover quickly from low numbers than at small sites. This may be a simple function of area, aslarger sites are likely to have a greater capacity to absorb recruits compared to small sites, or provide a larger target for potential colonists to arrive at. Alternatively, these results may also be caused by variation in habitat quality, heterogeneity or microclimate between large and small patches, which may lead to greater resources being available at large sites, enabling more rapid population growth following population decline (Oliver et al. 2010).

Somewhat counter-intuitively, populations in large woods were also more likely to show a significant decline from a high count. This negative density dependent feedback may be related to increased species movement in less fragmented landscapes, as outlined above. Potential negative impacts of fragmentation upon bird populations are being increasingly recognized as a result of reduced dispersal ability of individuals (reviewed by Lampila et al. 2005). Whilst there are examples illustrating how patch isolation may limit the dispersal of individuals across the landscape (Aldermann et al. 2005), the emigration of birds from particular isolated patches (Pearce-Higgins et al. 2007), and the probability of extinctions and colonizations (Bellamy et al. 1996a), the evidence from multi-species studies is that such effects are strongest for widespread generalist species (Dolman et al. 2007). This was also the case with our results: benefits associated with reduced distance between woodland patches were most apparent for generalist, rather than specialist woodland birds (Table 3). However, given the cross-correlations between these variables, it is difficult to be too definitive about the precise mechanisms underpinning the correlations we observed.

These general findings across species are supported by the individual species results for nuthatch, probably the woodland bird species for which there is the greatest evidence from previous work of its distribution and populations being limited by fragmentation. The occurrence of this species within woodland patches is consistently negatively associated with the degree of isolation of those patches from others (e.g. van Dorp & Opdam 1987, Bellamy et al. 1998, Villiard & Taylor 1994), and has been the subject of a number of spatial models to explore the consequences of this (Bellamy et al. 1998, van Langevelde 2000, Alderman et al. 2005), which indicate that isolation has restricted the occupancy of otherwise suitable habitat in eastern England, despite suitability of the climate for this species in the region (Bellamy et al. 1998). In our study, we found that nuthatch populations were more likely to exhibit positive population growth if they were located in wooded landscapes (a positive correlation between population growth and W5; Table 2), whilst in such landscapes, there was a greater probability of recovery from a small population size than in a less wooded landscape (negative W5*C interaction; Table 4). The net result from this is that the strongest nuthatch population growth is at a site in a well-wooded landscape recovering from a small count, whilst at isolated sites, population growth is more stable, or weakly positively related to count in the previous year (Figure 3). Thus, our results support these previous studies suggesting that this is a fragmentation sensitive species, which adds confidence to the robustness of our other conclusions. Within the bounds of concerns over multiple testing, the results presented in Tables 2-4 can therefore be used to identify other species most likely to benefit from both site and landscape site scale management to increase patch size and reduce patch isolation.

There was little evidence that the species populations were depressed where there was more woodland edge habitat. If anything there was better evidence, for some species at least, that recovery following population decline was more likely where there was more woodland edge habitat. The lack of a relationship for habitat specialists supports the idea that in our study there are few deep woodland specialists that benefit from large areas of woodland (although see Broughton et al. 2010, who highlighted the vulnerability of Marsh Tits to habitat fragmentation). This reflects the character of British woodlands where there are few large patches (Thomas et al. 1997).

et alOur results further suggest that fragmentation has reduced the movement of individuals between sites. Populations at more isolated sites appeared more sensitive to decline in response to unsuitable temperatures, whilst populations at large sites in more well wooded landscapes were more likely to recover from small populations, such as may be caused by adverse weather. Similar results have been found for a woodland butterfly species (Oliver et al. 2012b). Although we have not specifically considered the benefit associated with increased connectivity in facilitating the range expansion of woodland birds, or demonstrated that habitat fragmentation limits range expansion, as has been shown for woodland butterflies (Warren et al. 2001), our findings can still inform the debate over the potential for landscape-scale conservation to promote the range-expansion of species in response to climate change.

This study provides important evidence that both site and landscape scale effects can have a strong influence upon the sensitivity of bird populations to temperature. We have focused on the effects of winter temperature, the key climatic driver of populations over the time-period studied (Greenwood & Baillie 1991). Although this may be projected to become a less important driver with future climate change (Jenkins et al. 2009), there is some evidence that warming conditions in the Arctic may drive more frequent cold winters at temperate latitudes (Liu et al. 2012), indicating our results may be directly relevant to current climatic change. Aside from the precise form of future climatic changes that will occur in the UK, our results also demonstrate the important principle that variation in habitat characteristics may moderate the response of populations to temperature. This is consistent with the concept that reducing fragmentation of landscapes will increase the resilience of species' and populations to climate change, and specifically suggests that landscape-scale conservation interventions might help some woodland birds in England to adapt to climate change.

Nevertheless, it is worth emphasizing that these findings were not consistent across species, and it is likely that any adaptive landscape-scale conservation measures may only benefit a subset of woodland species. Measures to increase landscape connectivity may be most likely to benefit woodland generalists (although there is good evidence that nuthatch populations would also be likely to benefit from increased woodland cover across the landscape), whilst increasing the size of woodland areas may be most likely to benefit woodland specialists. Given that patch size and landscape connectivity are intrinsically linked in real landscapes, a strategy of habitat protection and creation to maximise woodland patch size and to reduce the distance between woodland patches would be likely to benefit the widest range of woodland species. These benefits will be incurred not only through the facilitation of range shifts under climate warming, as shown in previous studies, but also through improving the resilience of in-situ populations to increased climatic variability.

Acknowledgements

We would like to thank all the volunteer fieldworkers who contributed to the CBC and BBS surveys. The CBC was funded by the BTO and JNCC and the BTO by the BTO / JNCC and RSPB. This analysis was funded by Natural England (project NECR112). We are extremely grateful to Rob Fuller and two anonymous referees for comments on an earlier draft.

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Table 1. Bird species and information relevant to the analyses of CBC data. Species are grouped into broad-leaved / mixed woodland specialists and generalists and ordered within group according to declining preference (Jacobs' index) for this habitat.

Species (species code)	Jacobs' index	Number of sites in model	Total number of observations	Number of colonisation events	Number of Territories range (mean)
Broad-leaved / mixed woodland generalists					
Bullfinch, *Pyrrhula pyrrhula* (BF)	0.30	149	817	32	1-9 (2.97)
Great tit, *Parus major* (GT)	0.29	176	1,214	1	1-9 (3.54)
Blue tit, *Cianistes caeruleus* (BT)	0.27	175	1,204	2	1-9 (2.89)
Robin, *Erithacus rubecula* (R.)	0.26	178	1,236	1	1-9 (2.46)
Song thrush, *Turdus philomelos* (ST)	0.24	176	1,153	11	1-9 (3.96)
Wren, *Troglodytes troglodytes* (WR)	0.24	178	1,234	4	1-9 (2.68)
Coal tit, *Periparus ater* (CT)	0.17	167	977	18	1-9 (3.49)
Wood pigeon, *Columba palumbus* (WP)	0.15	115	506	26	1-9 (3.63)
Mistle thrush, *Turdus viscivorus* (M.)	0.14	162	728	60	1-7 (1.83)
Chaffinch, *Fringilla coelebs* (CH)	0.11	176	1,192	4	1-9 (3.32)
Blackbird, *Turdus merula* (B.)	0.09	177	1,232	0	1-9 (3.08)
Goldcrest, *regulus regulus* (GC)	0.08	140	657	58	1-9 (3.53)
Broad-leaved / mixed woodland specialists					
Marsh tit, *Poecile palustris* (MT)	0.58	120	623	29	1-9 (2.63)
Nuthatch, *Sitta europaea* (NH)	0.55	118	654	27	1-9 (2.80)
Lesser spotted woodpecker, *Dendrocopos minor* (LS)	0.54	52	84	33	1-7 (1.43)
Eurasian treecreeper, *Certhia familiaris* (TC)	0.54	145	734	36	1-8 (2.29)
Jay, *Garrulus glandarius* (J.)	0.47	171	994	18	1-9 (2.17)
Willow tit, *Poecile montanus* (WT)	0.46	67	157	31	1-7 (2.13)
Great spotted woodpecker, *Dendrocopos major*(GS)	0.45	157	862	28	1-9 (1.90)
Green woodpecker, *Picus viridis* (G.)	0.35	132	663	53	1-9 (1.69)
Long-tailed tit, *Aegithalos caudatus* (LT)	0.35	162	866	41	1-9 (2.31)

Table 2. **Direct effects**. Change in woodland bird populations in relation to environmental variables according to Common Birds Census data (1965-2000). P-values are: *<0.05, **<0.01, ***<0.001. Significant results are further highlighted in bold. W = percent woodland cover, D = distance between patches, E = site edgeness, C = count in previous year. The effects of MIN and C are averaged here across the four models. Full species names are given in Table 1. Note that one significant result (1/21 tests) for each variable would be expected by chance alone.

	Site attributes		Landscape attributes			
Species	W0.5	E0.5	W5	D5	MIN	C
Generalists						
B.	0.0016 (0.0012)	0.0275 (0.0875)	0.0029 (0.0019)	**-0.0066 (0.0024) ** **	-0.0272 (0.0139)	**-0.1102 (0.0100) *****
BF	**-0.0018 (0.0007) ** **	-0.0559 (0.0365)	-0.0012 (0.0010)	0.0007 (0.0019)	-0.0046 (0.0101)	**-0.0331 (0.0074) *****
BT	-0.0008 (0.0011)	-0.0341 (0.0732)	**-0.0033 (0.0016) ***	**0.0055 (0.0020) ** **	0.0061 (0.0120)	**-0.1031 (0.0118) *****
CH	0.0013 (0.0012)	0.0799 (0.0683)	0.0011 (0.0020)	**-0.0072 (0.0031) ***	-0.0012 (0.0130)	**-0.1161 (0.0111) *****
CT	0.0016 (0.0009)	0.0690 (0.0471)	**0.0038 (0.0011) *****	-0.0021 (0.0019)	**0.0224 (0.0116) ***	**-0.0851 (0.0100) *****
GC	-0.0017 (0.0016)	0.0449 (0.0577)	-0.0005 (0.0020)	-0.0037 (0.0039)	**0.0536 (0.0167) ** **	**-0.1068 (0.0140) *****
GT	-0.0003 (0.0013)	0.0207 (0.0502)	0.0009 (0.0017)	-0.0025 (0.0024)	-0.001 (0.0109)	**-0.1346 (0.0100) *****
M.	0.0001 (0.0008)	-0.0406 (0.0282)	0.0014 (0.0014)	-0.0044 (0.0037)	0.0088 (0.0095)	**-0.0550 (0.0212) ** **
R.	-0.0004 (0.0008)	0.0801 (0.0522)	0.0001 (0.0017)	0.0027 (0.0018)	0.0054 (0.0162)	**-0.1303 (0.0134) *****
ST	0.0000 (0.0007)	-0.0473 (0.0331)	0.0000 (0.0012)	0.0012 (0.0013)	0.0095 (0.0091)	**-0.1182 (0.0104) *****
WP	0.0010 (0.0013)	-0.0935 (0.0544)	-0.0005 (0.0025)	0.0038 (0.0057)	0.0376 (0.0204)	**-0.1127 (0.0136) *****
WR	0.0009 (0.0011)	0.0491 (0.0716)	-0.0010 (0.0020)	**0.0063 (0.0031) ***	-0.0294 (0.0196)	**-0.1550 (0.0147) *****
Weighted mean (se) [a]	0.0001 (0.0003)	-0.0009 (0.0176)	0.0004 (0.0000)	-0.0002 (0.0002)	0.0060 (0.0054)	**-0.1026 (0.0114)*****
Specialists						
G.	-0.0001 (0.0006)	0.0294 (0.0366)	0.0018 (0.0010)	-0.0012 (0.0025)	0.0136 (0.0124)	-0.0158 (0.0191)
GS	0.0001 (0.0004)	0.0124 (0.0550)	0.0001 (0.0008)	0.0005 (0.0013)	0.0061 (0.0094)	**-0.0301 (0.0151) ***
J.	0.0009 (0.0006)	0.0019 (0.0474)	0.0006 (0.0013)	-0.0009 (0.0012)	-0.0065 (0.0067)	**-0.0346 (0.0132) ** **
LS	**-0.0074 (0.0026) ** **	0.0188 (0.2328)	**-0.0095 (0.0049) ***	0.0044 (0.0088)	0.0383 (0.0485)	**0.0955 (0.0331) ** **
LT	-0.0012 (0.0008)	-0.0694 (0.0612)	-0.0025 (0.0014)	**0.0025 (0.0013) ***	**0.0306 (0.0087) *****	**-0.0681 (0.0153) *****
MT	0.0002 (0.0012)	0.0001 (0.0595)	-0.0008 (0.0015)	-0.0006 (0.0015)	0.0045 (0.0118)	**-0.0692 (0.0167) *****
NH	0.0011 (0.0008)	0.1037 (0.0847)	**0.0037 (0.0014) ** **	**-0.0132 (0.0034) *****	-0.0007 (0.0130)	**-0.0487 (0.0109) *****
TC	0.0012 (0.0007)	0.0074 (0.0644)	0.0013 (0.0009)	-0.0005 (0.0021)	0.0154 (0.0117)	**-0.0561 (0.0170) ** **
WT	-0.0040 (0.0028)	-0.1497 (0.2132)	-0.0034 (0.0047)	**0.0064 (0.0019) *****	0.0289 (0.0341)	-0.0234 (0.0404)
Weighted mean (se) [a]	-0.0001 (0.0004)	0.0048 (0.0153)	-0.0002 (0.0070)	0.0001 (0.0012)	0.0101 (0.0053)	**-0.0371 (0.0107) ** **

[a] Weighted by 1 / variance

Table 3. **Influence of habitat attributes on sensitivity to winter temperature**. Change in woodland bird populations in relation to winter temperature according to Common Birds Census data (1965-2000). P-values are: *<0.05, **<0.01, ***<0.001. Significant results are further highlighted in bold. W = percent woodland cover, D = distance between patches, E = site edgeness, C = count in previous year. The effects of C*MIN are averaged here across the four models. Full species names are given in Table 1. Note that one significant result (1/21 tests) for each variable would be expected by chance alone.

	Site attributes		Landscape attributes		
Species	W0.5*MIN	E05*MIN	W5*MIN	D5*MIN	C*MIN
Generalists					
B.	0.0001 (0.0004)	0.0157 (0.038)	0.0002 (0.0007)	0.0013 (0.0010)	0.0038 (0.0054)
BF	0.0002 (0.0005)	0.0308 (0.0183)	0.0009 (0.0007)	-0.0006 (0.0008)	0.0001 (0.0050)
BT	-0.0001 (0.0003)	0.0061 (0.0262)	**-0.0014 (0.0006)***	**0.0021 (0.0008)****	-0.0066 (0.0056)
CH	0.0003 (0.0006)	0.0263 (0.0394)	-0.0004 (0.0007)	0.0001 (0.0008)	-0.0002 (0.0064)
CT	-0.0007 (0.0005)	-0.0181 (0.0163)	-0.0003 (0.0005)	0.0003 (0.0010)	**0.0109 (0.0052)***
GC	0.0012 (0.0009)	-0.0030 (0.0346)	0.0015 (0.0012)	-0.0021 (0.0019)	-0.0037 (0.0067)
GT	0.0000 (0.0004)	-0.0233 (0.0221)	-0.0007 (0.0006)	0.0009 (0.0007)	-0.0050 (0.0056)
M.	-0.0004 (0.0004)	-0.0108 (0.0255)	-0.0004 (0.0005)	0.0023 (0.0013)	0.0013 (0.0088)
R.	-0.0010 (0.0008)	-0.0005 (0.0280)	-0.0020 (0.0015)	0.0012 (0.0014)	0.0022 (0.0075)
ST	0.0002 (0.0003)	-0.0091 (0.0178)	0.0008 (0.0005)	-0.0003 (0.0007)	-0.0111 (0.0058)
WP	-0.0004 (0.0009)	0.0304 (0.0738)	-0.0013 (0.0012)	**0.0051 (0.0023)***	**0.0168 (0.0083)***
WR	0.0001 (0.0008)	-0.0099 (0.0424)	-0.0008 (0.0011)	**0.0034 (0.0010)****	0.0099 (0.0091)
Weighted mean (se) [a]	0.0000 (0.0001)	-0.0009 (0.0176)	-0.0004 (0.0006)	**0.0010 (0.0004) ***	0.0014 (0.0017)
Specialists					
G.	-0.0002 (0.0005)	-0.0135 (0.0328)	-0.0004 (0.0007)	0.0001 (0.0022)	0.0032 (0.0047)
GS	0.0003 (0.0003)	0.0502 (0.0412)	**0.0015 (0.0006)****	-0.0002 (0.0006)	0.0152 (0.0085)
J.	-0.0002 (0.0002)	0.0051 (0.0247)	0.0001 (0.0004)	-0.0001 (0.0005)	0.0045 (0.0054)
LS	0.0014 (0.0022)	0.1870 (0.1427)	0.0013 (0.0037)	-0.0028 (0.0034)	**-0.0951 (0.0421)***
LT	0.0004 (0.0004)	-0.0078 (0.0194)	0.0001 (0.0006)	0.0004 (0.0003)	0.0072 (0.0079)
MT	-0.0011 (0.0006)	-0.0372 (0.0210)	-0.0010 (0.0006)	**0.0040 (0.0009)*****	-0.0027 (0.0087)
NH	0.0003 (0.0006)	-0.0064 (0.0330)	0.0019 (0.0010)	-0.0036 (0.0034)	0.0012 (0.006)
TC	0.0001 (0.0005)	0.0152 (0.0380)	0.0005 (0.0006)	**0.0026 (0.0012)***	0.0080 (0.0083)
WT	0.0003 (0.0020)	0.0979 (0.1050)	0.0048 (0.0030)	**-0.0032 (0.0009)*****	-0.0330 (0.0186)
Weighted mean (se) [a]	0.0000 (0.0002)	0.0048 (0.0116)	0.0004 (0.0003)	0.0002 (0.0006)	0.0009 (0.0035)

[a] Weighted by 1 / variance

Table 4. **Influence of habitat attributes on density-dependent population growth**. Change in woodland bird populations in relation to environmental variables according to Common Birds Census data (1965-2000). P-values are: *<0.05, **<0.01, ***<0.001. Significant results are further highlighted in bold. W = percent woodland cover, D = distance between patches, E = site edgeness, C = count in previous year. Full species names are given in Table 1. Note that one significant result (1/21 tests) for each variable would be expected by chance alone.

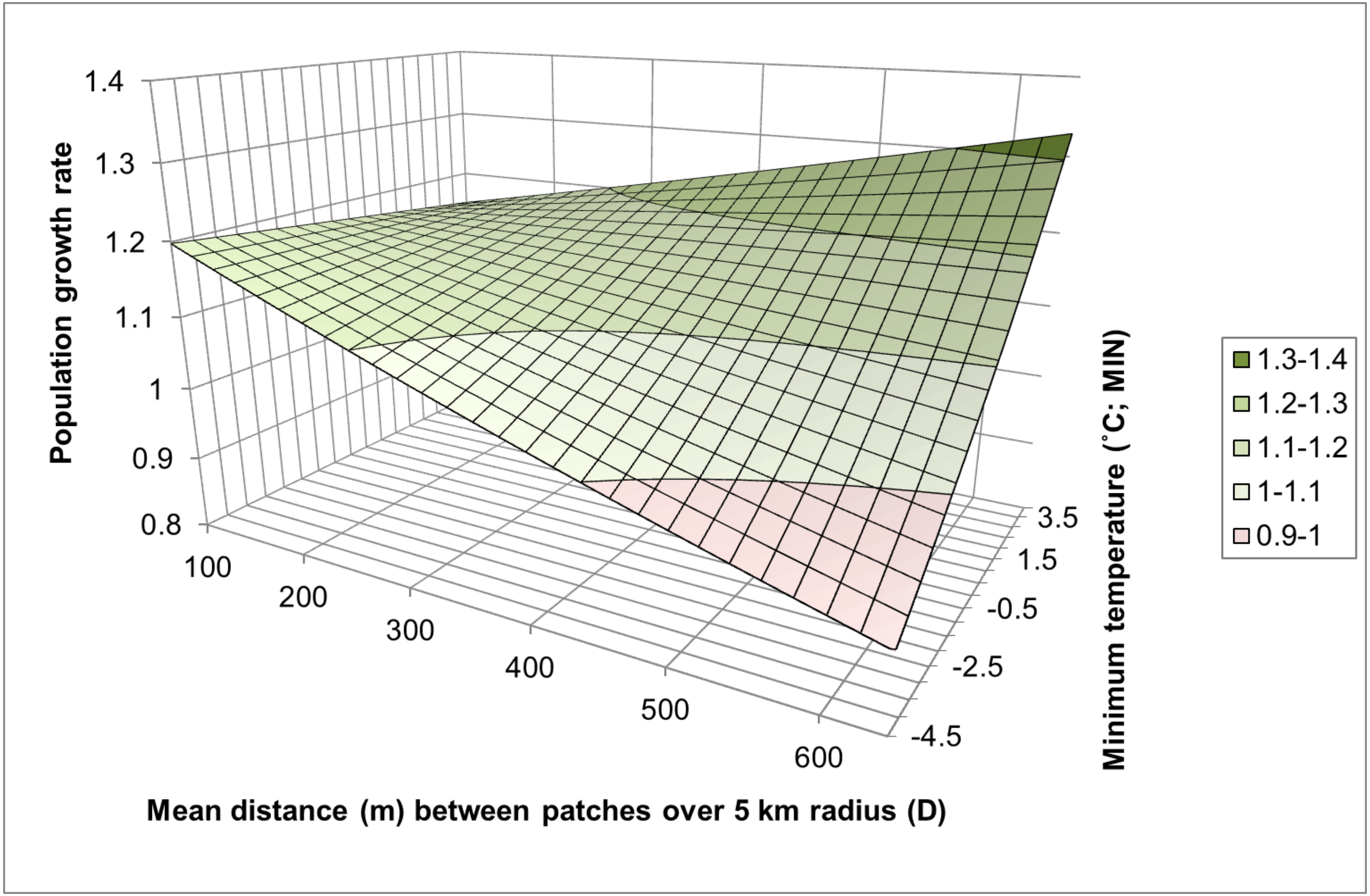
	Site attributes		Landscape attributes	
Species	W0.5*C	E0.5*C	W5*C	D5*C
Generalists				
B.	0.0002 (0.0004)	0.0131 (0.0289)	0.0001 (0.0007)	-0.00004 (0.00014)
BF	-0.0002 (0.0004)	0.0103 (0.0146)	0.0009 (0.0008)	0.00000 (0.00007)
BT	0.0001 (0.0005)	-0.0017 (0.0356)	0.0004 (0.0008)	-0.00014 (0.00011)
CH	**-0.0010 (0.0004) ***	**-0.0949 (0.0227) *****	-0.0014 (0.0007)	0.00032 (0.00019)
CT	0.0000 (0.0004)	-0.0093 (0.0304)	-0.0009 (0.0005)	0.00010 (0.00006)
GC	0.0009 (0.0007)	-0.0110 (0.0255)	-0.0001 (0.0009)	0.00008 (0.00020)
GT	-0.0001 (0.0004)	**-0.0692 (0.0246) ****	0.0004 (0.0006)	-0.00001 (0.00008)
M.	**-0.0018 (0.0007) ***	-0.0329 (0.0511)	**-0.0038 (0.0011) *****	0.00034 (0.00023)
R.	-0.0003 (0.0006)	-0.0236 (0.0382)	-0.0007 (0.0011)	0.00009 (0.00012)
ST	0.0002 (0.0003)	-0.0070 (0.0224)	-0.0001 (0.0005)	0.00009 (0.00005)
WP	-0.0002 (0.0005)	-0.0593 (0.0437)	-0.0007 (0.0007)	0.00004 (0.00015)
WR	0.0001 (0.0008)	0.0320 (0.0347)	-0.0007 (0.0010)	0.00007 (0.00014)
Weighted mean (se) [a]	-0.0002 (0.0002)	-0.0201 (0.0120)	-0.0005 (0.0003)	0.00006 (0.00003)
Specialists				
G.	**-0.0026 (0.0013) ***	0.0695 (0.0661)	-0.0007 (0.0020)	-0.00024 (0.00030)
GS	**-0.0016 (0.0007) ***	-0.0459 (0.0538)	-0.0010 (0.0009)	0.00009 (0.00020)
J.	0.0001 (0.0006)	0.0019 (0.0640)	0.0005 (0.0009)	0.00000 (0.00012)
LS	-0.0003 (0.0010)	0.6137 (0.3496)	-0.0017 (0.0018)	**0.00059 (0.00025) ***
LT	-0.0004 (0.0008)	-0.0518 (0.0469)	0.0003 (0.0010)	-0.00015 (0.00008)
MT	-0.0008 (0.0008)	**-0.1049 (0.0375) ****	-0.0002 (0.0008)	0.00001 (0.00012)
NH	**-0.0010 (0.0003) ****	0.0029 (0.0304)	**-0.0025 (0.0005) *****	0.00043 (0.00023)
TC	-0.0003 (0.0008)	-0.0172 (0.0535)	0.0003 (0.0012)	**-0.00041 (0.00015) ****
WT	-0.0008 (0.0022)	-0.0557 (0.1438)	**0.0089 (0.0045) ***	**-0.00093 (0.00018) *****
Weighted mean (se) [a]	**-0.0008 (0.0002) ****	-0.0160 (0.0231)	-0.0005 (0.0006)	-0.00010 (0.00012)

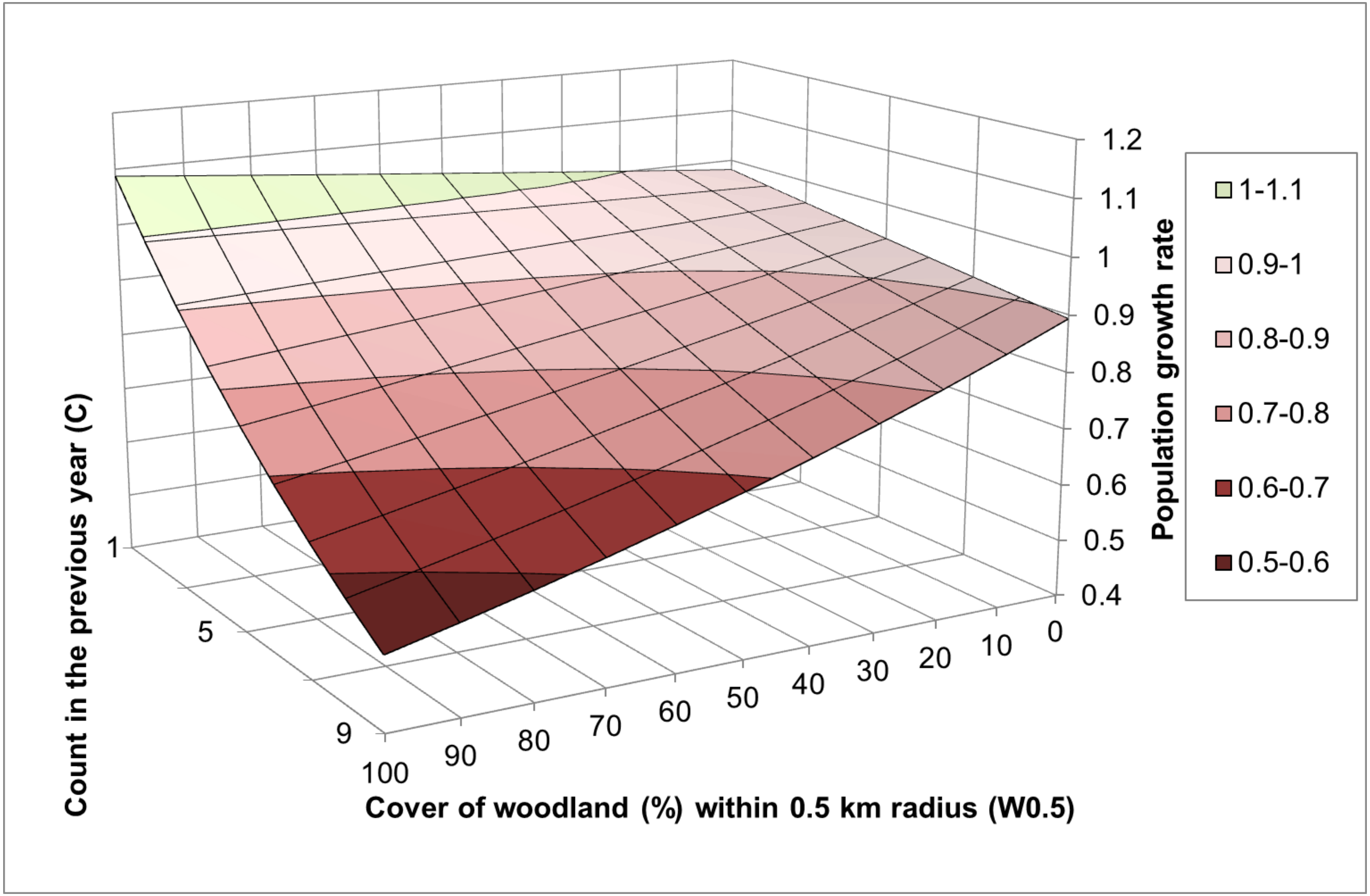
[a] Weighted by 1 / variance

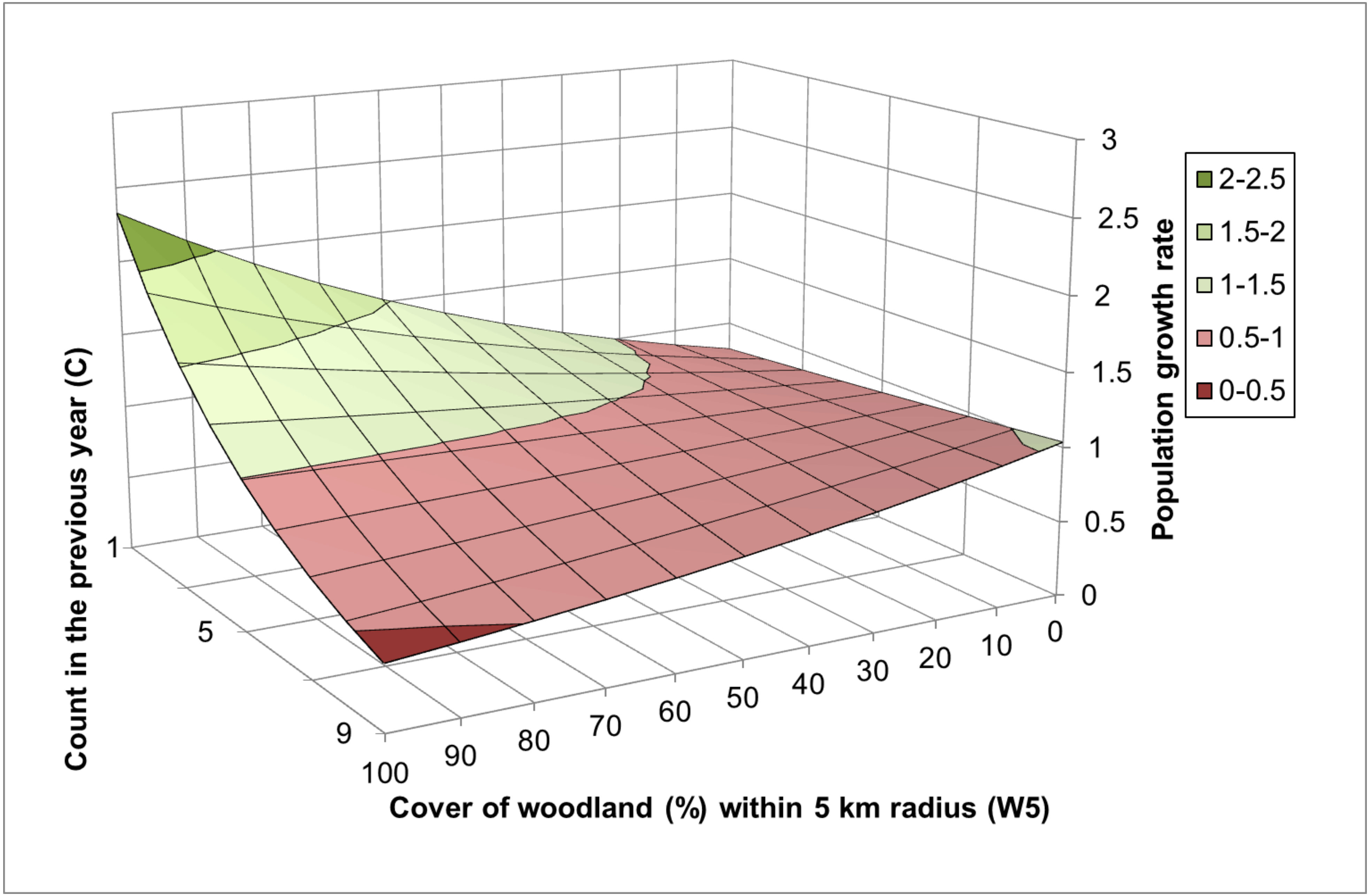
Figure 1. The sensitivity of generalist woodland birds to winter temperature increases with distance between woodland patches. Fitted model based on the parameters in Table 3.

Figure 2. The recovery of specialist woodland birds from small populations is greater at well-wooded sites. Fitted model based on the parameters in Table 4.

Figure 3. The recovery of nuthatch populations from small counts is enhanced in well-wooded landscapes. Fitted model based on the parameters in Table 4.


Population growth rate
1.4
1.3
1.2
1.1
1
0.9
0.8
100
200
300
400
500
600
Mean distance (m) between patches over 5 km radius (D)
3.5
1.5
-0.5
-2.5
-4.5
Minimum temperature (˚C; MIN)
1.3-1.4
1.2-1.3
1.1-1.2
1-1.1
0.9-1


1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
Population growth rate
1-1.1
0.9-1
0.8-0.9
0.7-0.8
0.6-0.7
0.5-0.6
Count in the previous year (C)
1
5
9
100
90
80
70
60
50
40
30
20
10
0
Cover of woodland (%) within 0.5 km radius (W0.5)


3
2.5
2
1.5
1
0.5
0
Population growth rate
2-2.5
1.5-2
1-1.5
0.5-1
0-0.5
Count in the previous year (C)
1
5
9
100
90
80
70
60
50
40
30
20
10
0
Cover of woodland (%) within 5 km radius (W5)