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Changes in the Structure of British Woodland Bird Communities Between the 1980s and 2003-04: An Analysis of Repeat Woodland Bird Survey Data

Authors

C. M. Hewson, R. J. Fuller, A. Amar & K. Smith

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British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU
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Executive Summary

Data on the population changes of birds in British woodland were collected in the Repeat Woodland Bird Survey (RWBS) to confirm the extent and patterns of population changes between the 1980s and 2003-04 (Amar *et al.* 2006). The data consisted of 252 sites surveyed by point counts (‘the RSPB data’) and 92 sites surveyed by territory mapping (‘the BTO data’). Potential causes of population changes were assessed through the collection of data on a number of covariates at each woodland site surveyed and through the collation of data on climate change and landscape structure. The results of RWBS analyses at the level of individual species suggested that habitat changes, possibly brought about by a reduction in the active management of woods and / or increases in deer grazing, were the most likely causes of declines. Against this background, further analyses were carried out looking at cross-species, community level patterns of change. The specific aims of this project were to examine the major axes of community structure and community changes in Britain between the 1980s and 2003-04 using RWBS data and to relate these measures to a set of covariates similar to those used in the RWBS (Amar *et al.* 2006) but expanded to include the effects of winter climate and an expanded set of species with which interspecific interactions (predation and competition) were hypothesised to have caused declines in some species. Part of these analyses included examining spatial patterns of community changes.

Analyses of community structure in 2003-04 across the 344 sites for which data were gathered found that the most important axes for both BTO and RSPB datasets described a gradient of abundance of increasing residents and middle-distance migrants. Abundances of declining species were not generally related to this gradient. For the RSPB dataset, this gradient was contrasted with the abundance of a suite of mostly nationally declining species associated with Scottish birch woods. There were relationships between both habitat and climatic variables and scores on the first axis for both datasets but each appeared most clearly related to the stature of woods, scores being higher in tall woods with big trees and well-developed understorey. Shifts of site scores on these axes that were calculated for individual woods between the 1980s and 2003-04 were more clearly related to climate change, movement towards to the positive end being related to warming of winters. The second most important axis for each dataset contrasted the abundance of increasing species associated with the understorey with those of species associated with old-growth woodlands. For each dataset, this axis was related to both climatic and habitat variables but shifts in site scores between the 1980s and 2003-04 were related only to habitat characteristics, sites moving towards communities expected based on their habitat in 2003-04.

The most important axis of change between the 1980s and 2003-04 for both datasets was one of increasingly positive changes for many widespread and increasing residents but some long-distance migrants were also weakly related to these axes. Site scores on this axis for the BTO dataset were related to few variables, although the results were consistent with climate change having caused population increases that resulted in an expansion into suboptimal habitat. For the RSPB dataset, relationships were mostly with variables that suggested a contrast between woods in the south and east of England and those elsewhere but there was no apparent effect of climate change. The second axis for the BTO dataset contrasted the changes of species associated with understorey with those of species primarily associated with old-growth woodland. Scores on this axis were related to habitat characteristics but not to climate change. For the RSPB dataset, the second axis contrasted the changes of two sets of species not readily assigned to discrete ecological groups, although one group consisted entirely of declining species. These changes were related to climate change and to the abundance of two potential nest predators / competitors. Geographical patterns of change varied between the two datasets and although spatial trends were evident, it was not possible to identify clear clusters of sites undergoing certain types of community change.

Analyses designed to investigate specific hypotheses proposed to explain population declines in woodland birds produced mixed results. In general but not in every case, more evidence came from analyses of the RSPB dataset than the BTO dataset. There was little direct, but some indirect, support for the hypothesis that increased deer grazing had been responsible for population declines. There was

more support for the idea that reductions in active management and the ageing of woods had played a role. Climate change was clearly related to the increases of several groups of species in a manner consistent with their different ecologies. There was also a suggestion that climate change may be indirectly related to the declines of long-distance migrants, probably via interactions with increasing resident species. However, there was little evidence that nest predation and competition between residents and long-distance migrants had been important processes affecting community changes.

It is concluded that both habitat change and climate change have likely been important in determining community shifts thorough population changes of species. Declining residents may have been affected by interspecific interactions but there is little evidence that climate change or habitat change has driven their declines. On the other hand, winter climate appears to be a driver of population increases in several widespread residents. Long-distance migrants may have been affected by habitat change as well as possibly by the indirect effects of winter climate change. However, observed associations between habitat and change in populations of long-distance migrants could arise through preferential occupation of optimal sites by a population reduced by factors operating outside the breeding areas.

2. INTRODUCTION

In recent years, there has been growing concern about declines in woodland bird populations in the UK, reflected in falls in the government's woodland bird indicator (Defra 2005) and the addition of a number of woodland breeding species to the red and amber lists of Birds of Conservation Concern (Gregory *et al.* 2002). The declines sparking these concerns have been detected by the national monitoring schemes but there was uncertainty about how habitat-specific the declines for woodland species were, since the schemes provided trends for all habitats, and whether turnover of sites and regional biases in the Common Birds Census (CBC) had influenced the results. Against this background, the Repeat Woodland Bird Survey (RWBS) was undertaken to provide accurate national, regional and habitat-specific trends for birds in broadleaved and mixed woodland. The population change results of this study area presented in Hewson *et al.* (2007) and Amar *et al.* (2006) provides further details, including an analysis of the covariates of population changes of species in individual woods. According to the RWBS, 8 and 11 species showed large national declines and increases respectively between the 1980s and the 2000s (Amar *et al.* 2006, Hewson *et al.* 2007). The species that declined were primarily long-distance migrants but some more specialised resident birds also declined. As a number of common resident species and middle-distance migrants have also increased, there have clearly been major changes to the structure of bird communities in British woodlands.

In contrast to farmland birds, for which there has been a huge amount of research dedicated to elucidating the causes of widespread declines (Aebischer *et al*. 2000, Vickery *et al*. 2004), there had until recently been very little work evaluating the possible causes of woodland bird declines. In a review of the potential causes of declines in woodland bird populations, Fuller *et al.* (2005) highlighted seven key hypotheses requiring further examination:

(1) Pressures may have acted on **long-distance migrants during winter or on migration**, to reduce survival for example through loss of habitat or climate change.

(2) **Climate change on the breeding grounds** may have affected breeding productivity, possibly through reduction in food or change in timing of food availability.

(3) A general **reduction of invertebrate food supplies** may have occurred on the breeding grounds possibly as a result of diffuse pollution, changes in land-use, climate change.

(4) **Changes in habitat quality and quantity may have occurred at the edges of woods**, or in the landscape adjacent to woods (e.g. hedgerow loss), which has acted to reduce survival or breeding productivity or both.

(5) **Reduction in management of lowland woods** may have resulted in increased shading, loss of open space and reduction of low vegetation causing deterioration of habitat quality.

(6) **Intensified grazing and browsing pressure**, especially by deer, may have resulted in reduction of understorey vegetation causing deterioration of habitat quality.

(7) **Nest predation** may have increased, as populations of corvids, great spotted woodpecker and grey squirrels have increased.

Other potential hypotheses were considered but thought to be unlikely drivers of the majority of population declines were:

(8) Deterioration in tree condition, mainly in terms of crown density, may have reduced food for woodland birds and possibly affected habitat quality in other ways.

(9) Fragmentation and loss of woodland may have caused habitat loss for woodland birds.

(10) The age structure has changed in woodland with a relatively small area of young woodland now compared with 20 years ago which may have resulted in less habitat for several species.

(11) Tree species composition may have changed with consequences for food resources and habitat availability.

(12) Increasing recreational pressure on woodland may have reduced habitat quality for some species.

(13) The increase in road traffic may have resulted in higher bird mortality and reduced habitat quality.

(14) Intensified game management, especially for pheasants, may have reduced habitat quality.

(15) Dead wood may have declined with consequences for habitat quality including nest sites for hole-nesters.

(16) Reduction of lichens may have occurred with loss of foraging sites for some species.

(17) Inter-specific competition may have increased between some species.

(18) Parasites and disease may have become important.

Amar *et al.* (2006) examined the pattern of population change of individual species across woods in the RWBS with respect to data on a number of covariates related to the above hypotheses and concluded that habitat change, perhaps as a result of a reduction in active management of woods and increases in the intensity of deer grazing, was the most likely driver of many of the declines. They could not, however, rule out the possibility that wider-scale factors, such as climate change, had caused a general reduction in populations of species that had in turn resulted in a contraction into the most suitable habitats. It should be stressed that the exact nature of declines may be species-specific and may involve multiple factors. Nevertheless broad habitat change does appear to affect many species (Fuller *et al.* 2007).

A number of potential pieces of further work on the RWBS dataset that could advance understanding of the causes of population changes over what had already been achieved were suggested by Amar *et al.* (2006). Of those suggested, this report examines shifts in woodland bird communities with respect to the hypotheses that have been proposed to explain changes in woodland bird populations. Responses to factors that are not evident on a species-by-species basis may be reflected in more-subtle, over-all changes in bird communities as a result of the common response of a number of species to a particular factor. Examining either over-all community level or multi-species responses to factors of interest may be valuable as it has the potential to overcome the unique ecologies of species and hence their likely individualistic responses to drivers of change.

The **key aims of this work** are to use RWBS data to:

1) Examine the major axes of change in bird communities between the 1980s and 2003-04.

2) Examine both community structure in 2003-04 and also change in community structure between the 1980s and 2003-04 with respect to a set of covariates, based on those used in Amar *et al.* (2006) to examine change in individual species. Here this list of covariates is expanded to include data on winter climate and winter climate change, potential avian nest predators and potential competitors for long-distance migrants.

3) Carry out analyses as above but based on ecological / functional groups of species, selected to give insight into the hypotheses proposed to explain changes in woodland bird populations.

4) Pay particular attention to geographical variation in community structure and community changes through the inclusion of geographical co-ordinates in modelling procedures, the production of maps showing spatial variation of community attributes and the investigation of clustering of sites showing similar community changes.

2. METHODS

2.1 Repeat Woodland Bird Survey Design and Study Sites

Historical data were available for two sets of sites; a sample of sites surveyed by point counts by the RSPB in a single year between 1982 and 1988 and a sample of sites originally covered as part of the Common Bird Census (CBC) during three periods, namely 1965 -1972, 1973 - 1980, and 1981 - 1988. For the purposes of this study, data was used only from those BTO sites for which data was available for the latter period (1981 – 1988), giving two sets of sites for which historical data was available from 1982 – 1988 (RSPB) or 1981 – 1988 (BTO). This historical survey period is referred to as 'the 1980s' within this report. Full details of the site selection procedure can be found in Hewson *et al.* (2007) and Amar *et al. (*2006). Data from a total of 252 RSPB sites and 92 BTO sites were used in this study.

For the re-survey, the RSPB sites were again surveyed mostly in just a single year of the RWBS (2003-04), with around 20% of sites in each region (n=56 in total) being surveyed in both years to provide information on inter-annual variation. Historical data were available for most CBC sites for multiple years within the 1980s, so two were chosen at random. 127 of the 153 CBC sites were re-surveyed in both 2003 and 2004, the remainder being surveyed in one year only. The resurvey consisted of just four visits for territory mapping (rather than the 8-10 visits used historically) and so the census maps for the selected historical years were re-interpreted, using four historical visits from the original 8-10 that most closely matched the periods of the resurvey. This made the numbers of 'territories' comparable with the results of the RWBS. To account for changes in phenology, in particular the fact that laying dates of birds in Britain advanced by an average of 8.8 days between 1971 and 1995 (Crick *et al.* 1997), visits that fell towards the early part of each period were selected whilst those that fell in the last five days were avoided. The four visits were then re-interpreted using the same criteria for assessing territory clusters as used to analyse the data collected during the RWBS.

For the RWBS, sites were classified into regions corresponding to Government Office Regions, with the exception that London was merged with Southeast and Yorkshire was merged with Northeast. For this study, regions were combined to ensure at least 10 sites in each region in the BTO dataset. The number of sites in each region for the BTO and RSPB datasets is given in table 2.1, together with region definitions in terms of Government Office Regions.

Region	RWBS regions incorporated	BTO	RSPB
East	East England, East Midlands	18	32
North	Northeast, Northwest	16	0
Southeast	Southeast	26	34
Southwest	Southwest	20	42
West	West Midlands, Wales	12	85
Scotland	Scotland	0	59

Table 2.1 Regional distribution of sites used in this study. 'Region' refers to the geographical division used in the current study. The second column gives the regions used in Amar *et al.* (2006) that were included in each current region.

2.1.1 Characteristics of the resurvey sites

A detailed examination of the characteristics and representativeness of the sites used in the RWBS is given in Amar *et al.* (2006). All study sites were either broadleaved or mixed woodland sites (sites where at least 20% of trees were broadleaved species). The percentage distribution of sites across regions was very similar to the distribution of broadleaved woodlands according to the National

Inventory of Woodlands and Trees (Forestry Commission 2003). Compared to the size distribution of ancient semi-natural woods in England and Wales given by Spencer and Kirby (1992), the RWBS sites over-sampled woods of > 100 ha and under-sampled those < 20 ha. However, as these discrepancies are based on number of woods falling into each size class rather than the area of woodland contributed by each, it is likely that our sites are in fact a more representative sample of woodland by area than these apparent biases suggests. Secondly, as each of the sites included in the RWBS must have been at the very least 15 years old (due to the interval between the end of the historical survey period and the start of the RWBS) new woodlands would not be included and therefore are not represented in the RWBS sample.

The size distributions of woodland blocks containing resurvey sites were similar for the BTO and the RSPB selections. However, a greater proportion of BTO sites fell in woods < 20 ha and a greater proportion of RSPB sites fell in woods 100 - 500 ha. Woodland blocks containing BTO sites also tended to be surrounded by more human-altered landscapes (e.g. arable / horticultural land, improved grassland, urban / suburban areas) than those containing RSPB sites. Differences in the geographical distributions of the two samples of sites (Table 2.1) meant the RSPB survey sites provided better coverage than the BTO of the ranges of species associated with deciduous oak *Quercus* woodlands in western Britain e.g. Pied Flycatcher *Ficedula hypoleuca*, Common Redstart *Phoenicurus phoenicurus* and Wood Warbler *Phylloscopus sibilatrix*). Therefore the population changes for these species derived from the RSPB data set are likely to be more reliable.

2.2 Bird Surveys

To ensure data collected during the resurvey were directly comparable with the historical data available for each site, survey methods were made as similar as possible to those used in the original surveys. The two resurveys therefore used two different census methods depending on the site – point counts in the case of the RSPB sites and four-visit mapping censuses in the case of the BTO surveys.

For the RSPB surveys, a random number table was used to select points based on their grid reference within the area sampled by the original surveys, with no point being closer than 50m to the edge of the wood and no two points being closer than 100m of each other. Points were marked on a map, located in the field using a GPS and then marked with flagging tape during a reconnaissance visit, to allow easy relocation. In most cases, 10 points were surveyed per site but there was some variation between sites and survey episodes. Two visits were made to each point, one in April or the first week of May and another in the last three weeks of May or first half of June. The timing of the two visits roughly corresponded with the historical survey but, where possible, was up to one week earlier to account for changes in phenology (Crick *et al.* 1997, Crick & Sparks 1999) since the 1980s. All bird counts were carried out in the morning, starting within one hour of dawn and were completed by midday. Counts were not made in heavy rain or in strong or cold winds. The order in which the points were visited was reversed for the second visit. On arrival at the point, observers waited five minutes then started counting all individuals seen or heard for five minutes. Birds were recorded in two distance categories although the distance bands are not used in the analyses presented here. Counts in visit 1 and visit 2 are treated separately in the analyses.

For the BTO surveys, observers carried out a reconnaissance visit during which they familiarised themselves with the site using a map showing its boundaries on which they marked prominent features using a GPS. This facilitated orientation during the bird surveys. The same territory mapping methods were used as for the original CBC surveys (Marchant 1983) except that four visits were made to each site rather than 8-10. The visits were spread between late March / early April and early June; visit one was made by 16 April, visit two by 8 May, visit three by 29 May and visit four by 15 June in each year. Criteria modified from those given by Marchant *et al.* (1983) were used for interpreting the census maps based on four rather than 8 - 10 visits. Full details of the criteria used can be found in Amar *et al.* (2006).

Note that we use the word ‘territories’ in this report to signify the clusters of registrations identified during map interpretation. These clusters are interpretations influenced by the criteria applied and the application of these criteria by the map analyst, as well as by the degree of survey effort applied. They are therefore ‘pseudo-territories’ that give an index of abundance for each species at each site rather than an absolute value of the number of territories present. A sole analyst carried out virtually all of the map interpretation for the project (both historical and resurvey maps) and applied consistent criteria throughout, so our data are internally consistent, making comparisons within the dataset robust.

2.3 Woodland Characteristics

To allow us to assess the possible causes of the major axes of variation in abundance in 2003-04 and change in abundance between the 1980s and 2003-04 across the study sites, data were collated on a number of potential covariates. These data fall into the following groups: habitat (including data on deer impacts); landscape structure; physical characteristics of woods; predator abundance and climate data. Details for each group are given below.

2.3.1 Habitat data

Habitat recording was undertaken at each point count station at RSPB survey sites. At BTO survey sites, it was done at up to 10 randomly chosen points within each site, with no point being allowed to be less than 50m from the edge of the wood and no two points being permitted within 100m of each other.

Each habitat survey location formed the centre of a 25m radius area in which habitat recording took place. Some measurements were recorded from the centre of the 25m plot, whilst others were recorded in four 5m radius subplots centred 12.5m north, east, south and west of the centre of the plot.

Prior to analysis, we took the mean of the four subplot measures at each habitat plot and then the mean of these 10 habitat plot measures was then taken to give a single summary score for each site. For plot level information, a mean across the 10 plot scores was taken.

2.3.1.1 Plot level information

From the centre of each point the following were recorded to best represent the area within the 25m plot:

Drainage	(None or presence/absence of: Stream <1m across, Stream 1-5m across, Stream >5m across, Bog, Flush, Pond)
Tracks	(None, Single, Double i.e. sufficient for a vehicle)
Trees	1) Basal area based on the number of stems of each tree species that scored according to a standardised relascope when viewed from the centre of the plot (Hamilton, 1975) 2) Presence of any woody species occurring in the plot but with no stems counting on the relascope measure. 3) Maximum diameter at breast height (dbh) of trees within the plot 4) Count of dead trees. 5) Maximum tree height.

2.3.1.2 Subplot level information

At each of the four subplots the following was recorded:

1) Horizontal Visibility: A 2.4m pole marked with alternate black and orange dm sections was placed in the centre of plot and viewed from the centre of each subplot. The number of orange bands that were at least 50% visible through the vegetation (maximum 12) was recorded. This method is described in detail in Wilson *et al*. (2005).

2) Canopy Cover: The number of 2 cm squares in a 4 x 4 wire grid that were at least 50% covered by canopy level foliage when viewed directly from below (maximum 16). The grid was held horizontally 60cm above the observer, on the end of a marked stick fitted with a plumb line. Canopy was defined as foliage at least 10m high so vegetation below that height was ignored.

3) Percentage Vegetation Cover in height classes (0.5 - 2m, 2 - 4m and 4 - 10m): Total cover by vegetation of the 5m subplot as if viewed from above, considering only the vegetation in each height band in turn.

4) Coppice height: Height of stools where appropriate.

5) Field layer cover: Percentage cover of each of the following: bramble, bracken, heather, bilberry, herb, grass, moss, leaf litter, rock, bare ground and ‘other’. Cover of each within 0.5m of the ground across the 5m subplot was recorded, with cover adding up to at least 100%.

6) Number of dead limbs > 20cm diameter (dead limbs still attached to trees at any height above the subplot)

7) Ground wood (number of pieces of dead wood on ground over 10cm diameter and 1m in length)

8) Lichen (none, present, frequent)

9) Stool count (number of coppice stools where applicable)

10) Burned (% of ground affected by burning)

11) Regenerating (tick if subplot regenerating from burning)

12) Nest boxes (count within the subplot)

13) Presence of shrub species (shrubs under 5m high only)

14) Deer slots (presence / absence)

15) Deer pellets (none, one group of pellets, more than one group of pellets)

16) Browse line (none obvious, present but not very clear, very obvious)

17) Height of browse line (estimated to nearest 0.5m)

18) Browsed bramble (no bramble present, no browsing, light browsing, heavy browsing)

19) Browsed stems (for non-bramble woody stems < 2m high: none present, no browsing, light browsing, heavy browsing)

20) Frayed stems (presence or absence of frayed stems for stems < 5m high)

For measures 16 - 19, observers noted when they suspected that browsing may have been due to domestic livestock rather than deer.

The dominant tree species for each site was obtained by calculating the proportion of the total number trees counted by the relascope at each habitat plot that was contributed by each species, then by taking the average of these 10 proportions and assigning the species with the highest mean value as the dominant. Relascope data were also used to assess basal area. An index of shrub diversity for each site was calculated by dividing the total number of shrub species recorded at any location within a site by the total number of shrub species recorded at all RWBS sites (36 species).

2.3.1.3 Deer trackway survey

Deer trackway counts were used to give an index of the presence and activity of deer. Systematic counts of deer trackways have been shown to be a potentially useful measure of deer presence in extensive surveys of woods (Mayle *et al*. 2000). At each site, trackways were counted along transects totalling at least 1000m where possible, which were made up of external edges, or internal rides/paths, or a mixture of both. The ideal would be to count 500m of external edge and 500m of internal ride. Where there was not sufficient length of suitable edges or rides/paths within the census plot itself, supplementary trackway counts were made in other woodland in the general area surrounding the survey plot. Rides/paths that were within 30m of the external woodland edge were not counted, nor were external edges or rides / paths where a deer-proof fence ran along the edge. Trackway counts were not made when snow obscured the ground. The number of trackways was recorded separately for different sections of edges and rides/paths along with the length of that section so that a density of trackways could be calculated.

2.3.2 Predator abundance

2.3.2.1 Grey squirrel abundance

At each site, fixed transects were established through the area of the wood surveyed by birds. Where possible the transect had a continuous length of 1000m but, if the shape or size of the wood dictated, a number of smaller transects totalling 1000m and not closer than 100m from each other if parallel, were established. The transect was divided into 100m sections and a code number assigned to each section.

Squirrel drey surveys were undertaken during March and April in 2003 and 2004 with each site being surveyed up to three times. Where multiple surveys were completed, the maximum score is used in the analyses. Transects were walked slowly, recording all active dreys visible from each 100m section separately. A drey was classified as active if it was >30cm in diameter and no light was visible through it. For each drey sighting, the perpendicular distance from the transect to the drey was measured using a laser rangefinder. Squirrel drey density estimates were computed using the software DISTANCE – full details can be found in Amar *et al.* (2006).

2.3.2.2 Avian nest predator abundance

For RSPB sites, great spotted woodpecker and jay abundance were taken as the maximum mean number of birds recorded per point during the 2003-04 surveys (calculated as in section 2.4.1). For BTO sites, jay abundance was taken as the maximum number of ‘territories’ and partial ‘territories’ recorded during 2003-04 (section 2.4.1). Great spotted woodpecker density at BTO sites was the maximum number of great spotted woodpecker ‘territories’ recorded during 2003-04 transformed using a regression equation derived from 18 woodland sites in England that were surveyed in 2002 using both the RSPB’s point count survey method (maximum from 2 visits) and the BTO territory mapping (Amar *et al.* in prep). This was done to make the counts from both sets of sites directly equivalent, as it was originally hoped to integrate both into a single analysis.

2.3.3 Landscape structure

The habitat composition around each site was assessed using Land Cover Map 2000 (LCM 2000) within Arc GIS version 9 to calculate the percentage composition of all habitat classes within circles of 3 km radius centred on the centre of each site. Full details are given in Amar *et al.* 2006. Individual variables were grouped into 8 broader categories – broadleaved woodland, coniferous woodland, dwarf shrub heath, improved grass, other grass, arable and horticultural, urban/suburban and water inland. These data were then used in a Principal Components Analysis (PCA) to extract the main axes of variation in landscape composition (see table 2.3).

2.3.4 Climate data

Climate data for the 5km square containing each of the study sites were obtained from the UKCIP web-site (**http://www.metoffice.gov.uk/research/hadleycentre/obsdata/ukcip/index.html**). Data were divided into spring climate and winter climate categories. For spring climate, we extracted the mean monthly temperature, amount of rainfall and number of days with rain (where rainfall >=1mm) for April and May between 1980 and 1999. These spring months were chosen as they were considered likely to have the greatest direct effect on bird populations, as they were the months over which most woodland birds would be nesting and / or in the case of migratory species, selecting breeding sites. For winter climate, the maximum and minimum temperatures and amount of rainfall was extracted for January, February and March of each year between 1980 and 2004. These months were chosen as they were considered those that were mostly likely to affect bird populations, as they are the coldest months, as food is scarce during late winter and as many resident birds begin breeding at this time and middle-distance migrants arrive on the breeding grounds towards the end of this period.

Measures of spring weather were calculated by taking the mean between 1996 and 1999 for each 5 km square. Measures of winter climate were calculated by taking the mean between 2001 and 2004 for each 5 km square. These were the last four years for which data were available for each set of parameters at the time that these measures were calculated. Measures of change for each climate parameter were calculated by regressing the values against year, with 1980 being year 1 in each case, and using the coefficient obtained (Kirby *et al.* 2005). The predominant direction of change across all 5 km squares for each parameter is given is table 2.1. In most cases, changes were of the same direction in all or nearly all squares.

Winter climate change		**Spring climate change**	
Variable	**Direction of trend**	**Variable**	**Direction of trend**
ChJan_maxt	+	ChApr_temp	+
ChFeb_maxt	+	ChMay_temp	+
ChMar_maxt	+	ChApr_cmRain	+
ChJan_mint	+	ChMay_cmRain	(-)
ChFeb_mint	+	ChgApr_Raindays	+
ChMar_mint	+	ChgMay_Raindays	-
ChJan_cmRain			
ChFeb_cmRain			
ChMar_cmRain			

Table 2.2 Direction of trends of climate change. Derived from regression coefficients of each variable against year. In most cases, changes were in the same direction across all sites – change signs in brackets indicate the direction of the average trend where there was variation between sites. See table 2.4 for definition of variables.

2.3.5 Change in density of potential competitor species

In order to assess the likelihood of competitive effects having contributed to the declines of long-distance migrants, measures of the population change of increasing species considered to be potential competitors were calculated for individual sites. These changes were calculated as in section 2.4.1 and were used as independent factors in analyses of scores from PCAs of population change. Resident gleaners selected were blue tit, great tit and chaffinch. Middle-distance migrants selected were blackcap and chiffchaff. When calculating change in combined densities of middle-distance migrant and resident foliage gleaners, the abundance of all relevant species was summed before calculating change.

2.3.6 Summary variables

In order to create variables that summarised the variance in several logical groups of the covariates collected, PCAs were carried out. Table 2.3 shows the loadings of variables on the PCA axes created, together with the amount of variance explained by each.

Table 2.3 Loadings for six principal components analysis of four aspects of woodland habitat structure (field layer, under-storey, tree structure, deadwood and deer impacts) and one large-scale component (landscape composition) for the RWBS sites. The loading of each variable on each component is shown and all loadings >0.3 are shown in bold. For each analysis, an explanation of what each axis describes is also given. (Adapted from Smart *et al. in prep*)

PCA	Variables included	Axis 1 score	Axis 2 score
Field layer	Bracken	**-0.40**	-0.26
	Bramble	**+0.34**	-0.03
	Herb	+0.16	**+0.63**
	Grass	**-0.53**	+0.10
	Moss	**-0.45**	+0.06
	Leaf litter	**+0.40**	**-0.56**
	Bare ground	+0.25	**+0.45**
	Variation explained	33%	17%
Axis 1 explanation	High grass, moss and bracken (birch) from those with high leaf litter and bramble (other woods)		
Axis 2 explanation	High herb and bare ground (ash) from high leaf litter (beech).		
Under-storey	Cover 05-2m	**-0.52**	+0.24
	Cover 2-4m	**-0.60**	-0.17
	Cover 4-10m	**-0.46**	**-0.66**
	Horizontal viz	**+0.40**	**-0.70**
	Variation explained	56%	23%
Axis 1 explanation	Gradient from an open to closed low under-storey.		
Axis 2 explanation	Gradient - open low and closed high under-storey to a closed low and open high under-storey.		
Tree structure	Canopy cover	**-0.54**	**-0.31**
	Basal area	**-0.44**	**-0.63**
	DBH	**-0.45**	**+0.67**
	Max Height	**-0.57**	+0.26
	Variation explained	54%	22%
Axis 1 explanation	Woods with tall trees and closed canopy from woods with small trees and open canopy.		
Axis 2 explanation	Woods with many young trees (high basal and low DBH) from those with few, old trees.		
Deadwood	Dead trees	**-0.43**	**+0.89**
	Dead limbs	**-0.62**	**-0.40**
	Ground wood	**-0.65**	-0.21
	Variation explained	48%	30%
Axis 1 explanation	Woods with trees with many dead limbs and dead ground wood to those with little deadwood.		
Axis 2 explanation	Woods with many dead trees to those with few dead trees.		

PCA	Variables included	Axis 1 score	Axis 2 score
Deer impacts	Slots	**0.41**	-0.01
	Pellets	**0.48**	-0.21
	Browse line presence	**0.60**	-0.27
	Browse line height	**0.58**	**-0.31**
	Browsed bramble	**0.35**	**0.92**
	Browsed non-bramble stems	**0.97**	-0.08
	Frayed stems	**0.36**	0.10
	Variation explained	48%	30%
Axis 1 explanation	Woods with few signs of deer impacts to woods with greater prevalence of all impacts, especially browsed stems, with a high and well-developed browse line.		
Axis 2 explanation	Woods with little browsed bramble to woods with much browsed bramble but few other signs of deer impacts.		
Landscape	Broadleaved woodland	-0.00	**-0.72**
	Improved grass	**+0.33**	+0.17
	Arable/horticultural	**+0.46**	+0.08
	Coniferous woodland	**-0.42**	**-0.42**
	Other grass	**-0.32**	**+0.46**
	Urban/suburban	+0.25	-0.10
	Dwarf shrub heath	**-0.51**	+0.07
	Inland water	-0.29	+0.24
	Variation explained	28%	17%
Axis 1 explanation	Woods set in an agriculture landscape to those set in a more natural landscape.		
Axis 2 explanation	Woods set in a wooded landscape to those in a less wooded, grassier landscape.		

Table 2.3 Continued**.**

2.4 Statistical Methods

2.4.1 Data methods

The use of a simplified, binary measure of population change for individual species in Amar *et al* (2006) allowed data from BTO and RSPB sites to be combined into a single analysis examining the relationship of population changes of individual species to a set of covariates. In the present study, it was necessary to use quantitative rather than qualitative information on bird abundance and population change to examine community structure and changes in community structure. This meant that separate analyses had to be carried out for each data set due to differences in the survey methods and hence measures of abundance between BTO and RSPB sites. To derive estimates of abundance in the 1980s and 2003-04, maximum counts during each period were taken for each species at each site. For the RSPB sites, the maximum count per point during any visit or year was taken. For the BTO sites, the maximum count of ‘territories’ or ‘partial territories’ per hectare during any year was taken. Measures of population change at each site were calculated by dividing the maximum count in 2003-04 by the sum of the maximum counts in 2003-04 and in the 1980s. This gave a value between 0 and 1, this being 0 where a species went extinct between the two survey periods, 1 where it invaded a site between the two periods and 0.5 where the population remained stable.

2.4.2 Principle Components Analysis

Two possible approaches to examining relationships between bird community data and environmental variables are 1) the use of unconstrained ordination (such as PCA or DCA) followed by relating the axes produced to the environmental variables and 2) the use of constrained ordination (such as RDA or CCA), in which the ordination of species data is undertaken directly with respect to their relationship to the environmental data. Constrained ordination finds the major axes in a multivariate dataset that are related to the environmental variables, whereas unconstrained ordination finds the major axes in the multivariate dataset independently of the explanatory variables, and these independent axes are then related to the environmental data to test hypotheses. The former approach is used in this study as results of constrained ordination can be difficult to interpret with respect to specific hypotheses.

Principal components analysis was carried out using the package CANOCO to extract the key axes of variation in abundance and change in abundance across sites. Scores on these axes for each site were used as dependent variables in the modelling procedure described below. In each case, data were analysed using the option to centre and standardise scores for each species. This is equivalent to using a correlation rather than a covariance matrix, as the scores of abundance or change in abundance for each species are set to have a mean of zero and a variance of 1. Using this option means that species with a greater variance in their scores do not dominate the axes.

Site scores from PCAs were used as dependent variables in statistical analyses (see below). Three initial sets of analyses were conducted using: a) abundance of all species in 2003-04, b) shifts between the 1980s and 2003-04 in the space defined by the first two axes of the PCA of abundance in 2003-04 as dependent variables and c) change in abundance of all species between the 1980s 2003-04. It was not possible to directly analyse abundance in the 1980s in relation to environmental factors as no covariate data was available for the 1980s for BTO sites and only a subset of variables was available for the RSPB sites. In addition PCAs were also carried out to extract the key axes of variation in the change in abundance of groups of species defined by their relevance to the key hypotheses explaining population declines in woodland birds. This approach is effectively intermediate between relating species-level change to environmental covariates (as in Amar *et al.* 2006) and looking at change across all species (as in the analyses described above). The species level approach may be limited as multiple characteristics of species may influence their population changes and thus the response of any one species to a particular driver may not be clear. The whole-community level approach is limited as PCAs across all species may not distil the variation in the species most likely to respond to the drivers responsible for each hypothesis, since the strongest statistical gradients across all species are unearthed (Lepš & Šmilauer 2003). By choosing groups of species predicted to be affected by certain processes in certain ways, it may be possible to detect relationships between changes in their abundance and explanatory variables.

One difficulty in using PCA axis scores of bird abundance as dependent variables lies in interpreting what gradient, if any, in species composition the axis represents. To facilitate this, at the beginning of each section the ecological meaning of the dependent variable axis is interpreted as far as is possible based on the species' loadings. The loadings of each species on an axis represent the slope of a linear regression of its abundance or change scores along that axis (Jongman *et al.* 1985). For the purposes of this study, any loading less than +/- 0.3 is not considered an important loading and is not discussed in the axis interpretation. Loadings of +/- 0.3 – 0.4 are discussed as weak associations, those of +/- 0.4 – 0.6 as moderate associations and those > +/- 0.6 as strong associations. In the interpretation of an axis, greater weight is placed on stronger loadings.

PCA can be viewed as a simultaneous regression of all variables (in this case species abundance / change in abundance scores) across a set of sites (Jongman *et al.* 1995). The solution for each axis is the combination of individual site scores that minimises the summed deviance when all variables are regressed against this axis. As PCA is a linear technique, strictly speaking only linear explanatory variables should be modelled against the scores from PCA axes. This could be a problem in this study as the measure of population change used is not a completely linear measure, as values are constrained at either end of the scale (at values of 0 and 1). Importantly, however, this measure is monotonic, i.e. the direction of change is constant across the range of values even though the rate of change is not. Also, it is approximately linear over most of its range, specifically the central part where most values lie. Because of this, there is only a minimal chance of type I, and no chance of type III, errors occurring because of the non-linearity of the change measure (S. Freeman pers. comm.).

In addition to using the PCA of change scores to investigate patterns of change across all species, shifts between the 1980s and 2003-04 in the multivariate space described by the first two axes of the PCA of abundance in 2003-04 were calculated. This was to allow us to examine change in bird communities independently of the method used to calculate change scores for species (section 2.4.1). This analysis effectively examines changes in bird communities as if the underlying axes were the same in the 1980s and 2003-04, although of course this is not the case if changes have occurred so there are limitations to the approach. Shifts were calculated by applying the species loadings derived from the PCA of 2003-04 abundance data to the data for abundance at the sites during the 1980s to create a new set of site scores. The shift in site scores on each axis was then calculated by subtracting the site score derived from abundance in the 1980s from the site score derived from abundance in 2003-04. The calculation of these shifts was one important reason for examining community structure in 2003-04. However, some species were not counted in all regions during the 1980s RSPB surveys. Therefore for this dataset only those species for which data was available for all regions in both the 1980s and 2003-04 were included in analysis of community structure in 2003-04 even though all species had been counted during the later set of surveys.

2.4.3 Species groupings for dependent variables

The species included in the PCAs used to create dependent variables relevant to each hypothesis, together with the rationales for the inclusion of species, are shown below. Only declining species were selected for inclusion (defining a declining species as one which showed a negative population change between the 1980s and 2003-04 in the RWBS according to either the BTO or RSPB datasets) except in some analyses relating to climate change, where increasing species were also included to ascertain whether they may be responding to climate. Results are discussed with respect to conditions under which the predominant direction of change for species included in each dependent variable is likely to occur. In addition to the rationale stated below, results from section 3.4 of Amar *et al.* (2006) were used to identify species that may have been affected by a reduction in active management. In practice, this was only applied to the inclusion of pied flycatcher and willow tit. It could be argued that the use of results from Amar *et al.* (2006) in species-selection introduces some circularity into the analytic process. However, in this instance it was felt that the inclusion of these species was justified as it was important to include as wide a range of species as possible given the complexity of the potential changes to woodland brought about by a reduction of management. The first two axes of each PCA were used as dependent variables, although only the first was used where the amount (%) of variance explained by the second axis was less than 100 / number species include.

Hypothesis One: *Declines of some species are driven by increased deer browsing.*

Reasoning: Species nesting and / or foraging preferentially in dense vegetation below 2 metres (such as brambles) are most likely to be negatively impacted by excessive deer browsing / grazing (Fuller 2001, Gill & Fuller 2007).

Species included: bullfinch, dunnock, garden warbler, willow warbler.

Hypothesis Two: *Changes in woodland management have driven declines.*

Reasoning: Changes in woodland management (including ageing of stands) may have caused increases in canopy cover, maximum DBH of trees, basal area and cover in the upper understorey and decreases in vegetation below 2 metres. Species for which these changes may have reduced habitat quality are included.

Species included: bullfinch, dunnock, garden warbler, willow warbler, willow tit and pied flycatcher.

<u>Hypothesis Three:</u> *Climate change is responsible for observed population changes (increases and decreases).*

Reasoning: Different species respond to climate change in different ways according to their ecology (Greenwood & Baillie 1991, Leech & Crick 2007). Increasing and decreasing species may respond to climate change in different ways. For this reason, species were placed in a number of groups in the following way: A) Long-distance migrants may be particularly adversely affected by climate change on the breeding grounds, due to temporal mismatching of seasonally available resources (Both *et al.* 2006) and interactions with resident species (Herrera 1978) B) Resident foliage gleaners may respond differently than migrants to spring rainfall (Leech & Crick *in prep.*) and may be positively affected by ameliorating winter conditions (Greenwood & Baillie 1991). C) It is unclear whether middle-distance migrants should respond like residents or long-distance migrants so they are included as a separate group. D) Thrushes may respond positively to increases in spring rainfall and winter temperatures as these parameters affect the availability of soil invertebrates and thus survival and productivity (Leech & Crick 2007 and references therein). E) Small insectivorous passerines may be vulnerable to low winter temperatures and particularly snow cover (Greenwood & Baillie 1991, Marchant *et al.* 1990).

Species included:

group A Resident foliage gleaners (blue, great, coal and long-tailed tits, chaffinch, goldcrest, nuthatch)
group B Middle-distance migrants (blackcap, chiffchaff)
group C Long distance migrants (garden warbler, pied flycatcher, redstart, spotted flycatcher, tree pipit, willow warbler, wood warbler)
group D Thrushes (blackbird, song thrush, mistle thrush)
group E Small insectivorous residents (dunnock, goldcrest, long-tailed tit, robin, wren,)

<u>Hypothesis Four:</u> *Increased levels of predation have been responsible for population declines.*

Reasoning: Open-nesting species (especially canopy-nesters) are generally considered to be most vulnerable to grey squirrel and jay predation. Hole nesting species may be most vulnerable to great spotted woodpeckers.

Hole-nesters: marsh tit, willow tit, pied flycatcher, lesser spotted woodpecker.

Open-nesters: chaffinch, hawfinch, mistle thrush, willow warbler, wood warbler, garden warbler, dunnock.

<u>Hypothesis Five:</u> *Competition between resident and migratory species has been responsible for their declines.*

Reasoning: Long-distance migrant foliage-gleaners are the species most likely to suffer from competition with their resident equivalents (O'Connor 1981 & 1985). See section 2.3.5 for competitor species selected.

Long-distance migrant foliage gleaners: willow warbler, wood warbler, garden warbler, redstart, pied flycatcher.

2.4.3 Modelling of covariate effects

Modelling of measures of community composition was carried out using General Linear Mixed Models (GLMMs). The site scores for one PCA axis comprised the dependent variable in each case (as described in section 2.4.2) and one environmental covariate acted as the independent in each case, with Region included as a random factor. Region was not included in models for latitude and longitude due to the systematic variation of these variables across space. However, the inclusion of region as a random factor in models examining the effects of climatic variables, for instance, allows us to estimate the effects of these variables whilst taking into account both their gross geographical variation and the spatial autocorrelation between sites in each region.

It was not possible to relate changes in bird communities to changes in woodland characteristics as covariate data was not available for the 1980s, except for a subset of habitat variables for RSPB sites and climate data for all sites. Instead, changes in bird communities are modelled with respect to data on environmental conditions collected in 2003-04 with the exception of independent variables relating to changes in the abundance of potential competitors and climate change. Results are shown for each variable that could be validly modelled against the dependent. Models were excluded when the independent variable was partially dependent on the dependent – i.e. a PCA axis representing a community measure including a certain species could not be modelled against an independent variable including a measure of that species' abundance. Specifically this means that great spotted woodpecker density could not be measured against axes including all species for the BTO dataset, for instance. Measures of climate during 1996 –1999 (spring) or 2001-2004 (winter) were used for modelling community structure in 2003-04 but measures of climate change were used to model all PCAs of species change values or shifts in PCA scores between the 1980s and 2003-04.

For analyses of PCA axes of abundance of all species or change in abundance for all species, all effects significant at P< 0.05 are discussed in full. For analyses of PCA axes of change in abundance of subsets of species relevant to specific hypotheses (section 2.4.3), only effects of variables relevant to the hypothesis that the dependent variable PCA was carried out for are discussed in full and others are summarised (but are given in full in tables). A full list of the independent variables used in the analyses, together with the abbreviations for them used in the tables, is given in table 2.4.

Table 2.4 List of all independent variables used during analyses. 'Name' gives the name or abbreviation used for the variable in tables within this report. 'Definition' defines the variable.

Name	Definition
Latitude	easting, British National Grid
Longitude	northing, British National Grid
Field Layer	(see section 2.3.1.2 for details of each measurement)
Bracken	% cover of bracken
Bramble	% cover of bramble
Herb	% cover of herb
Grass	% cover of grass
Moss	% cover of moss
LeafLitter	% cover of leaf litter
BareGround	% cover of bare ground
p1flayer	scores on field layer PCA axis 1 (table 2.3)
p2flayer	scores on field layer PCA axis 2 (table 2.3)
Woodland Structure	(see section 2.3.1.2 for details of each measurement unless stated)
Cover05_2	% vegetation cover between 0.5 and 2 metres
Cover2_4	% vegetation cover between 2 and 4 metres
Cover4_10	% vegetation cover between 4 and 10 metres
Horizivisibility	horizontal visibility
understpc1	scores on understorey PCA axis 1 (table 2.3)
understpc2	scores on understorey PCA axis 2 (table 2.3)
CanopyCov	canopy cover

Name	Definition
BasalArea	basal area (section 2.3.1.1)
MaxDBH	maximum DBH (section 2.3.1.1)
MaxHeight	maximum tree height (section 2.3.1.1)
treestructurepc1	tree structure PCA axis 1 (table 2.3)
treestructurepc2	tree structure PCA axis 1 (table 2.3)
Dominantsp	dominant tree species
Tree condition	(see section 2.3.1.2 for details of each measurement unless stated)
Lichen	presence of lichen
Ivy	presence of ivy
ShrubDiversity	shrub diversity
DeadTree	count of dead trees (section 2.3.1.1)
DeadLimbs	count of dead tree limbs
GroundWood	count of ground wood
deadwoodpc1	scores on dead wood PCA axis 1 (table 2.3)
deadwoodpc2	scores on dead wood PCA axis 2 (table 2.3)
Deer impacts	
Trackwaysper100m	deer trackways per 100m (section 2.3.1.3)
DeerPCAAxis1	scores on deer impact PCA axis 1 (table 2.3)
DeerPCAAxis2	scores on deer impact PCA axis 1 (table 2.3)
Landscape group	
threekmHabPCA1	scores on 3 km landscape PCA axis 1 (section 2.3.3)
threekmHabPCA2	scores on 3 km landscape PCA axis 2 (section 2.3.3)
Physical features	
Drainage	presence of drainage features (section 2.3.1.1)
Altitude	metres above sea-level of centre of plot
Contigarea	area of contiguous woodland block that plot is embedded within
Tracks	presence of tracks (section 2.3.1.1)
Spring climate	(see section 2.3.4 for details of each measurement)
AprTemp	mean daily temp for April averaged between 1996 - 1999
MayTemp	mean daily temp for May averaged between 1996 - 1999
AprRainfall	cms of rainfall in April averaged between 1996 - 1999
MayRainfall	cms of rainfall in May averaged between 1996 - 1999
AprRaindays	number of days with rain in April averaged between 1996 - 1999
MayRaindays	number of days in May averaged between 1996 - 1999
Winter climate (see section 2.3.4 for details of each measurement)	
Jan_minT	average daily min temp for Jan 1980 - 2004
Jan_maxT	average daily max temp Jan 1980 - 2004
Jan_cmRain	average number of cm of rain in Jan 1980 - 2004

Name	Definition
Feb_minT	average daily min temp for Feb 1980 - 2004
Feb_maxT	average daily max temp Feb 1980 - 2004
Feb_cmRain	average number of cm of rain in Feb 1980 - 2004
Mar_minT	average daily min temp for Mar 1980 - 2004
Mar_maxT	average daily max temp Mar 1980 - 2004
Mar_cmRain	average number of cm of rain in Mar 1980 - 2004
Spring climate change (see section 2.3.4 for details of each measurement)	
ChgAprTemp	change in mean daily temp for April averaged between 1996 - 1999
ChgMayTemp	change in mean daily temp for May averaged between 1996 - 1999
ChgAprRainfall	change in cms of rainfall in April averaged between 1996 - 1999
ChgMayRainfall	change in cms of rainfall in May averaged between 1996 - 1999
ChgAprRaindays	change in number of days with rain in April averaged between 1996 - 1999
ChgMayRaindays	change in number of days in May averaged between 1996 - 1999
Winter climate change (see section 2.3.4 for details of each measurement)	
ChJan_minT	Change in average daily min temp for Jan 1980 - 2004
ChJan_maxT	Change in average daily max temp Jan 1980 - 2004
ChJan_cmRain	Change in the number of cm of rain in Jan 1980 - 2004
ChFeb_minT	Change in average daily min temp for Feb 1980 - 2004
ChFeb_maxT	Change in average daily max temp Feb 1980 - 2004
ChFeb_cmRain	Change in the number of cm of rain in Feb 1980 - 2004
ChMar_minT	Change in average daily min temp for Mar 1980 - 2004
ChMar_maxT	Change in average daily max temp Mar 1980 - 2004
ChMar_cmRain	Change in the number of cm of rain in Mar 1980 - 2004
Predation	
DreyDensity	Density of squirrel dreys (section 2.3.2.1)
CalGRSWO	Change in great spotted woodpecker density (section 2.3.2.2)
JAY	Change in jay density (section 2.3.2.2)
Competition	
BTch	Change in blue tit density (section 2.3.5)
GTch	Change in great tit density (section 2.3.5)
CHch	Change in chaffinch density (section 2.3.5)
CCch	Change in chiffchaff density (section 2.3.5)
BCch	Change in blackcap density (section 2.3.5)
resFGch	Change in the density of the above 3 resident foliage gleaners (section 2.3.5)
MDMFGch	Change in the density of above 2 middle-distance migrant foliage gleaners (section 2.3.5)
ResMDMFGch	Change in the density of resident and middle-distance migrant foliage gleaners (section 2.3.5)

Table 2.4 Continued.

3. FULL RESULTS

The results presented in this section are complex and so in places can be difficult to follow. A brief single paragraph capsule is therefore included at the start of each section outlining the results obtained in broad terms before subsequent detailed presentation of the results.

3.1 Community Structure During 2003/04

The amount of variation accounted for by first two axes of the PCA of 2003/04 data was 23.1% and 10.5% for the BTO dataset and 19.5% and 10.9% for the RSPB dataset, comprising data on the abundance of 35 and 29 species respectively. Loadings for the first two axes of PCA of abundance in 2003-04 for the RSPB and BTO datasets are summarised in tables 3.1 & 3.4 and are given in full in Appendix 1. The relationships between explanatory variables and the site scores on these axes are summarised in tables 3.2 & 3.5 and shown in full in tables 3.3 and 3.6.

3.1.1 BTO sites

Capsule: The first axis represents a single gradient of increasing abundance of common resident and middle-distance migrant species associated with more mature, possibly managed woodlands. The second axis represents a bidirectional gradient with species associated with understorey increasing at sites towards the negative end and species associated with woodlands with little understorey, such as occurs where livestock grazing is intense in the west of England and Wales, increasing in sites towards the positive end.

Axis 1

Table 3.1 shows the first axis of the PCA of BTO data has strong or moderate positive loadings for several common resident species and the two middle-distance migrants. Long-distance migrants and declining resident species were not clearly related to this axis (with the exception of spotted flycatcher which was moderately positively related). There were no negative associations. This axis therefore represents a single directional gradient from sites with low density of residents and middle-distance migrants to sites with high density of residents and middle-distance migrants.

Table 3.3 shows that scores on this axis were negatively related to longitude and therefore scores were higher in the west, although figure 3.1 shows that there is no strong separation of sites from different regions. Table 3.2 shows that scores on this axis were most frequently related to variables describing woodland structure (4 variables), and that there was also one association with variables relating to winter climate change, spring climate change, physical characteristics of the woodlands, tree condition and field layer composition.

Specifically, there were positive associations with cover between 2 and 4 metres, maximum tree DBH and maximum tree height and a negative association with scores on tree structure PCA axis 1, meaning scores were highest in woods with tall trees and a closed canopy (table 3.3). Scores were also higher in woods with low cover of bracken in the field layer, a small number of dead trees and a greater presence of water features. Together, these results indicate that mature woods with a well-developed mid-understorey and few dead trees (and that may therefore be actively managed) are associated with high densities of residents and middle distance migrants. Although the proportion of climate variables with significant relationships to this axis was low, scores were positively related to minimum temperature in January and number of days with rainfall in May. High scores on this axis were therefore found especially in woods located in areas with damp late springs and mild mid winters.

Axis 2

Table 3.1 shows that the second axis of the PCA of BTO data has moderate negative loadings for blackcap and chiffchaff (two middle-distance migrants associated with understorey in mature woodlands) and moderate negative relationships for dunnock and long-tailed tit (residents also associated with understorey). The species with strong and moderate positive loadings (mistle thrush, marsh tit, treecreeper and coal tit) are species generally more associated with mature woodland, as are three of four long-distance migrants that were weakly positively loaded (pied flycatcher, wood warbler and redstart). This axis therefore describes a bidirectional gradient with species associated with the understorey increasing in woods located towards the negative end of the axis and species associated with mature woodland increasing in woods towards the positive end.

This axis was negatively related to longitude and therefore scores were higher in the west than in the east (table 3.3), although figure 3.1 shows that there is no strong separation of sites from different regions. Table 3.2 shows that compared to the first axis, scores were more frequently related to variables describing field layer cover (4) and to winter (3) and spring (4) climate change but that there are still 4 relationships with variables describing woodland structure, as well as with one physical attribute and one landscape composition variable.

The structural associations show the negatively loaded species were associated with high cover at 2-4 metres, low horizontal visibility and low scores on understorey PCA 1 (potentially also indicating an association with high cover in the 0.5 – 2 metres and 4-10 metre zones). The positively loaded species were therefore associated with the reverse (low cover in the understorey and high horizontal visibility). The field layer associations (including the relationships to the field layer PCA axes) show that the negatively loaded species were associated with high cover of leaf litter, bramble cover, herbs and bare ground whilst the positively loaded species were associated with high cover of bracken, leaf litter, grass and moss. These results therefore accord with the interpretation of this axis as a gradient related to species occupancy of sites with different understorey compositions. The climatic associations show that the positively loaded species were strongly associated with high rainfall in both winter and spring. They were also associated with low presence of water features and (due to the negative axis relationship with landscape PCA axis 1) to more natural landscapes as opposed to the landscapes dominated by agriculture and urban areas that the negatively loaded species were associated. Together, these results suggest this axis is separating sites comprised of mature woodland with little understorey (possibly due to grazing from livestock) as is often found in the west of England and in Wales, from more disturbed sites with a better developed understorey found elsewhere.

Loading	**AXIS 1 (23.1%)**	**AXIS 2 (10.5%)**
-0.5 - -0.4		BLACA, CHIFF
-0.4 - -0.3		DUNNNO, LOTTI
-0.3 - -0.2	**TREPI**	BULLF, GREWO, GRSWO
-0.2 - -0.1	SISKI, **GARWA**, *HAWFI*	WREN, *JAY*, NUTHA, MAGPI, *WILTI*, CHAFF, JACKD, **SPOFL**
-0.1 - 0	**REDST**, **WOOWA**	ROBIN, BLABI, **GARWA**, GRETI
0 - 0.1	**PIEFL**, *LESWO*, *REDPO*, *WILTI*	*REDPO*
0.1 - 0.2	GREWO	SISKI, BLUTI, *HAWFI*
0.2 - 0.3	MAGPI, JACKD, *JAY*, **WILWA**	SONTH, *LESWO*, GOLDC, **TREPI**
0.3 - 0.4	GRSWO, MARTI, BULLF	**PIEFL**, **WOOWA**, **WILWA**, **REDST**
0.4 - 0.5	DUNNO, **SPOFL**, MISTH	
0.5 - 0.6	LOTTI, COATI, NUTHA, CHIFF	COATI
0.6 - 0.7	TREEC, BLACA, GOLDC, GRETI	TREEC
0.7 - 0.8	CHAFF, WREN, ROBIN, SONTH	MARTI, MISTH
0.8 - 0.9	BLABI, BLUTI	

Table 3.1 Summary of species loadings on the first two axes of the PCA of abundance for BTO sites in 2003-04. Long-distance migrants are shown in bold. Strongly declining residents (defined as species showing a decline of > 20% according to results from the RWBS for both BTO and RSPB datasets or a significant decline according to one dataset) are shown in italics. Species are listed in ascending order of their loading. See Appendix 2 for species codes.

Variable group	**Axis 1**	**Axis 2**
Geographical location (2)	**1** (50)	**1** (50)
Field layer (9)	**1** (11)	**4** (44)
Structure (13)	**4** (31)	**4** (31)
Tree condition (7)	**1** (14)	**0**
Deer impacts (3)	**0**	**0**
Landscape (2)	**0**	**1** (50)
Physical features (4)	**1** (25)	**1** (25)
Spring weather (6)	**1** (17)	**4** (67)
Winter weather (9)	**1** (11)	**3** (33)
Predation (1)	**0**	**0**

Table 3.2 Summary of significant relationships between explanatory variables and site scores on the first two axes of the PCA of abundance in 2003-04 at BTO sites. The number of variables in each group is shown in brackets after each variable group name. For each PCA axis, the number of significant relationships is shown in bold followed in brackets by the percentage of variables in that group with significant relationships.

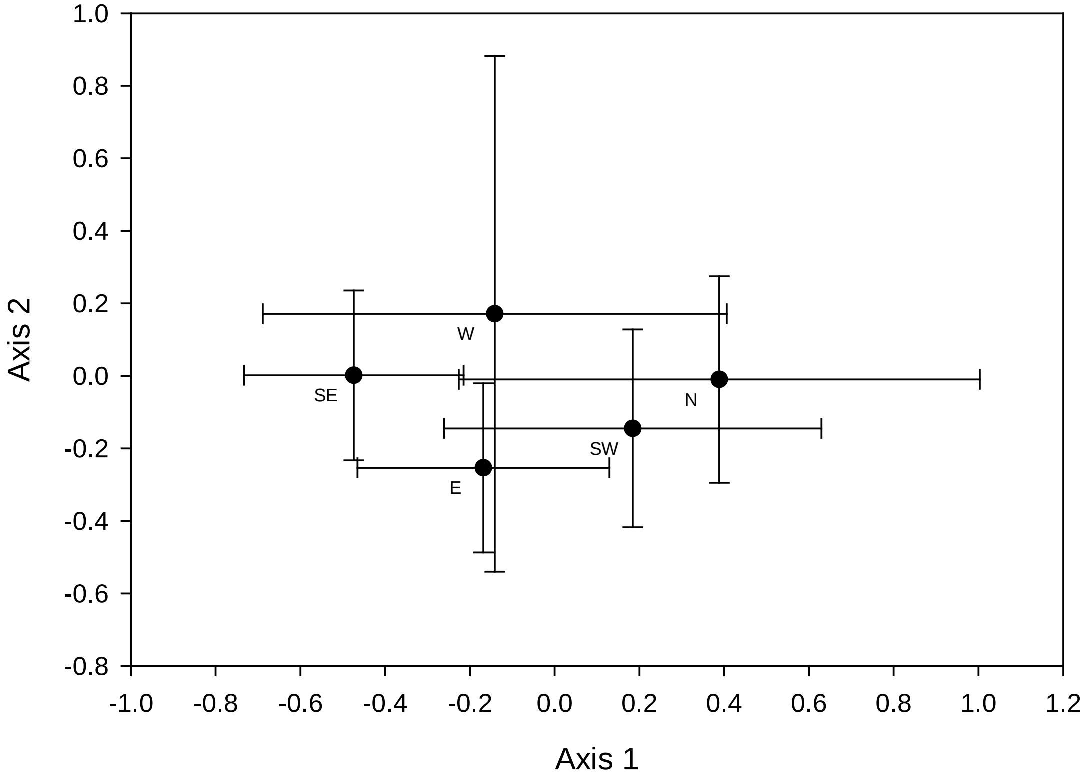

Figure 3.1 Mean scores per region on first two axes of PCA of abundance at BTO sites in 2003-04. The mean for each region is shown together with its 95% confidence interval. [N= North; E= East; W= West; SE= South-east; SW= South-west]

Effect	Axis 1	Axis 2	Effect	Axis 1	Axis 2
Location			**Deer impacts**		
Longitude	- ***	- ***	Trackwaysper100m		
Latitude			DeerPCAAxis1		
			DeerPCAAxis2		
Field layer					
Bracken	- **				
Bramble			threekmHabPCA1		- ***
Herb	+ *	- ***	threekmHabPCA2		
Grass		+ ***			
Moss			**Physical features**		
Leaf Litter			Water features	+ ***	- ***
BareGround			Altitude		+ *
p1flayer		- ***	Contigarea		
p2flayer		- **	Tracks		
Structure			**Spring weather**		
Cover05_2			AprTemp		- *
Cover2_4	+ **	- **	MayTemp		
Cover4_10		- *	AprRainfall		+ ***
Horizivisibility		+ **	MayRainfall		+ ***
understpc1		+ ***	AprRaindays		+ ***
understpc2	- *		MayRaindays	+ ***	+ ***
CanopyCov					
BasalArea			**Winter weather**		
MaxDBH	+ **		Jan_minT	+ **	
MaxHeight	+ **		Feb_minT		
treestructurepc1	- **		Mar_minT		
treestructurepc2	+ *		Jan_MaxT		
Dominantsp		*	Feb_MaxT		
			Mar_MaxT		
Tree condition			Jan_cmRain		+ ***
Lichen		+ *	Feb_cmRain		+ ***
Ivy			Mar_cmRain		+ ***
ShrubDiversity	- *	- *			
DeadTree	- **		**Predation**		
DeadLimbs			DreyDensity		
GroundWood					
deadwoodpc1					

Table 3.3 Direction and significance of effects of variables on site scores of sites from PCA bird abundance in 2003-04 at BTO sites. + = positive relationship; - = negative relationship. * = P<0.1; ** P< 0.05; ***= P< 0.01. All effects are calculated from mixed models including region as a random effect and each variable shown as the sole fixed effect.

3.1.2 RSPB sites

Capsule: The first axis contrasts the open upland woods of Scotland (containing high densities of willow warbler and tree pipit in particular) with mature lowland woods with high densities of common resident and middle-distance migrant species. The second axis contrasts mature upland oak woods with little understorey, whose typical species increase towards the positive end, with the less mature woods with more understorey of the east, whose typical species such as chiffchaff and dunnock increase towards the negative end.

Axis 1

Table 3.4 shows several common residents and middle-distance migrants are positively associated with the first axis of the RSPB PCA of data for abundance in 2003-04. This is much the same as for the equivalent BTO axis. However, whereas no species were negatively loaded on the BTO equivalent, tree pipit and willow warbler are strongly, and redpoll and chaffinch weakly, negatively loaded in the RSPB axis. It therefore represents an extended ecological gradient with high abundance of two long-distance migrants and one declining resident species (plus chaffinch) associated with upland birch woodland at the negative end and high abundance of common residents and middle-distance migrants at the positive end.

Scores on this axis varied with both latitude and longitude, being higher in the east and the south, as well as with altitude, being higher in the lowlands (table 3.6). Figure 3.2 shows that the regional separation on this axis is largely due to the very low mean score for Scotland. The negatively loaded species are therefore associated with upland woods in the north. Table 3.5 shows that scores were also related to a wide variety of other factors. These include 4 variables describing field layer cover, 6 woodland structure and spring and winter climate, as well as 2 tree condition variables, 1 deer impact variable, 2 landscape variables, 1 physical characteristic and the abundance of 2 potential nest predators.

Table 3.6 shows that in the field layer, positively loaded species were associated with sites that had more bramble and (according to the relationship with field layer PCA axis 1) leaf litter cover whilst negatively loaded species were associated with sites that had more grass, moss and (according to the same PCA axis) bracken cover. Structurally, woods at the positive end of the axis had taller trees with larger DBH and greater cover in the 0.5 – 2 metre and 2 – 4 metre zones. They correspondingly had lower horizontal visibility, as well as higher shrub diversity, greater amounts of ground dead wood and higher scores on deer impact PCA axis 2 (dominated by high levels of grazed bramble). They were set in less wooded landscapes that were more dominated by agricultural and urban areas than sites at the negative end of the axis. High densities of the positively loaded common residents and middle-distance migrants are therefore associated with mature woodlands with a well-developed understorey whilst the negatively loaded species were associated with woods with smaller trees and a more open understorey. Positively loaded species were associated with sites that had lower spring but higher winter rainfall and in general higher spring temperatures, but lower March maximum temperatures, than sites at the negative end of the gradient. Grey squirrel drey densities and interpolated great spotted woodpecker densities were also higher in sites with higher scores on this axis, potentially suggesting a negative predatory impact on the negatively loaded species or, more likely, shared ecological determinants of density with the positively loaded species.

Together, these results indicate that this axis is describing an axis from open upland woods (probably primarily birch woods) at the negative end of the spectrum to sites comprised of mature woodland with a well-developed understorey (and therefore likely managed by e.g. thinning) at the positive end.

Axis 2

The second axis is similar to the equivalent BTO axis in that species associated with understorey are negatively loaded, although only two species are weakly associated with this end of the axis (chiffchaff and dunnock) (table 3.4). The positively loaded species are, as for the equivalent BTO axis, generally associated with mature woodland. The three species most strongly positively loaded (wood warbler, pied flycatcher and redstart) are typical of mature oak woods that were, in contrast, only weakly associated with the equivalent end of the BTO axis. This axis therefore describes a similar bidirectional gradient to the BTO equivalent, running from species associated with understorey at the negative end to species associated with mature woodland with little understorey at the positive end.

Table 3.6 shows that scores on this axis were negatively related to longitude and positively related to altitude and were therefore higher in the west and in the uplands. Figure 3.2 shows that there is a clear distinction of scores on this axis between the east (especially) and other regions. According to table 3.5, there were associations with a wide variety of other types of variables including 7 relating to field layer cover, 6 relating to woodland structure, 5 to tree condition, all 3 measures of deer impacts, 2 to spring weather and 3 to winter weather as well as 1 physical feature and the abundance of grey squirrel dreys.

Table 3.6 shows the associations with individual variables. In the field layer, woods at the positive end of the axis had greater cover of bracken, grass and moss and woods at the negative end had greater cover of bramble, herb and potentially also (according to the associations with field layer PCA axes 1 and 2) bare ground. Amongst variables related to woodland structure, woods at the positive end of the axis had higher maximum DBH, basal area and horizontal visibility and lower scores on understorey PCA axis 2 (meaning they had an open lower and closed upper understorey) and tree structure PCA axis 1 (meaning they had large trees and a closed canopy). These are all characteristics of old growth woodland, such as the heavily grazed oak woodlands of the western uplands, whilst the reverse characteristics of woods at the negative end of the axis are typical of younger and more open woods. This interpretation is confirmed by the positive effect of dominant tree species, with oak woodlands scoring more highly on this axis than all other woods.

The woods with high scores on this axis also had higher shrub diversity and numbers of dead limbs and dead trees but less ground wood and, presumably due to this, higher scores on dead wood PCA axis 1. Other characteristics of these woods were higher numbers of deer track ways (possibly in fact track ways caused by livestock as these woods lie outside the areas of high deer abundance in Britain) but lower scores on deer impact PCAs 1 and 2, meaning they had fewer signs of deer grazing such as browsed stems, browse lines and browsed brambles, than woods with low scores. The relationships with climatic variables indicate that woods with high scores on this axis had higher May temperatures and number of days with rain in April as well as higher amounts of ran fall in all three winter months. They also had higher densities of grey squirrel dreys.

Loading	AXIS 1 (19.5%)	AXIS 2 (10.9%)
-0.8 - -0.7	**WILWA**	
-0.7 - -0.6	**TREPI**	
-0.6 - -0.5		
-0.5 - -0.4		
-0.4 - -0.3	*REDPO*, CHAFF	CHIFF, DUNNO
-0.3 - -0.2		
-0.2 - -0.1	**REDST**, **WOOWA**	*WILTI*, MARTI
-0.1 - 0		BLACA, ROBIN, BLABI
0 - 0.1	**SPOFL**, **PIEFL**, COATI, LOTTI, MISTH, **GARWA**, *LESWO*	*JAY*, SONTH, *REDPO*, *LESWO*
0.1 - 0.2	*HAWFI*, *WILTI*	**WILWA**, WREN, *HAWFI*, GOLDC, LOTTI
0.2 - 0.3		**GARWA**, COATI, GRETI, **TREPI**, CHAFF, **SPOFL**
0.3 - 0.4	DUNNO, TREEC, WREN	NUTHA
0.4 - 0.5	GRETI, GOLDC	BLUTI
0.5 - 0.6	SONTH, *JAY*, ROBIN, BLUTI, MARTI, NUTHA	TREEC, MISTH
0.6 - 0.7	BLACA, CHIFF	**WOOWA**, **PIEFL**
0.7 - 0.8	BLABI	**REDST**

Table 3.4 Summary of species loadings on the first two axes of the PCA of abundance for RSPB sites in 2003-04. Long-distance migrants are shown in bold. Strongly declining residents (defined as species showing a decline of > 20% according to results from the RWBS for both BTO and RSPB datasets or a significant decline according to one dataset) are shown in italics. Species are listed in ascending order of their loading. See Appendix 2 for species codes.

Variable group	Axis 1	Axis 2
Geographical location (2)	**2** (100)	**1** (50)
Field layer (9)	**4** (44)	**7** (78)
Structure (13)	**6** (46)	**6** (46)
Tree condition (7)	**2** (29)	**5** (71)
Deer impacts (3)	**1** (33)	**3** (100)
Landscape (2)	**2** (100)	**0**
Physical (4)	**1** (25)	**1** (25)
Spring weather (6)	**3** (50)	**2** (33)
Winter weather (9)	**2** (22)	**3** (33)
Predation (1)	**2** (100)	**1** (50)

Table 3.5 Summary of significant relationships between explanatory variables and site scores on the first two axes of the PCA of abundance in 2003-04 at RSPB sites**.** The number of variables in each group is shown in brackets after each variable group name. For each PCA axis, the number of significant relationships is shown in bold followed in brackets by the percentage of variables in that group with significant relationships.

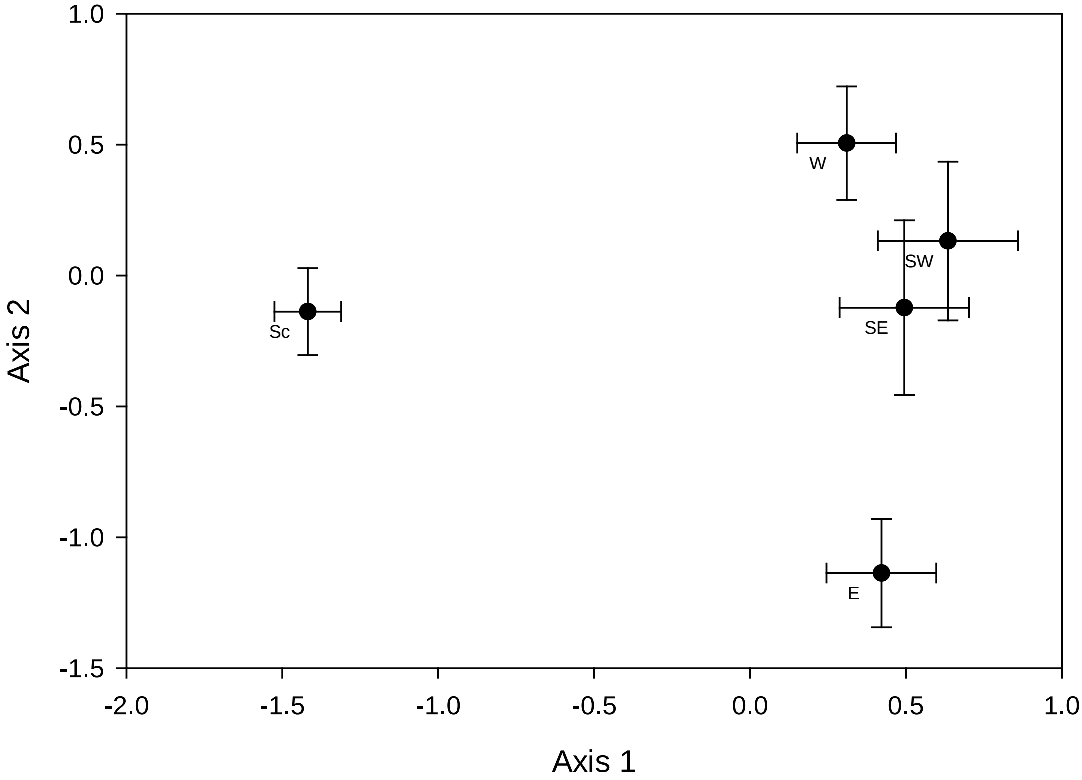

Figure 3.2 Mean scores per region on first two axes of PCA of abundance at RSPB sites in 2003-04. The mean for each region is shown together with its 95% confidence interval. [Sc=Scotland; E= East; W= West; SE= South-east; SW= South-west]

Effect	Axis 1	Axis 2	Effect	Axis 1	Axis 2
Location			**Deer**		
Longitude	+ ***	- ***	Trackwaysper100m		+ ***
Latitude	- ***		DeerPCAAxis1		- ***
			DeerPCAAxis2	+ **	- ***
Field Layer					
Bracken		+ ***	**Landscape structure**		
Bramble	+ ***	- **	threekmHabPCA1	+ ***	- *
Herb		- ***	threekmHabPCA2	- ***	
Grass	- **	+ **			
Moss	- ***	+ **	**Physical features**		
LeafLitter			Drainage		
BareGround		- *	Altitude	- ***	+ **
p1flayer	+ ***	- ***	Contigarea		
p2flayer		- **	Tracks		
Structure			**Spring weather**		
Cover05_2	+ ***		AprTemp	+ *	
Cover2_4	+ ***		MayTemp	+ *	+ **
Cover4_10			AprRainfall	- **	
Horizivisibility	- *	+ ***	MayRainfall	- **	
understpc1	- ***		AprRaindays	- **	+ **
understpc2		- ***	MayRaindays		- *
CanopyCov					
BasalArea		+ **	**Winter weather**		
MaxDBH	+ **	+ ***	Jan_mint		
MaxHeight	+ ***		Feb_minT		
treestructurepc1		- **	Mar_minT		
treestructurepc2	+ **		Jan_MaxT		
Dominantsp		***	Feb_MaxT	- *	
			Mar_MaxT	- **	
Tree condition			Jan_cmRain	+ **	+ **
Lichen	- *		Feb_cmRain		+ **
Ivy	+ *		Mar_cmRain	+ *	+ ***
ShrubDiversity	+ ***	+ ***			
DeadTree		+ ***	**Predation**		
DeadLimbs		+ ***	DreyDensity	+ ***	+ ***
GroundWood	+ **	- ***	CalGRSWO	+ ***	
deadwoodpc1		+ ***			

Table 3.6 Direction and significance of effects of variables on site scores from PCA bird abundance in 2003-04 at RSPB sites. + = positive relationship; - = negative relationship. * = P<0.1; ** P< 0.05; ***= P< 0.01. All effects are calculated from mixed models including region as a random effect and each variable shown as the sole fixed effect.

3.1.3 Comparison between community structure in 2003-04 from BTO sites and RSPB sites

The PCAs of abundance of birds in 2003-04 at BTO and RSPB sites produced broadly similar axes despite the different samples of sites included and the different field methods and measures of abundance used. The first axes describe a gradient from open upland to closed mature lowland woods whilst the second axis describes a gradient from closed mature upland to open lowland woods. These can be readily interpreted in terms of both woodland attributes and geographical co-ordinates and represent fundamental patterns of variation in the composition of British broadleaved woodland bird communities.

The first axis for both datasets described a gradient of increasing abundance of common resident and middle-distance migrant species that was associated with an increase in the stature of the woods and cover in the understorey. The RSPB axis, however, contrasted this gradient with the abundance of a group of species (primarily willow warbler and tree pipit but also redpoll and chaffinch) that reach high abundances in open, upland woods such as Scottish birch woods. The almost complete absence of this end of the gradient in the BTO dataset is due to the absence of sites from Scotland in this sample of sites.

The second axis for both datasets describes an axis from species associated with understorey at the negative end to species associated with mature woodlands with little understorey at the positive end. Compared to the BTO axis, the RSPB axis has stronger positive loadings for the three species typical of closed-canopy Atlantic oak woods (pied flycatcher, redstart and wood warbler) due to inclusion of a larger sample of sites from the uplands of Wales in this dataset. Although the loadings of the smaller number of species associated with sites at the negative end of the axis were less strong for the RSPB dataset, there was a stronger geographical distinction on the axis for this dataset due to the smaller number of sites comprising upland oak woods in the BTO sample.

3.2 Shifts Between Episodes One and Two

3.2.1 BTO sites

Capsule: Site scores on axis one increased between the 1980s and 2003-04, reflecting the increase of a number of common resident species away from the southeast in particular. These shifts were not related to the characteristics of woods in a clearly interpretable way. Although the fact that sites in the north showed the greatest increase is potentially consistent with them being driven by climate change, the results for individual variables did not support this. Site scores on axis two decreased slightly on average but these changes occurred away from the southern regions (southeast and southwest), reflecting the greater increase of middle-distance migrants away from these regions. Results are consistent with habitat change driving these shifts.

At BTO sites, scores on axis 1 were on average 0.562 higher for 2003-04 data than in the 1980s (confidence limits 0.270 – 0.853 higher) and scores on axis 2 were on average 0.084 lower than in the 1980s (confidence limits 0.026 – 0.141 lower). There was thus a significant shift across all sites towards the positive end of axis 1 and a significant but small shift towards the negative end of axis 2. Overall, sites therefore had more common resident and middle-distance migrant species and, to some extent, fewer long-distance migrants and other species associated with mature woodland in 2003-04. This accords with the results for individual species from Amar *et al.* 2006.

The mean shifts for sites in each region are shown in figure 3.3. There was a significant difference between regions in the degree of shift on both axes, although for axis 2 this was marginal (Axis 1: 4 df, F 4.26, P= 0.003; Axis 2: 4 df, F 2.64, P= 0.039). On axis 1, the mean shift was significantly greater than zero for the southwest and the north, whilst on axis 2, the mean shift of east, west and north were significantly less than zero.

Table 3.7 shows that in addition to the geographical differences in shifts on axis 1 (shifts being higher in the north and west), the degree of change was related to 2 variables pertaining to the structure of woods, 1 physical characteristic and 1 to spring and 2 to winter climate change. According to table 3.8, sites with low cover between 4 and 10 metres, smaller maximum DBH of trees and lower prevalence of drainage features showed greater increases in scores on this axis. These sites tended to be in areas where increases in March minimum temperature and May temperature had been smallest but where the increase in March maximum temperature had been greatest. The conflicting results for March minimum and maximum temperatures appear unintuitive but may be due to these areas experiencing more frequent or stronger high-pressure systems at this time of year, with resulting diurnal fluctuations in temperature. Overall, there was not a strong relationship between shifts on this axis and characteristics of the woods themselves or the locations in which they were situated given the number of relationships relative to the number of variables modelled and the lack of clearly interpretable patterns. The habitat characteristics of the woods are not clearly those predicted to benefit the increasing species creating the observed community shifts. It is possible that this indicates a move into sub-optimal areas by these common species already at high densities in many woods. The pattern of relationships with March temperature could indicate that occurrence of warm weather at this time, when many resident species are either beginning to breed or are preparing to do so and the middle-distance migrants are arriving on the breeding grounds, is important in determining community shifts.

Table 3.7 shows in addition to shifts on axis 2 being more negative in the north than in the south, there were more relationships with variables relating to the characteristics of the woods themselves than for axis 1. These were with 2 variables describing the field layer, 5 describing woodland structure, 1 variable describing tree condition and 2 related to winter climate change. According to table 3.8, the greatest shifts towards the negative end of the axis occurred in woods with higher bramble and lower grass cover, lower horizontal visibility, maximum DBH of trees and total basal area and higher vegetation cover between 0.5 and 2 metres and shrub diversity. Broadly speaking, this suggests that the woods that showed the greatest shift towards the negative end of the axis were those whose habitat in 2003-04 was most suitable for the negatively loaded species. The climatic associations show that the greatest of these shifts towards the negative end of the axis occurred where March rainfall decreased most and February maximum temperature increased least.

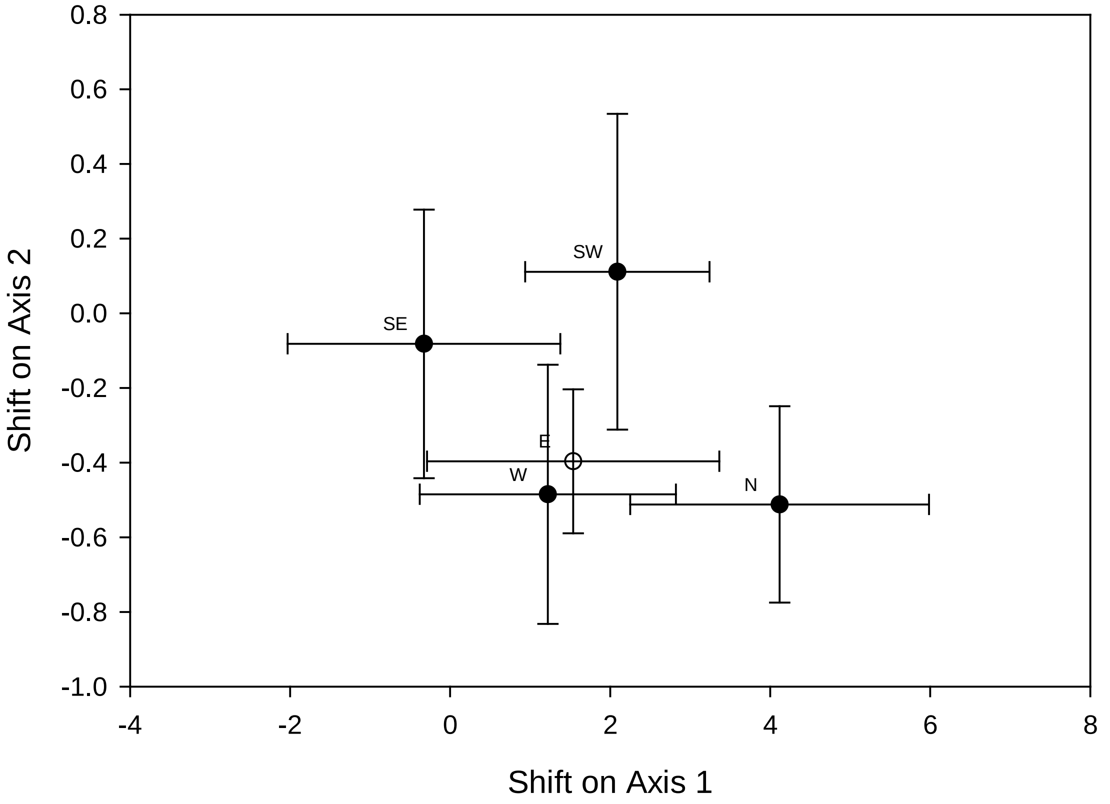

Figure 3.3 Shifts between 1980s and 2003-04 of mean BTO site scores per region in multivariate space defined by the first two axes of the PCA of abundance data from 2003-04. The mean for the shifts across all sites in each region is shown together with its 95% confidence intervals. [N= North; E= East; W= West; SE= South-east; SW= South-west]

Variable group	Axis 1	Axis 2
Location (2)	**2** (100)	**1** (50)
Field layer (9)	**0**	**2** (22)
Structure (13)	**2** (15)	**5** (38)
Tree condition (7)	**0**	**1** (14)
Deer (3)	**0**	**0**
Landscape (2)	**0**	**0**
Physical features (4)	**1** (25)	**0**
Spring climate change 6)	**1** (17)	**0**
Winter climate change (9)	**2** (22)	**1** (11)
Predation (1)	**0**	**0**

Table 3.7 Summary of significant relationships between explanatory variables and shifts in site scores between the 1980s and 2003-04 on the first two axes of the PCA of abundance in 2003-04 at BTO sites. The number of variables in each group is shown in brackets after each variable group name. For each PCA axis, the number of significant relationships is shown in bold followed in brackets by the percentage of variables in that group with significant relationships.

Effect	Axis 1	Axis 2	Effect	Axis 1	Axis 2
Location			**Deer**		
Longitude	- **		Trackwaysper100m		
Latitude	+ ***	- ***	DeerPCAAxis1	+ *	
			DeerPCAAxis2		
Field layer					
Bracken			**Landscape structure**		
Bramble		- **	threekmHabPCA1		
Herb			threekmHabPCA2		- *
Grass		+ ***			
Moss			**Altitude etc**		
LeafLitter			Drainage	- **	
BareGround			Altitude		
p1flayer			Contigarea		
p2flayer			Tracks		
Structure			**Spring climate change**		
Cover05_2		- *	ChApr_temp		- *
Cover2_4			ChMay_temp	- ***	+ *
Cover4_10	- **		ChApr_cmRain		
Horizivisibility		+ **	ChMay_cmRain		
understpc1			ChgApr_Raindays		
understpc2		- **	ChgMay_Raindays		+ *
CanopyCov					
BasalArea		+ **	**Winter climate change**		
MaxDBH	- **	+ *	ChJan_minT		
MaxHeight			ChFeb_minT		
treestructurepc1		- ***	ChMar_minT	- **	
treestructurepc2			ChJan_maxt		
Dominantsp			ChFeb_maxt		- **
			ChMar_maxt	+ **	
Tree condition			ChJan_cmRain		
Lichen			ChFeb_cmRain		
Ivy			ChMar_cmRain		- ***
ShrubDiversity		- **			
DeadTree			**Predation**		
DeadLimbs			DreyDensity		
GroundWood					
deadwoodpc1					

Table 3.8 Effects of variables on shifts in site scores between 1980s and 2003-04 on axes defined by PCA of bird abundance in 2003-04 at BTO sites. + = positive relationship; - = negative relationship. * = P<0.1; ** P< 0.05; ***= P< 0.01. All effects are calculated from mixed models including region as a random effect and each variable shown as the sole fixed effect.

3.2.2 RSPB sites

Capsule: Sites in all regions shifted towards the positive end of axis 1. These shifts appear to be particularly associated with increases in winter temperatures. There was no change across all regions on axis 2 but sites in the west shifted further towards the positive end of the axis and those in Scotland and the southeast shifted towards the negative end. These shifts were not associated with climate change but were to some extent associated with a variety of woodland characteristics.

At RSPB sites, scores on axis 1 were 2.798 higher in 2003-04 than in the 1980s (confidence limits 2.533 - 3.062 higher) and scores on axis 2 were 0.018 lower than in the 1980s (confidence limits 0.156 lower to 0.119 higher). There was thus a significant shift across all sites towards the positive end of axis 1 but no significant shift in scores on axis 2. This means that on average across all regions sites had greater abundances of common resident and middle-distance migrant species and lower abundance of willow warbler and tree pipit in 2003-04 compared to the 1980s, a result in accordance with the species results in Amar *et al.* 2006.

The mean shifts for sites in each region are shown in figure 3.4. There was a significant difference between regions in the degree of shift on both axes (Axis 1: 4 df, F 33.94, P<0.0001; Axis 2: 4 df, F 4.93, P= 0.0008). On axis 1, the mean shifts for all regions were significantly greater than zero. On axis 2, the mean shifts for Scotland and the southeast were significantly less than zero and that for west significantly greater than zero but there was no significant shift for east and the southwest. Sites in Scotland and the southeast therefore had higher abundances of chiffchaff and dunnock and/or lower abundances of the bird species associated with mature woodland at the positive end of axis 2. The reverse was true on average for sites in the west, where positively loaded species had higher abundances in 2003-04. The three species with the strongest positive loadings on this axis were long-distance migrants that declined strongly over this period according to Amar *et al.* 2006, including in this region. The modest positive shift on this axis in the west must therefore be due to the increases of other positively loaded species (treecreeper, mistle thrush, blue tit and nuthatch) outweighing these declines.

Table 3.9 shows that there were no associations of shifts on axis 1 with the characteristics of the woods themselves other than an association with dominant tree species (shifts in woods dominated by beech being higher than shifts in woods dominated by oak or birch) and the fact that shifts were most positive in woods with greater amounts of dead wood and those set in more wooded landscapes. Relationships with climatic variables show that shifts were more positive where the number of days with rain in May decreased least and where maximum temperatures in all three winter months and minimum temperatures in February increased most. It seems likely that increased winter temperatures may have benefited the positively loaded species.

Shifts on axis 2 did not vary systematically with geographical co-ordinates despite the differences between regions outlined above (tables 3.9 and 3.10). Table 3.9 shows that there were 2 associations with field layer variables, 3 with structural variables, 5 tree condition variables, 1 measure of deer impact and 1 physical feature. According to table 3.10, shifts were most negative where there was a higher cover of bare ground and possibly (due to the relationship with understorey PCA axis 1) also bramble and litter, and where horizontal visibility was lower and the maximum height of trees was greater. These characteristics of woods are amongst those favoured by the increasing and negatively loaded chiffchaff. There was also less dead wood and a lower prevalence of lichen in these woods and scores on deer impact PCA 2 were higher, meaning that there was a greater prevalence of browsed bramble. These results are most likely to be due to the greatest declines of the three positively loaded long-distance migrants having occurred in the east and southeast of England, where deer densities are highest. These woods also had greater prevalence of drainage features and lower great spotted woodpecker density.

3.2.3 Summary of community shifts

For both the BTO and RSPB datasets, there was a positive shift across all sites on axis 1 – that is, densities of common residents and middle-distance migrants increased. This shift in community structure occurred in all regions except the southeast according to the BTO dataset and was greatest either in the north (BTO dataset) or where winters warmed most (RSPB dataset). There were shifts towards the negative end of the second axis (associated with high abundance of species dependent on understorey in each case but more strongly in the BTO dataset) in all regions except the southeast and southwest for the BTO dataset and in Scotland and southeast for the RSPB dataset. Only the west for the RSPB dataset shifted towards the positive end of the axis (associated with high abundance of mature woodland species). Relationships with woodland characteristics were consistent with habitat change driving these shifts.

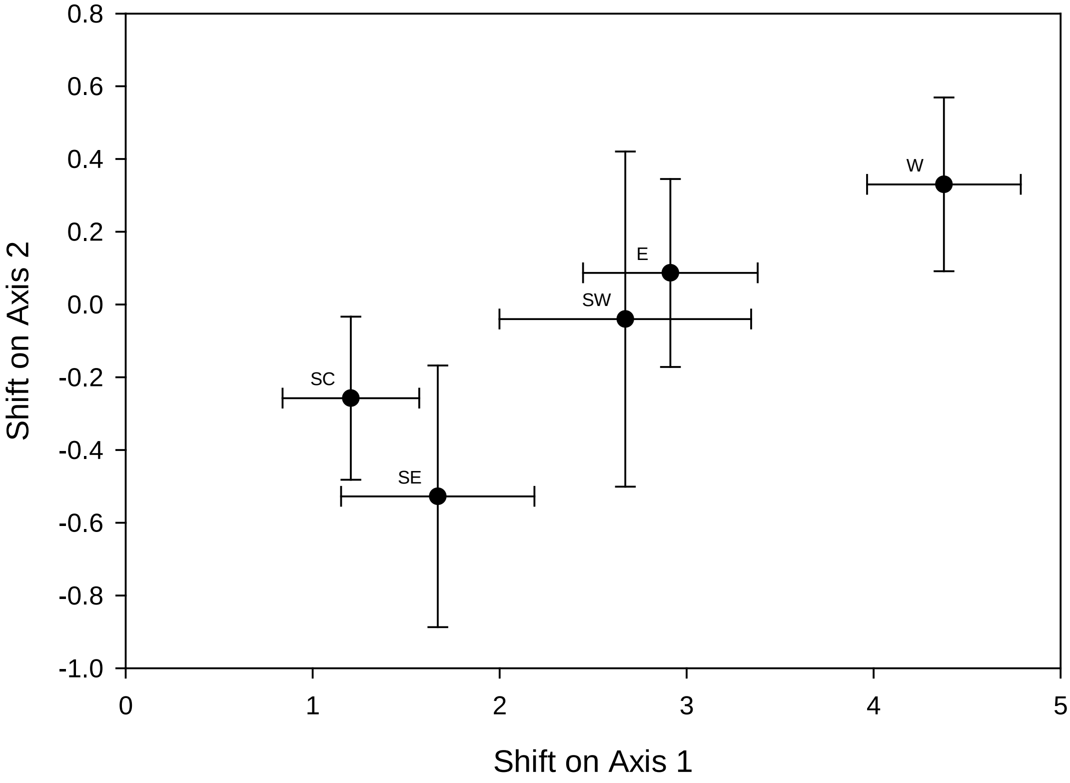

Figure 3.4 Shifts between 1980s and 2003-04 of mean RSPB site scores per region in multivariate space defined by the first two axes of the PCA of abundance data from 2003-04. The mean for the shifts across all sites in each region is shown together with its 95% confidence intervals. [Sc=Scotland; E= East; W= West; SE= South-east; SW= South-west]

Variable group	Axis 1	Axis 2
Location (2)	**1** (50)	**0**
Field layer (9)	**0**	**2** (22)
Structure (13)	**1** (8)	**3** (23)
Tree condition (7)	**2** (29)	**5** (71)
Deer (3)	**0**	**1** (33)
Landscape (2)	**1** (50)	**0**
Physical features (4)	**0**	**1** (25)
Spring climate change (6)	**1** (17)	**0**
Winter climate change (9)	**4** (44)	**0**
Predation (2)	**1** (50)	**1** (50)

Table 3.9 Summary of significant relationships between explanatory variables and shifts in site scores between the 1980s and 2003-04 on the first two axes of the PCA of abundance in 2003-04 at RSPB sites. The number of variables in each group is shown in brackets after each variable group name. For each PCA axis, the number of significant relationships is shown in bold followed in brackets by the percentage of variables in that group with significant relationships.

Table 3.10 Effects of variables on shifts in site scores between 1980s and 2003-04 on axes defined by PCA of bird abundance in 2003-04 at RSPB sites. + = positive relationship; - = negative relationship. * = P<0.1; ** P< 0.05; ***= P< 0.01. All effects are calculated from mixed models including region as a random effect and each variable shown as the sole fixed effect.

Effect	Axis 1	Axis 2		Axis 1	Axis 2
Location			**Deer**		
Longitude			Trackwaysper100m		
Latitude	- ***		DeerPCAAxis1		+ *
			DeerPCAAxis2		- **
Field Layer					
Bracken			**Landscape structure**		
Bramble			threekmHabPCA1		
Herb			threekmHabPCA2	- ***	
Grass					
Moss			**Physical features**		
LeafLitter			Drainage		- ***
BareGround		- **	Altitude		
p1flayer		- **	Contigarea		
p2flayer			Tracks		
Structure			**Spring climate change**		
Dominantsp	***		ChApr_temp		
Cover05_2			ChMay_temp		
Cover2_4			ChApr_cmRain		
Cover4_10			ChMay_cmRain		
Horizivisibility		+ **	ChgApr_Raindays		
understpc1			ChgMay_Raindays	+ ***	
understpc2		- **			

Effect	Axis 1	Axis 2		Axis 1	Axis 2
CanopyCov			**Winter climate change**		
BasalArea			ChJan_minT	+ *	+ *
MaxDBH			ChFeb_minT	+ **	+ *
MaxHeight		- ***	ChMar_minT		
treestructurepc1			ChJan_MaxT	+ ***	
treestructurepc2			ChFeb_MaxT	+ **	
			ChMar_MaxT	+ ***	
Tree condition			ChJan_cmRain		- *
Lichen		+ **	ChFeb_cmRain		
Ivy			ChMar_cmRain		
ShrubDiversity					
DeadTree	+ *	+ ***	**Predation**		
DeadLimbs	+ ***	+ ***	DreyDensity	+ *	
GroundWood	+ *	+ **	CalGRSWO	+ ***	+ ***
deadwoodpc1	- ***	- ***			

Table 3.10 Continued**.**

3.3 Patterns of Change Across All Species in BTO Data

The amount of variation accounted for by the first two axes of the PCA of scores for change between the 1980s and 2003-04 was 19.4% and 6.9% for the BTO dataset and 11.3% and 7.2% for the RSPB dataset. Loadings for the first two axes of PCA of these change scores for the RSPB and BTO datasets are summarised in tables 3.11 & 3.14 and are given in full in Appendix 1.

3.3.1 BTO sites

Capsule: Axis 1 describes a gradient of increasingly positive changes of common resident and middle-distance migrant species particularly, but also some declining residents and long-distance migrants. Scores on this axis were not related to many woodland characteristics but they were positively related to the extent that winter conditions became warmer and there was also some evidence of increases being greater in suboptimal habitat. Sites at the negative end of axis 2 had more positive changes of three species associated with understorey whilst sites at the positive end of that axis had more positive changes of several species associated in general with clearer understorey. Variables describing woodland structure were most often related to scores on this axis.

Axis 1

Table 3.11 shows that 18 species of common resident and middle-distance migrant species, including the declining jay, are moderately or strongly positively loaded on the first axis, with a further eight species (including four long-distance migrants and declining resident lesser spotted woodpecker) showing weak positive loadings along. No species were negatively loaded. This axis therefore shows a unidirectional gradient with sites where these species showed more positive population changes (greater increases or smaller decreases) falling towards the positive end of the axis. Most of these species were positively related to the first axis of the PCA of abundance but the relationships for the declining pied flycatcher, willow warbler, garden warbler and lesser spotted woodpecker were stronger.

Table 3.13 shows that scores on this axis were positively related to latitude, so species with positive loadings on it did better in the north than in the south (see also figure 3.5). Table 3.12 shows that otherwise scores on this axis were related only to one variable describing woodland structure and to one spring and two winter climate change variables.

According to table 3.13, there was a negative relationship to maximum DBH, meaning that the positively loaded species did better in woods where the maximum size of trees was smaller. This contrasts with the finding that scores on BTO abundance PCA axis 1 were greater where maximum DBH was greater but supports the finding that the size of positive shifts on that axis were negatively associated with maximum DBH, suggesting that populations of the positively loaded species are increasing to a level where they are spilling over into sub-optimal habitat. There were some relationships with climatic variables – a negative relationship with change in May temperature and positive relationships with change in maximum temperature in January and March. The species with positive loadings on this axis therefore did better where maximum temperature in January and March increased most– in other words, where winter conditions ameliorated most. This finding is consistent with increased over-winter survival or condition in spring due to milder winters having increased the populations of these species. Also, these species did least well where temperature in May increased most – in other words, where late spring warmed most. Assuming that the degree of spring warming dictates the advance of phenology of invertebrate prey, this result is consistent with resource asynchrony having a negative impact on population changes (Buse *et al.* 1999).

Axis 2

Table 3.11 shows that the second axis has a strong negative loading for chiffchaff, a moderate one for blackcap and a weak one for wren – one resident and two middle-distance migrant species associated with the understorey, especially bramble. There are moderate positive loadings for spotted flycatcher and redpoll and weak ones for wood warbler and tree pipit – a group of species not associated with understorey.

According to table 3.13, scores on this axis were related negatively to both latitude and longitude, so positively loaded species did better in the south and west and negatively loaded species did better in the north and east (see also figure 3.6). Table 3.12 shows that there were several relationships with woodland characteristics, including 7 with woodland structure but also 2 with both field layer variables and deer impact scores and one each with a landscape composition variable and a physical feature.

In the field layer, the negative association with bracken and the positive association with field layer PCA1 (table 3.13) suggest that the positively loaded species declined most where its cover was higher. For woodland structure, the positive associations with horizontal visibility, canopy cover, basal area and tree maximum height, and the negative association with scores on understorey PCA axis 2 and tree structure PCA axis 1 all indicate that the positively loaded species declined least in tall, closed canopy woods with an open lower understorey and that negatively loaded species increased least in these woods. The species at both ends of the axis therefore appear to have done best in conditions that resemble their preferred habitats. There is therefore no evidence of the increasing middle-distance migrants expanding into sub-optimal habitat, although their expansion does not seem to be driven by habitat availability since the association with understorey structure was not strong and there was no association with e.g. bramble cover. The fact that there was to some extent a positive association between the population change scores of the strongly declining positively loaded species and the apparent habitat suitability for these species in woods, it is possible that habitat change has driven their declines. However, it is also possible that wider-scale factors have caused population changes, resulting in a contraction into their optimum habitat due to proportionately greater decline elsewhere.

The positive association with two deer impact variables – density of track ways and scores on deer impact PCA 1 (table 3.13) – both suggest that the negatively loaded species did less well where deer impacts had been greatest (consistent with deer browsing impacts impeding population growth of the negatively loaded species at some sites) and/or that the positively loaded species did better where deer impacts were higher. The positive association with landscape PCA axis 1 and the negative association with area of contiguous woodland (table 3.13) together suggest the positively loaded species did better in smaller woods in more agricultural landscapes. Amongst climatic variables, there was a positive relationship with change in the number of days in April with rain and a negative relationship with change in April temperature. This means that the positively loaded species did better where April rainfall showed greater increases and April temperatures increased least, with the converse being true for the negatively loaded species (i.e. they did better where April rainfall showed least increase and temperature showed greatest increase).

Loading	Axis 1 (19.4%)	Axis 2 (6.9%)
-0.7 - -0.6		CHIFF
-0.6 - -0.5		
-0.5 - -0.4		BLACA
-0.4 - -0.3		WREN
-0.3 - -0.2		DUNNO, **WILWA**, **GARWA**, SISKI, ROBIN
-0.2 - -0.1		WILTI, **PIEFL**
-0.1 - 0		MAGPI, BLABI, GREWO
0 - 0.1	**TREPI**, *HAWFI*	LOTTI, CHAFF, *JAY*, GRETI, BLUTI
0.1 - 0.2	SISKI, *REDPO*, *WILTI*, **WOOWA**, **REDST**, GREWO	BULLF, GRSWO, MISTH, COATI, NUTHA
0.2 - 0.3	MAGPI	MARTI, JACKD, *LESWO*, SONTH, *HAWFI*, GOLDC, **REDST**, TREEC
0.3 - 0.4	**PIEFL**, *LESWO*, SONTH, MISTH, **WILWA**, **SPOFL**, **GARWA**, GOLDC	**WOOWA**, **TREPI**
0.4 - 0.5	*JAY*, NUTHA, BULLF, CHIFF, JACKD, GRSWO, LOTTI	*REDPO*
0.5 - 0.6	TREEC, CHAFF, MARTI, BLACA, BLABI	**SPOFL**
0.6 - 0.7	COATI, ROBIN, DUNNO	
0.7 - 0.8	WREN, GRETI, BLUTI	

Table 3.11 Summary of species loadings on the first two axes of the PCA of change in abundance between 1980s and 2003-04 at BTO sites. Long-distance migrants are shown in bold. Strongly declining residents (defined as species showing a decline of > 20% according to results from the RWBS for both BTO and RSPB datasets or a significant decline according to one dataset) are shown in italics. Species are listed in ascending order of their loading. See Appendix 2 for species codes.

Variable group	Axis 1	Axis 2
Location (2)	**1** (50)	**2** (100)
Field layer (9)	**0**	**2** (22)
Structure (13)	**1** (8)	**7** (54)
Tree condition (7)	**0**	**0**
Deer (3)	**0**	**2** (67)
Landscape (2)	**0**	**1** (50)
Physical features (4)	**0**	**1** (25)
Spring climate change (6)	**1** (17)	**0**
Winter climate change (9)	**2** (22)	**0**
Predation (1)	**0**	**0**

Table 3.12 Summary of significant relationships between explanatory variables and site scores on the first two axes of the PCA of change between the 1980s and 2003-04 at BTO sites. The number of variables in each group is shown in brackets after each variable group name. For each PCA axis, the number of significant relationships is shown in bold followed in brackets by the percentage of variables in that group with significant relationships.

Effect	Axis 1	Axis 2	Effect	Axis 1	Axis 2
Location			**Deer**		
Longitude		- **	Trackwaysper100m		+ ***
Latitude	+ ***	- ***	DeerPCAAxis1		+ ***
			DeerPCAAxis2		
Field layer					
Bracken		- ***	**Landscape structure**		
Bramble			threekmHabPCA1		+ **
Herb		+ *	threekmHabPCA2		
Grass					
Moss			**Physical features**		
LeafLitter			Drainage		
BareGround		+ *	Altitude		
p1flayer		+ **	Contigarea		- **
p2flayer		+ *	Tracks		
Structure			**Spring climate change**		
Cover05_2		- *	ChApr_temp		- **
Cover2_4			ChMay_temp	- ***	
Cover4_10			ChApr_cmRain		+ *
Horizivisibility		+ **	ChMay_cmRain		
understpc1			ChgApr_Raindays		+ **
understpc2		- ***	ChgMay_Raindays		
CanopyCov		+ ***			
BasalArea		+ ***	**Winter climate change**		
MaxDBH	- **		ChJan_minT	+ *	
MaxHeight		+ ***	ChFeb_minT		
treestructurepc1		- ***	ChMar_minT		
treestructurepc2	- *	- *	ChJan_MaxT	+ **	
Dominantsp			ChFeb_MaxT		
			ChMar_MaxT	+ **	
Tree condition			ChJan_cmRain		+ *
Lichen	+ *		ChFeb_cmRain		
Ivy			ChMar_cmRain		
ShrubDiversity					
DeadTree			**Predation**		
DeadLimbs			DreyDensity		
GroundWood					
deadwoodpc1					

Table 3.13 Direction and significance of effects of variables on site scores of sites from PCA of change in abundance between the 1980s and 2003-04 at BTO sites. + = positive relationship; - = negative relationship. * = P<0.1; ** P< 0.05; ***= P< 0.01. All effects are calculated from mixed models including region as a random effect and each variable shown as the sole fixed effect.

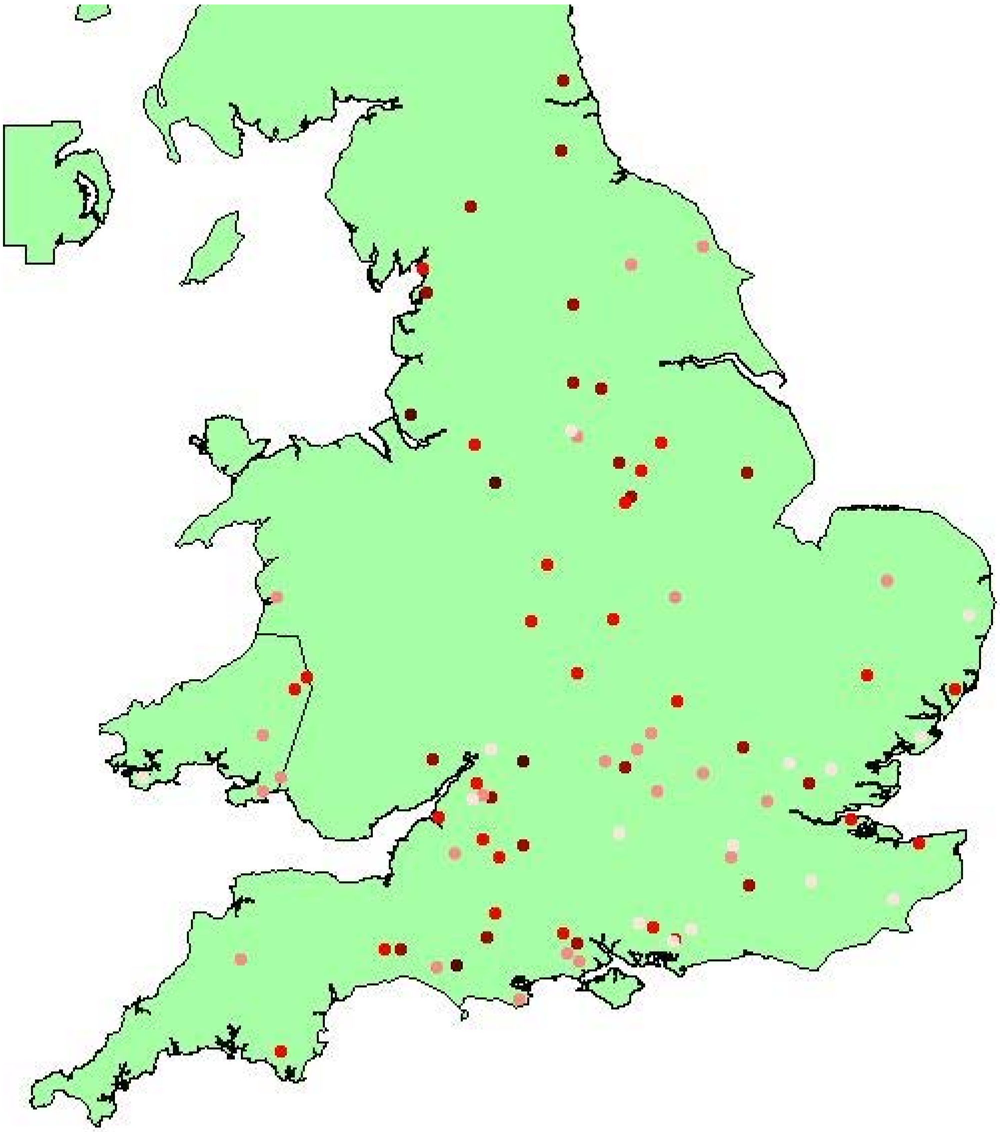

Figure 3.5 Scores on the first axis of the PCA of change values for all species (BTO sites). Sites are graduated monochromatically by colour, those shown in pale pink having the lowest scores and those in dark red the highest. Little geographical patterning is apparent although there was a tendency for scores to be higher in the north than south and away from the southeast.

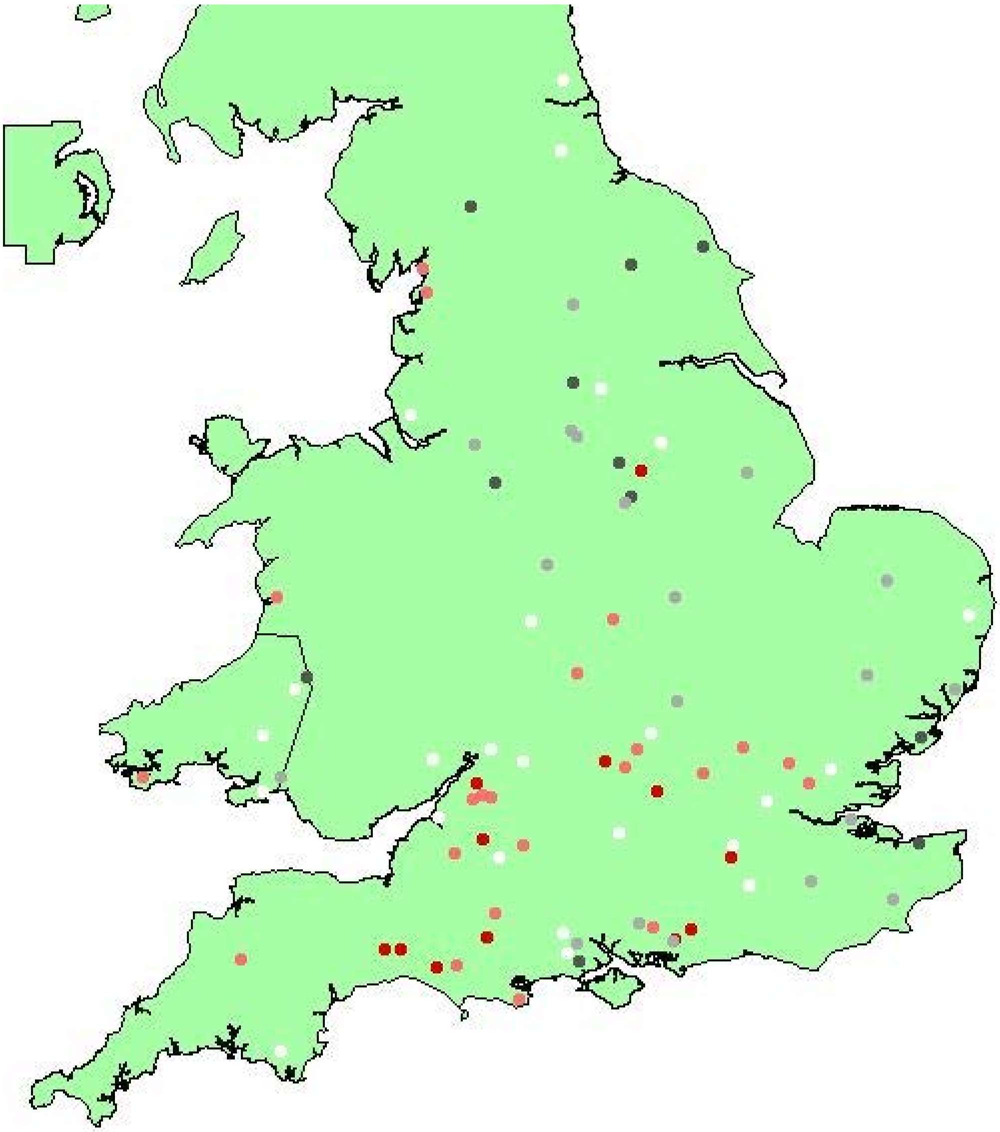

Figure 3.6 Scores on the second axis of the PCA of change values for all species (BTO sites). Sites are graduated by colour, those shown in dark grey having the most negative scores and those in dark red the highest. There are no clear geographical divisions but scores are highest towards the south and west.

3.3.2 RSPB sites

Capsule: Axis 1 describes a gradient with a number of both resident and migratory species doing best at the positive end, these species having done less well in the south than the north. However, there was little evidence of relationships of this axis with climate change, most correlates reflecting the differences in structure and field layer composition between woods in the south and elsewhere. Axis 2 describes a bidirectional gradient with several declining species being negatively loaded and with four increasing residents plus redstart being positively loaded. This axis was related mostly to climate change, with the increasing species doing better where temperatures increased most and rainfall increased least, but also to the density of two potential nest predators / competitors of negatively loaded species.

Axis 1

Table 3.14 shows that chaffinch is strongly positively loaded on the first axis of the PCA of change scores at RSPB sites and 8 species (including three long-distance migrants) are moderately positively loaded and 5 additional residents are weakly positively loaded. This axis therefore represents a gradient of increasingly positive changes of many of the species associated with axis 1 of the PCA abundance in 2003-04 (table 3.4) plus willow warbler, wood warbler and garden warbler.

Table 3.16 shows that scores on this axis were positively related to latitude and negatively related to longitude, so the species associated with it did better in the north and west than south and east (see also figure 3.7). Table 3.15 shows that this axis was most often related to habitat characteristics of the woods themselves, there being relationships with 5 field layer variables, 4 variables describing woodland structural and 6 tree condition variables. In addition, there were single relationships with a measure of deer impacts, landscape composition and spring climate change.

Table 3.15 shows that in the field layer, there were positive relationships with bracken and moss and negative relationships with leaf litter, bare ground and scores on field layer PCA axis 1 - the species associated with this axis therefore did better in woods with more moss and bracken cover and less cover of leaf litter and bare ground. Amongst variables describing woodland structure, there were negative relationships with the maximum DBH and maximum height of trees and with scores on tree structure PCA axis 1. The species associated with this axis therefore did better in woods with smaller trees. These results are consistent with the species doing better in northern birch woods in particular.

Other results show that these species did better in woods with more dead limbs of trees, dead trees and more dead ground wood, greater prevalence of lichen and lower prevalence of ivy and with higher scores on deer impact PCA axis 1 (meaning where there was a higher prevalence of non-bramble browsed stems). The negative relationship with landscape PCA axis 1 suggests these species did better in more natural, less agricultural / urban landscapes. Overall, these results are consistent with the species doing better in less managed woods situated in the rural areas of Scotland and Wales. The relationship with deer impact axis 1 may in fact reflect the presence of grazing by livestock in these woods. There was a negative association with change in the number of days with rain in April, so these species also did better at sites where there was a smaller increase in the frequency of rain in April.

Axis 2

Three residents are moderately positively loaded on the second axis and two further species (one resident and the long-distance migrant redstart) are weakly positively loaded (table 3.14). Hawfinch is moderately negatively loaded on this axis, whilst four further species (two long-distance migrants and two declining residents) are weakly negatively loaded (table 3.14). The species associated with the two ends of this axis do not appear to be associated with a particular type of woodland or woodland structure and this axis is not easily interpretable based solely on species’ loadings.

Scores on this axis were negatively related to latitude and positively related to longitude (table 3.16), positively loaded species therefore doing better in the south and east and negatively loaded species doing better in the north and west (see also figure 3.8). Table 3.15 shows that there were few relationships with characteristics of the woodlands themselves, there being only one each with variables describing field layer and deer impacts. There was also one relationship with landscape structure and one with each of great spotted woodpecker density and grey squirrel drey density. There were more relationships with climate change, however – four with spring climate change and 6 with winter climate change.

The positive relationship with herb cover, negative relationship with deer track way density and negative relationship with scores on landscape PCA axis 1 (table 3.16) indicate that the positively loaded species did better in woods with greater herb cover and lower density of deer track ways, set in more wooded, less grassy landscapes, and that the opposite was true for the negatively loaded species.

The relationships with climate change include negative relationships with changes in amount of rain in January, February and April and number of days with rain in April and May and positive relationships with changes in February minimum temperatures, January and March maximum temperatures and April temperature. These results indicate that positively loaded species did better where winter and spring temperatures increased most, January, February and April rainfall increased least and the frequency of rain in May rain decreased most. The reverse is the case for negatively loaded species. The negative relationship with change in minimum temperature in March appears to be counter to this, although the opposite trends for change in minimum and maximum temperatures in March may be due to the prevalence of high pressure systems causing low minimum temperatures at night and high maximum temperatures during the day in some regions.

The relationships with grey squirrel drey density and great spotted woodpecker density indicate that negatively loaded species declined most where these species occurred at higher densities in 2003-04. This could indicate an effect of nest predation for hawfinch and lesser spotted woodpecker in particular (although the latter is also likely to be affected by competition from great spotted woodpeckers).

Loading	Axis 1 (11.3%)	Axis 2 (7.2%)
-0.6 - -0.5		*HAWFI*
-0.5 - -0.4		
-0.4 - -0.3		**GARWA**, *LESWO*, **WILWA**, *REDPO*
-0.3 - -0.2		BLABI, ROBIN
-0.2 - -0.1		*JAY*, SONTH, DUNNO
-0.1 - 0		MISTH, WREN, BLUTI, **SPOFL**
0 - 0.1	*WILTI*, **REDST**, *HAWFI*, **TREPI**	*WILTI*, CHAFF, GOLDC
0.1 - 0.2	*JAY*, COATI, *REDPO*, MARTI, **SPOFL**, CHIFF, **PIEFL**	COATI, **WOOWA**, **TREPI**, NUTHA, **PIEFL**
0.2 - 0.3	LOTTI, *LESWO*, DUNNO, SONTH	BLACA, CHIFF
0.3 - 0.4	TREEC, NUTHA, ROBIN, GOLDC, MISTH	LOTTI, **REDST**
0.4 - 0.5	**WOOWA**, **WILWA**, BLUTI, GRETI, **GARWA**, BLABI	TREEC, MARTI
0.5 - 0.6	WREN, BLACA	GRETI
0.6 - 0.7	CHAFF	

Table 3.14 Summary of species loadings on the first two axes of the PCA of change in abundance between 1980s and 2003-04 at RSPB sites. Long-distance migrants are shown in bold. Strongly declining residents (defined as species showing a decline of > 20% according to results from the RWBS for both BTO and RSPB datasets or a significant decline according to one dataset) are shown in italics. Species are listed in ascending order of their loading. See Appendix 2 for species codes.

Variable group	Axis 1	Axis 2
Location (2)	**2** (100)	**2** (100)
Field layer (9)	**5** (56)	**1** (11)
Structure (13)	**3** (23)	**0**
Tree condition (7)	**6** (86)	**0**
Deer (3)	**1** (33)	**1** (33)
Landscape (2)	**1** (50)	**1** (50)
Physical features (4)	**0**	**0**
Spring climate change (6)	**1** (17)	**4** (67)
Winter climate change (9)	**0**	**6** (66)
Predation (2)	**0**	**2** (100)

Table 3.15 Summary of significant relationships between explanatory variables and site scores on the first two axes of the PCA of change between the 1980s and 2003-04 at RSPB sites. The number of variables in each group is shown in brackets after each variable group name. For each PCA axis, the number of significant relationships is shown in bold followed in brackets by the percentage of variables in that group with significant relationships.

Effect	Axis 1	Axis 2	Effect	Axis 1	Axis 2
Location			**Deer**		
Longitude	- ***	+ ***	Trackwaysper100m	+ *	- **
Latitude	+ ***	- ***	DeerPCAAxis1	+ ***	
			DeerPCAAxis2		
Field Layer					
Bracken	+ **		**Landscape structure**		
Bramble			threeekmHabPCA1	- ***	
Herb		+ ***	threekmHabPCA2		- ***
Grass					
Moss	+ **		**Physical features**		
LeafLitter	- ***		Drainage	- *	
BareGround	- ***	- *	Altitude		
p1flayer	- ***		Contigarea		
p2flayer			Tracks	- *	
Structure			**Spring climate change**		
Cover05_2			ChApr_temp		+ ***
Cover2_4			ChMay_temp	- *	
Cover4_10			ChApr_cmRain		- ***
Horizivisibility			ChMay_cmRain		- *
understpc1			ChgApr_Raindays	- **	- ***
understpc2			ChgMay_Raindays		- **
CanopyCov					
BasalArea	- *		**Winter climate change**		
MaxDBH	- **		ChJan_minT		
MaxHeight	- ***		ChFeb_minT		+ **
treestructurepc1	+ ***		ChMar_minT		- ***
treestructurepc2			ChJan_MaxT		+ **
Dominantsp	*		ChFeb_MaxT		
			ChMar_MaxT		+ ***
Tree condition			ChJan_cmRain		- ***
Lichen	+ **		ChFeb_cmRain		- **
Ivy	- **		ChMar_cmRain		
ShrubDiversity					
DeadTree	+ **		**Predation**		
DeadLimbs	+ **		DreyDensity		+ **
GroundWood	+ **		CalGRSWO	+ *	+ **
deadwoodpc1	- ***				

Table 3.16 Direction and significance of effects of variables on site scores of sites from PCA of change in abundance between the 1980s and 2003-04 at RSPB sites. + = positive relationship; - = negative relationship. * = P<0.1; ** P< 0.05; ***= P< 0.01. All effects are calculated from mixed models including region as a random effect and each variable shown as the sole fixed effect.

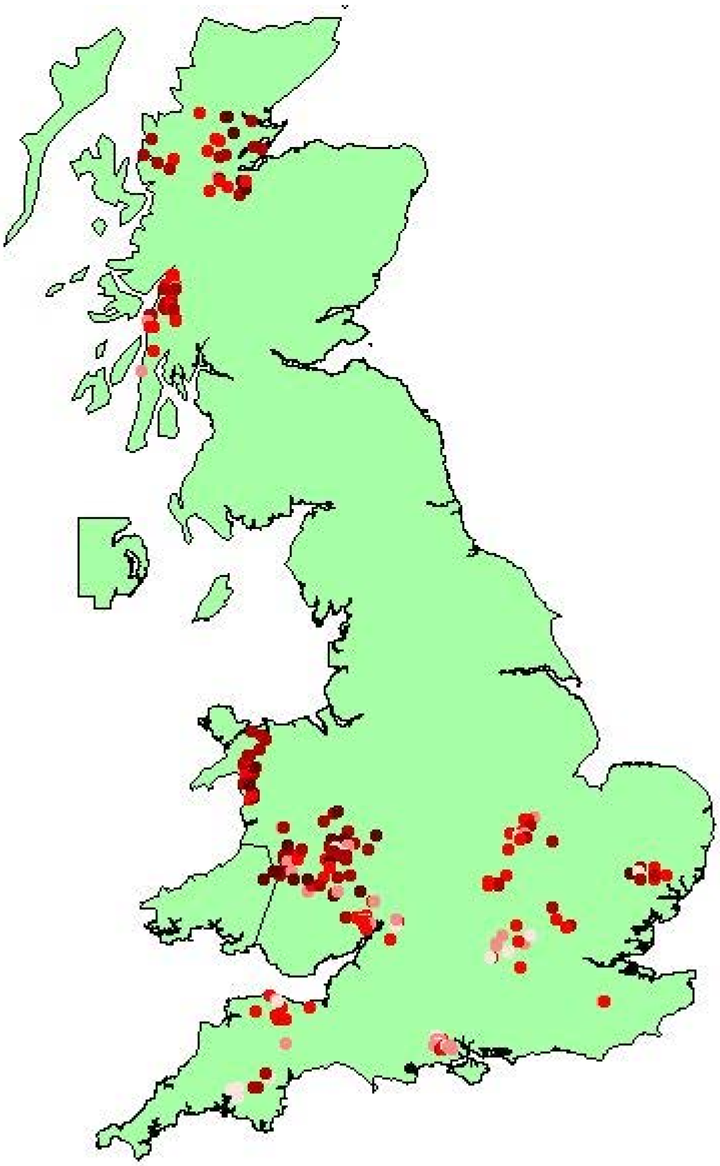

Figure 3.7 Scores on the first axis of the PCA of change values for all species (RSPB sites). Sites are graduated by colour, those shown in pale pink having the lowest scores and those in dark red the highest. Note that there are no clear-cut geographical divisions but the scores of sites in Scotland and Wales were more consistently higher than those elsewhere.

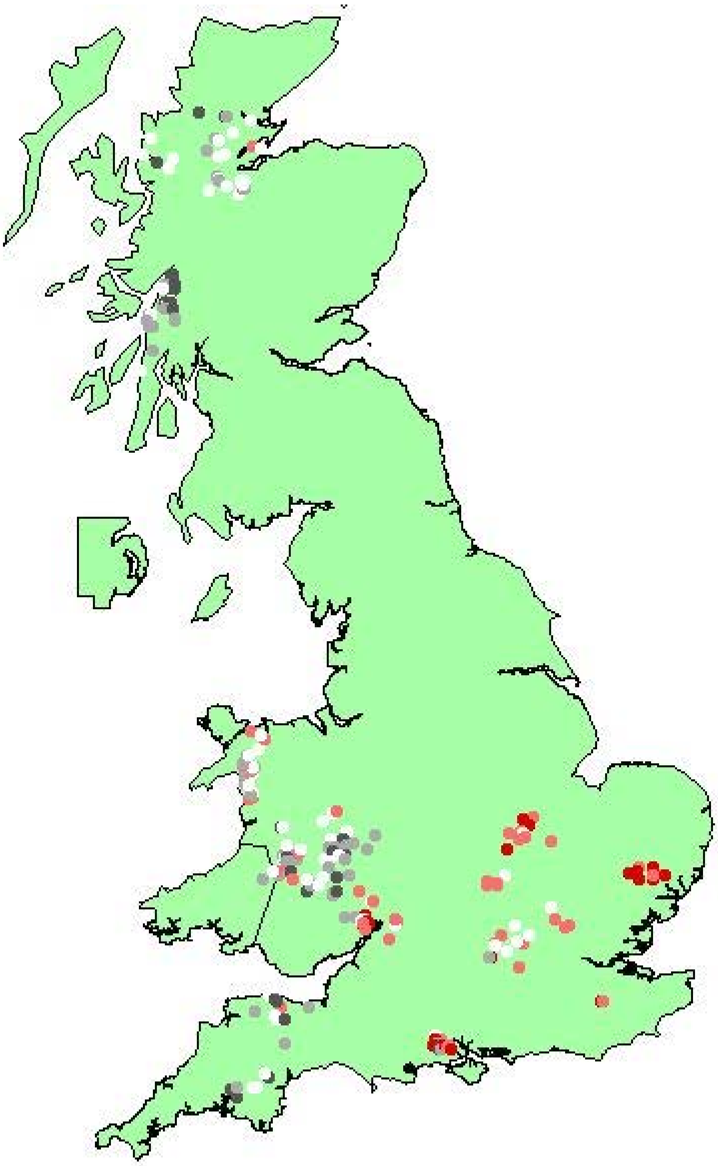

Figure 3.8 Scores on the second axis of the PCA of change values for all species (RSPB sites). Sites are graduated by colour, those shown in dark grey having the lowest scores, those in white intermediate scores and those in dark red the highest. Note that the highest scores were found in England away from the southwest peninsula and the lowest in Devon, Wales and Scotland. The pattern is similar to that for the scores on sites on the first axis except that here the scores of sites in the southwest peninsular of England were similar to those in Wales and Scotland.

3.3.3 Comparison of factors relating to change in abundance at BTO and RSPB sites

The PCAs of change scores for both datasets produce a unidirectional first axis and a bidirectional second axis. Broadly speaking, the first axes are similar in that a variety of increasing residents and a few long-distance migrants including willow warbler and garden warbler are amongst those with important relationships to this axis. In both cases, these species did better in the north and declining residents are not strongly related to the axis. Many of the species that had relatively high loadings on this axis also did on the first axes of the PCAs of abundance (section 3.1) for each dataset. It is noteworthy, however, that scores on those abundance axes were either not related to latitude (BTO) or were higher in the south than the north (RSPB). Therefore those species with important loadings on the first axes for both change and abundance PCAs showed more positive trends away from their centres of abundance. The associations between site scores on these two equivalent first axes of the PCAs of change and the characteristics of the woods and their locations differ between the datasets. Scores on this axis for the BTO dataset were associated with increases in winter temperatures and few other variables, whilst on the RSPB axis there are several relationships with field layer cover, woodland structure and tree condition variables but only one with spring and none with winter climate change. In contrast to this, there was some evidence from both datasets, but especially the RSPB dataset, that whilst the first axes of the PCAs of abundance were related primarily to habitat characteristics (section 3.1), shifts on these axes were related more to winter climate change (section 3.2). In each case, axis 2 of the abundance PCAs was related to both habitat characteristics and climate but shifts were related entirely or almost entirely to habitat characteristics. Note, however, that whilst the abundance axes were modelled with data on recent climate, the shifts were modelled with data on climate change.

The second axes of the PCA for the two datasets contrast in certain respects. For the BTO dataset, this axis separates out species on the basis of their habitat associations, some increasing species associated with understorey being negatively loaded and some decreasing species mainly associated with woods with little understorey being positively loaded. The variables that are related to site scores on this axis largely reflect the fact that each group of species has done better in woods where the habitat is most suitable for them. In contrast, the species positively and negatively loaded on the RSPB axis do not fall into readily interpretable ecological groups and most associations with this axis are climatic rather than with characteristics of the woods themselves. Figure 3.8 shows that there was a strong geographical patterning to this axis, with the negatively loaded species decreasing most in south and east England away from Devon (i.e. from the Forest of Dean and the New Forest eastwards).

3.3.4 Geographical patterning of change scores

To examine cross-site patterns of change, various forms of cluster analysis were performed on both datasets in SAS, both on the change scores for all species and only those for declining species. However, in all cases the analyses failed to find any significant clusters. This suggests that change patterns vary continuously across sites and that there are no distinct demarcations between groups of sites in their patterns of change.

Figures 3.5 to 3.8 show that there was some geographical patterning in the scores on the PCA axes of change in abundance at BTO and RSPB sites. For the BTO datasets, both the shifts on axis 1 of the PCA of abundance (fig. 3.3) and the scores on axis 1 of change in abundance (fig. 3.5) suggest that sites in the southeast have behaved differently from other sites, increasing species having done less well here. For shifts on axis 2 of the PCA of abundance, sites in the southwest and to some extent the southeast showed more positive changes than other regions. A similar situation exists with scores on axis 2 of the PCA of change, scores being more positive for sites in the southwest and also the southeast away from Kent and the New Forest (fig. 3.6). For the RSPB dataset, sites in Scotland and the southeast behaved differently to other sites with respect to shifts on the two axes of the PCA of abundance in 2003-04 as they showed lower increases on axis 1 (Scotland in particular) and showed negative shifts on axis 2 (fig. 3.4). Sites in the west showed the most positive shifts on both axes (fig. 3.4). Figure 3.7 shows that sites in the southwest and southeast (with several exceptions) tended to score less highly on axis 1 of the PCA of change in abundance for the RSPB dataset than sites in other areas. On axis 2, sites in the southwest (excluding the Forest of Dean), Wales and Scotland had lower scores than sites in the rest of England except Buckinghamshire.

3.4 Evidence Relating to Specific Hypotheses Proposed to Explain Change in Woodland Bird Populations

PCAs were carried out for each of the selected groups of species (section 2.4.3) in order to identify axes to act as summary variables for change in that group. Where all species have important positive loadings the axis is a good surrogate for the variation in the species included to the extent indicated by the percentage of variance accounted for by the axis. At the beginning of each section, the loadings of species on the dependent variable PCA axes are briefly outlined.

3.4.1 Hypothesis One: *Declines of some species are driven by increased deer browsing.*

Capsule: There was no evidence from the BTO dataset of deer impacts causing declines. There was no direct evidence from the RSPB dataset but this may be due to the measures of deer impact used. Relationships between patterns of change of ‘deer impact species’ in the RSPB dataset and habitat characteristics were consistent with deer impacts driving declines.

Table 3.17 shows that for both the BTO and RSPB dataset, all species included are moderately or strongly positively loaded on the first axis (note that bullfinch is not included in the RSPB dataset), which therefore represents a gradient along which change scores of all these species become more positive.

Table 3.18 shows that the BTO axis was related only to 1 tree condition variable, 1 spring and 1 winter climate change variable and all variables related to the changes of potential competitors (all were positive relationships). There were no relationships with deer impact variables and as none of the variables with significant relationships (table 3.19.1) are likely to be related to the effects of deer impacts, there is no evidence from this dataset that declines in these species have been influenced by deer browsing. It is notable that there were so many positive relationships with the changes of potential competitors yet so few with characteristics of the woods themselves or their locations. This suggests that some factor not measured by these variables has caused the species included in the dependent and independent variables to share similar changes at individual sites. This effect holds even though the spatial autocorrelation of sites within regions is taken into account and is found for a number of other dependent variables discussed later in this report.

The scores on the equivalent RSPB axis were related to numerous variables (table 3.18), including latitude, longitude, 4 field layer and 9 structural variables, 2 out of 3 deer impact scores, 1 measure of landscape structure, 5 winter climate change variables and the changes of 3 potential competitors. Table 3.19.2 shows that the two relationships with deer impacts were in fact positive relationships between scores on this axis and trackways per 100 metres and deer impact PCA axis 1 scores. This means that the ‘deer impact species’ included in this PCA in fact declined least where there were more deer trackways and higher numbers of non-bramble browsed stems – the opposite of the direction predicted by the hypothesis.

A likely explanation for this is that ‘deer impact species’ have generally done well at sites where the habitat is suitable for both themselves and deer. According to this view, deer are in the process of impacting these sites and thus may not yet have reduced the habitat suitability for the species they are predicted to impact. Sites that have already been impacted would have fewer browsed stems, and may no longer have high densities of deer as habitat suitability for deer, as well as the predicted bird species, is reduced due to the impact of their heavy grazing. Our deer impact measures may be unsuitable as they are indicators of sites about to be or in the process of being impacted rather than of those that have recently been impacted. Examination of the relationships between the scores on this axis and the habitat characteristics of woods for the RSPB data supports this (table 3.19.2). These results show that the ‘deer impact species’ declined more where bramble cover was lower and leaf litter was higher and where cover in the 0.5 – 2 metre and 2 – 4 metre zones was lower. These are the characteristics of woodlands that have been impacted by deer (Gill & Fuller 2007). However, two caveats are important: 1) these relationships could arise because the species have done well where the habitat is suitable for them, rather than badly where it is not; 2) these sites are also those where canopy cover (as well as basal area and the maximum height of trees) is higher and thus deer grazing may not have been the sole factor in creating these conditions.

	BTO	**RSPB**
Loading	**Deer Axis 1**	**Deer Axis 1**
	43.1	**49.2**
0 - 0.1		
0.1 - 0.2		
0.2 - 0.3		
0.3 - 0.4		
0.4 - 0.5		
0.5 - 0.6	**BULLF**	**DUNNO**
0.6 - 0.7	**WILWA, DUNNO**	
0.7 - 0.8	**GARWA**	**WILWA, GARWA**
0.8 - 0.9		

Table 3.17 Summary of species loadings on the first two axes of the PCA of change in abundance between 1980s and 2003-04 of species predicted to be vulnerable to effects of deer grazing at BTO and RSPB sites. Species are listed in ascending order of their loading. See Appendix 2 for species codes.

	BTO	**RSPB**
Variable group	**Deer1**	**Deer1**
Location (2)	**0**	**2** (100)
Field layer (9)	**0**	**4** (44)
Structure (13)	**0**	**9** (69)
Tree condition (7)	**1** (14)	**0**
Deer (3)	**0**	**2** (67)
Landscape (2)	**0**	**1** (50)
Physical features (4)	**0**	**0**
Spring climate change 6)	**1** (17)	**0**
Winter climate change (9)	**1** (11)	**5** (55)
Predation (3)	**0**	**0**
Competition (8)	**8** (100)	**3** (38)

Table 3.18 Summary of significant relationships between explanatory variables and site scores on the first two axes of the PCA of change between the 1980s and 2003-04 at BTO and RSPB sites of declining species predicted to be vulnerable to impacts of deer grazing. The number of variables in each group is shown in brackets after each variable group name. For each PCA axis, the number of significant relationships is shown in bold followed in brackets by the percentage of variables in that group with significant relationships.

Effect	Deer1	Man1	Man2	Effect	Deer1	Man1	Man2
Location				**Landscape**			
Longitude	- *	- *		threekmHabPCA1			
Latitude		+ **		threekmHabPCA2			
Field layer				**Altitude etc**			
Bracken				Drainage			
Bramble				Altitude			
Herb				Contigarea			
Grass			- *	Tracks			
Moss							
LeafLitter				**Spring CC**			
BareGround				ChApr_temp			
p1flayer			+ *	ChMay_temp		- **	
p2flayer				ChApr_cmRain			
				ChMay_cmRain			- *
Structure				ChgApr_Raindays			
Cover05_2				ChgMay_Raindays	+ ***	+ *	
Cover2_4							
Cover4_10				**Winter CC**			
Horizivisibility				ChJan_minT			
understpc1				ChFeb_minT			
understpc2				ChMar_minT			
CanopyCov			+ *	ChJan_MaxT		+ *	
BasalArea				ChFeb_MaxT			
MaxDBH				ChMar_MaxT			
MaxHeight				ChJan_cmRain			
treestructurepc1			- **	ChFeb_cmRain			
treestructurepc2				ChMar_cmRain	- **		
Dominantsp							
				Predation			
Tree condition				DreyDensity			
Lichen	+ ***	+ ***		CalGRSWO			
Ivy				JAY			
ShrubDiversity							
DeadTree				**Competition**			
DeadLimbs				BTch	+ ***	+ ***	
GroundWood				GTch	+ ***	+ ***	
deadwoodpc1				CHch	+ **	+ **	
				CCch	+ ***	+ ***	
Deer				BCch	+ ***	+ ***	
Trackwaysper100m				resFGch	+ ***	+ ***	
DeerPCAAxis1				MDMFGch	+ ***	+ ***	
DeerPCAAxis2				ResMDMFGch	+ ***	+ ***	

Table 3.19.1 Direction and significance of effects of variables on site scores of sites from PCA of change in abundance of declining species vulnerable to the effects of deer grazing and changes in management between the 1980s and 2003-04 at BTO sites. + = positive relationship; - = negative relationship. * = P<0.1; ** P< 0.05; ***= P< 0.01. All effects are calculated from mixed models including region as a random effect and each variable shown as the sole fixed effect.

	Deer1	Man1	Man2	Effect	Deer1	Man1	Man2
Location				**Landscape**			
Longitude	- ***	- ***		threekmHabPCA1	- ***	- ***	
Latitude	+ ***	+ ***		threekmHabPCA2			
Field Layer				**Altitude etc**			
Bracken	+ *	+ *		Drainage			
Bramble	+ *		- ***	Altitude			
Herb	- ***	- ***		Contigarea			
Grass				Tracks			
Moss	+ *	+ *					
LeafLitter	- ***	- ***		**Spring CC**			
BareGround	- **	- **		ChApr_temp		- *	
p1flayer	- **	- ***		ChMay_temp			
p2flayer				ChApr_cmRain			
				ChMay_cmRain			- *
Structure				ChgApr_Raindays			
Cover05_2	+ **	+ **		ChgMay_Raindays	+ ***		
Cover2_4	+ *	+ *					
Cover4_10			+ *	**Winter CC**			
Horizivisibility				ChJan_minT			
understpc1	- **	- **		ChFeb_minT	- ***	- ***	
understpc2			- *	ChMar_minT	+ *	+ **	
CanopyCov	- ***	- ***		ChJan_MaxT	- **	- ***	
BasalArea	- ***	- ***		ChFeb_MaxT	- ***	- ***	
MaxDBH				ChMar_MaxT	- ***	- ***	- **
MaxHeight	- **	- **		ChJan_cmRain			
treestructurepc1	+ ***	+ ***		ChFeb_cmRain		+ ***	
treestructurepc2	+ ***	+ ***		ChMar_cmRain	- **	- **	
Dominantsp	*						
				Predation			
Tree condition				DreyDensity			
Lichen			+ ***	CalGRSWO			
Ivy				JAY			
ShrubDiversity							
DeadTree			+ **	**Competition**			
DeadLimbs			+ *	BTch	+ ***		
GroundWood	+ *	+ **		GTch	+ ***		
deadwoodpc1		- **	- **	CHch	+ **	+ *	
				CCch	+ ***		
Deer				BCch	+ ***	+ ***	
Trackwaysper100m	+ **	+ **		resFGch	+ ***		
DeerPCAAxis1	+ ***	+ ***		MDMFGch	+ ***	+ ***	
DeerPCAAxis2				ResMDMFGch	+ ***	+ **	

Table 3.19.2 Direction and significance of effects of variables on site scores of sites from PCA of change in abundance of declining species vulnerable to the effects of deer grazing and changes in management between the 1980s and 2003-04 at RSPB sites. + = positive relationship; - = negative relationship. * = P<0.1; ** P< 0.05; ***= P< 0.01. All effects are calculated from mixed models including region as a random effect and each variable shown as the sole fixed effect.

3.4.2 Hypothesis Two: *Changes in woodland management have driven declines in some species.*

Capsule: There was little evidence from the BTO dataset that clearly related declines to possible changes in woodland management. There was more support for the hypothesis from the RSPB dataset, results being consistent with a possible role for reduction in active management and increases in the age of stands but not for reductions in stand condition.

Predicted relationships between reduction in active management and individual habitat measures, together with the predicted direction of relationships with individual species population changes, are given in Amar *et al.* (2006) [table 3.4.6]. These are outlined below where necessary for interpreting the results from the present analyses.

Table 3.20 shows that axis 1 for the BTO and RSPB datasets is similar, with all species except willow tit (BTO axis) or willow tit and pied flycatcher (RSPB axis) having important positive loadings and no species having negative loadings. These axes therefore represent a gradient of increasingly positive change for these species, particularly dunnock, garden warbler and willow warbler (plus bullfinch for the BTO dataset). The RSPB axis in particular is therefore very similar to the deer impact species axis. Axis 2 for the BTO dataset contrasts the moderately negative willow warbler and the weakly negative garden warbler with the moderately positive willow tit and pied flycatcher. The RSPB axis 2 contrasts the moderately negative dunnock with the strongly positive pied flycatcher and willow tit. The RSPB and BTO axes are therefore similar, but with dunnock replacing the two warblers at the negative end of the RSPB axis and both axes contrasting the willow tit and pied flycatcher with species strongly associated with dense low understorey / field layer.

Tables 3.19.1 and 3.21 shows that scores on BTO axis 1 were related to latitude and longitude and single tree condition and spring climate variables (as well as positively to the changes in all potential competitor species as in the case of the hypothesis 1 analyses). The tree condition result is a positive relationship with lichen prevalence, which probably reflects the fact that the change scores for these species were more positive in moist unpolluted areas of the north and west and is unlikely to be related to woodland management. There was thus no support from relationships with this axis for the idea of reduction in management driving species declines.

The sole relationship for the second axis was a negative relationship with tree structure PCA axis 1, which suggests that willow warbler and garden warbler did worse in woods with larger trees and a closed canopy whilst the reverse was true for pied flycatcher, willow tit and to some extent bullfinch. This is in contrast with the single species results for pied flycatcher and bullfinch in the binary analysis of population change across both datasets in Amar *et al.* (2006) that found that these species, along with willow warbler and garden warbler, were more likely to decline where canopy cover was higher. There is thus some support from this dataset for the hypothesis that increased canopy cover due to reductions in management have caused decreases in some species, namely willow warbler and garden warbler but contradictory evidence for willow tit and pied flycatcher.

Tables 3.19.2 and 3.21 show that there were numerous relationships for scores on RSPB axis 1. Scores were related to latitude and longitude, 4 field layer, 9 structural, 2 tree condition and 2 deer impact variables as well as 1 measure of landscape structure and 5 of winter climate change as well as to the densities of 5 potential competitors.

The axis scores were lower where there was a higher cover of herb, leaf litter and bare ground and there was less ground deadwood, meaning the species included declined more under these conditions. Herb cover is predicted to decline under reduced active woodland management so this relationship is not consistent with the hypothesis. According to Amar *et al.* (2006), the result for leaf litter supports reduction in stand management driving declines (an increase in leaf litter is predicted) but does not support the role of deterioration of stand condition (leaf litter predicted to decrease). The ground deadwood result is also contrary to the predictions of the stand condition hypothesis. The relationships with woodland structure show that scores were lower (i.e. declines were greater) where there was less cover in the 0.5 – 2 metre zone and canopy cover, basal area and maximum height of trees were all greater. These relationships are broadly supportive of the role of a reduction in active management and an increase in stand age negatively impacting these species according to Amar *et al.* (2006). Overall, relationships with this axis support the idea that increases in stand age and a reduction in active management may have driven declines in these species but provide contradictory evidence to the idea that reduction in stand condition (according to the definition of Amar *et al.* 2006, table 3.4.6) has driven declines.

Table 3.21 shows that axis 2 was related to 1 field layer, 3 tree condition and 1 winter climate change variable. According to table 3.19.2, dunnock declined most where there was lower cover of bramble whilst willow tit and pied flycatcher did declined most where there was lower prevalence of lichens and dead trees and lower scores of deadwood PCA axis 1 (meaning where there were more dead trees and limbs and ground deadwood). These results support the idea that reduction in active management may have contributed to declines of the dunnock, since bramble cover is predicted to decrease. They also support the idea that dunnock had declined due to a reduction in stand condition as measured by deadwood abundance but this seems unlikely given the general habitat associations of the species.

	BTO		**RSPB**	
Loading	**Axis 1**	**Axis 2**	**Axis 1**	**Axis 2**
	30.01	**19.35**	**29.84**	**23.05**
-0.5 - -0.4		**WILWA**		**DUNNO**
-0.4 - -0.3		**GARWA**		
-0.3 - -0.2				
-0.2 - -0.1				
-0.1 - 0				GARWA
0 - 0.1				WILWA
0.1 - 0.2	WILTI	BULLF, DUNNO	PIEFL	
0.2 - 0.3			WILTI	
0.3 - 0.4	**PIEFL**			
0.4 - 0.5				
0.5 - 0.6	**WILWA, BULLF**		**DUNNO**	
0.6 - 0.7	**GARWA**	**WILTI, PIEFL**		**WILTI**
0.7 - 0.8	**DUNNO**		**GARWA, WILWA**	**PIEFL**

Table 3.20 Summary of species loadings on the first two axes of the PCA of change in abundance between 1980s and 2003-04 of species predicted to be vulnerable to effects of changes in the degree of active management at BTO and RSPB sites. Species are listed in ascending order of their loading. See Appendix 2 for species codes.

	BTO		RSPB	
Variable group	**Man1**	**Man2**	**Man1**	**Man2**
Location (2)	**2** (100)	**0**	**2** (100)	**0**
Field layer (9)	**0**	**0**	**4** (44)	**1** (11)
Structure (13)	**0**	**1** (8)	**9** (69)	**0**
Tree condition (7)	**1** (14)	**0**	**2** (29)	**3** (43)
Deer (3)	**0**	**0**	**2** (67)	**0**
Landscape (2)	**0**	**0**	**1** (50)	**0**
Physical features (4)	**0**	**0**	**0**	**0**
Spring climate change (9)	**1** (17)	**0**	**0**	**0**
Winter climate change (9)	**0**	**0**	**7** (77)	**1** (11)
Predation (3)	**0**	**0**	**0**	**0**
Competition (8)	**8** (100)	**0**	**3** (38)	**1** (13)

Table 3.21 Summary of significant relationships between explanatory variables and site scores on the first two axes of the PCA of change between the 1980s and 2003-04 for declining species predicted to be vulnerable to impacts of changes in active management of woods at BTO and RSPB sites. The number of variables in each group is shown in brackets after each variable group name. For each PCA axis, the number of significant relationships is shown in bold followed in brackets by the percentage of variables in that group with significant relationships.

3.4.3 Hypothesis Three: *Climate change is responsible for observed population changes (increases and decreases).*

Capsule: There was some evidence that changes in each group of species were related to climate change. According to both datasets, resident foliage gleaners and middle-distance migrants did best where winter warmed most. Long-distance migrants declined most where spring warmed most (consistent with the effects of spring advance resource asynchrony) and where winters warmed most (potentially consistent with indirect effects via interspecific interactions), although most evidence came from the RSPB dataset. Changes in thrushes were positively related to changes in spring rainfall and negatively related to changes in April temperature according to both datasets and were, according to the BTO dataset, positively related to changes in winter temperature and winter rainfall. There was evidence from both datasets of a positive relationship between changes of small insectivorous residents and changes in winter temperatures and, from the RSPB dataset, of complex relationships between their changes and change in rainfall.

3.4.3.1 Resident foliage gleaners

Table 3.22.1 shows that axis 1 for the BTO dataset had strong positive loadings for blue tit, great tit, long-tailed tit, coal tit and chaffinch and moderate positive loadings for marsh tit, goldcrest and nuthatch. This axis therefore represents a single gradient of increasingly positive population changes for these species. Axis 1 for the RSPB dataset represents a similar gradient of increasingly positive changes for the strongly positively loaded great tit and chaffinch, the moderately positive blue tit, goldcrest and nuthatch and the weakly positively loaded long-tailed tit. Willow tit, coal tit and marsh tit did not have important loadings on this axis, however. Axis 2 for the BTO dataset has a strong negative loading for willow tit and moderate negative loadings for marsh tit and nuthatch, other species not having important loadings on this axis that therefore represents a gradient of increasing negative scores for these three species. The RSPB axis 2 contrasts the changes of the moderately negatively loaded blue tit and weakly negative nuthatch with the changes of the moderately positive long-tailed tit, marsh tit and coal tit.

Table 3.23.1 shows that axis 1 for the BTO dataset was related to latitude, 1 field layer variable and 1, in addition to measures of the changes of two potential competitor species. There was 1 relationship with spring climate change and 4 with winter climate change. Table 3.24.1 shows that scores on this axis were higher where May temperatures had increased least. They were higher where January and February minimum and March maximum temperatures had increased most, but where March minimum temperatures had increased least. This last result contrasts with the result for March maximum temperature and may be due to the prevalence of anti-cyclonic conditions, as discussed elsewhere. Overall, however, there is evidence that resident gleaners increased most where winters warmed most. Axis 2 was related to 3 structural variables and 1 measure of deer impacts (table 3.23.1). It was also related to single measures of spring and winter climate change. Table 3.24.1 shows that scores were more positive (so the negatively loaded willow and marsh tit decreased most and nuthatch increased least) where the number of days with rain in May decreased most and where January maximum temperatures increased least.

Table 3.23.2 shows that axis 1 for the RSPB dataset was related to 2 field layer, 3 structural, 2 tree condition variables and 1 deer impact variable as well as to the abundance of 2 potential nest predators and 2 measures of the change of potential competitors. There was 1 relationship with spring and 5 with winter climate change. Table 3.24.2 shows that the positively loaded species increased most where May temperatures increased least and where February minimum and January and March maximum temperatures increased most but where March minimum temperatures increased least and where January rainfall increased least. As for the BTO dataset, there was thus evidence that the positively loaded species increased most where winters had warmed most. Axis 2 was related to longitude (table 3.24.2), 3 structural variables1 measure of landscape composition and 1 physical feature, as well as to the change in abundance of 1 competitor species (table 3.23.2). There were also two relationships with each of spring and winter climate. According to table 3.24.2, the positively loaded species (coal tit, long-tailed tit and marsh tit) did better where both the number of days with rain and amount of rain in April increased least, with the reverse being true for the negatively loaded species (blue tit and nuthatch). The positively loaded species also did better where February maximum temperature and the amount of rain in January increased least, so the negatively loaded species did best where these measures increased most.

3.4.3.2 Middle-distance migrants

Both blackcap and chiffchaff were strongly positively loaded onto the PCA axis (table 3.22.2), this axis therefore effectively summarises their collective population changes. The loadings were higher for the BTO dataset, suggesting that the changes of the two species covaried more closely in this set of sites.

The BTO axis was related to latitude (tables 3.23.1 and 3.24.1), to 4 woodland structure variables and to 1 variable related to each of field layer cover, tree condition and deer impacts as well as to 4 measures of the change of potential competitors. There was one relationship to spring and none to winter climate change, these species increasing most where May temperatures increased least (table 3.24.1).

Table 3.23.2 shows that the RSPB axis was related to latitude and longitude, 2 woodland structure variables and single variables relating to field layer cover, tree condition, deer impacts, landscape composition and the abundance of grey squirrel dreys, as well as 3 measures of the population change of potential competitors. There were 3 relationships with spring climate change and 2 with winter climate change. These suggest (table 3.24.2) that these middle-distance migrants increased most where April temperatures showed the greatest rise and where changes in April and May rain fall were most negative. Both of these sets of conditions are likely to increase the breeding success of these early breeding species. They also increased most where February and March maximum temperatures increased most. This is the same pattern as shown by resident foliage gleaners (section 3.4.3.1) and the reverse shown by long-distance migrants (section 3.4.3.3). Although these conditions are likely to promote higher levels of over winter survival and pre-breeding body condition in these species, the wintering population of blackcaps does not breed here and it is unclear what proportion of the wintering chiffchaff population does (Greg Conway *pers. comm.).* However, the breeding population of chiffchaffs begins to arrive from mid-February and the blackcaps from mid-March so it is likely that they would benefit from increasing mild conditions at this time.

3.4.3.3 Long-distance migrants

The first axis for the BTO dataset has a strong positive loading for redstart and moderate positive loadings for tree pipit, spotted flycatcher and wood warbler (table 3.22.3). No species have important negative loadings so this axis represents a unidirectional gradient of increasingly positive change scores for these species. The equivalent RSPB axis has a strong positive loading for willow warbler, moderate positive loadings for tree pipit, garden warbler, pied flycatcher and wood warbler and a weak positive loading for spotted flycatcher and so represents a gradient of increasingly positive scores for all species except redstart. Axis 2 for the BTO dataset contrasts the changes of the strongly positive willow warbler and garden warbler with those of the moderately negative tree pipit, whilst the RSPB equivalent contrasts willow warbler (moderately positively loaded) and garden warbler (weakly positively loaded) with the strongly negative redstart and weakly negative spotted flycatcher.

Table 3.23.1 shows that axis 1 of the BTO data was related to 2 field layer, 1 structural and 1 tree condition variable, 1 physical feature, 1 measure of landscape structure and to 5 variables relating to changes of potential competitor species. There was a single relationship with climate change – the long-distance migrants declined more where maximum temperature in February increased most (table 3.24.1). These species are not present on the breeding sites at this time of year so cannot be directly affected by this climatic variable. It is possible, though, that they could be affected indirectly via competitive effects with residents that are influenced by winter conditions (see below & section 3.4.5) but as this is a single relationship, no strong inference can be drawn. Axis 2 was related to latitude (table 3.24.1), 2 field layer, 3 structural and 1 tree condition variable, as well as 1 deer impact measure and 6 measures of potential competitor changes. There was 1 relationship with spring climate change – a negative relationship with change in May temperature (table 3.24.1) that suggests that garden and willow warblers declined most where May temperatures increased most, and tree pipit declined most where it increased least.

RSPB axis 1 was related to latitude and longitude, 4 variables related to each of field layer cover, structure and tree condition, 1 measure of deer impacts and 2 measures of landscape structure, in addition to 6 measures of the change of potential competitor species (table 3.23.2). There were several relationships with measures of climate change – 2 for spring and 6 for winter. Table 3.24.2 shows that scores on this axis were lower (i.e. declines of species with important positive loadings were greater) where the number of days with rain in April and the mean temperature in May increased most. Assuming that springs have advanced most where they have warmed most, the latter result is potentially consistent with migrants having suffered from resource asynchrony. Amongst winter climate variables, declines were greater where minimum temperature in January and maximum temperature in January, February and March increase most, as well as where February rainfall increased most and March rainfall decreased least. The relationships with winter temperature add weight to the finding from the BTO dataset and suggest that the long-distance migrants could be affected by competition from resident species benefiting from climatic amelioration in winter. This is supported quite strongly by the fact that the main axis for variation in population change of resident foliage gleaners showed opposite relationship – i.e. they increased most in the same climatic conditions that long-distance migrants declined most (table 3.24.2 & section 3.4.3.1).

According to table 3.23.2, axis 2 was related to latitude and longitude, 4 structural variables and 1 variable related to each of deer impacts, landscape structure and the physical characteristics of woods, as well as to 1 measure of the changes of potential competitors. There were 3 relationships with each of spring and winter climate change, suggesting there may be a difference in the way different species responded to climate change. The spring climate relationships suggest (table 3.24.2) that positively loaded willow and garden warblers declined most where April and May temperatures increased most (potentially indicative of resource asynchrony as above) and where the number of days with rain in May decreased most, with the negatively loaded spotted flycatcher and redstart declining most where April and May temperatures increased least and May rain days decreased least. Winter climate relationships suggest that the positively loaded species declined most where February minimum and maximum temperatures increased most and where January and February rainfall increased least, with the reverse being true for the negatively loaded species.

3.4.3.4 Thrushes

For both datasets, all three species have positive loadings the PCA axis (table 3.22.4), those of song thrush and blackbird being strong and that of mistle thrush moderate on the BTO axis and mistle thrush and blackbird being strong and song thrush weak for the RSPB axis. The axes therefore summarise the changes of these species well, although least well for song thrush in the RSPB dataset.

The BTO axis was related to longitude (table 3.24.1), 1 variable describing each of field layer cover and woodland structure, 2 tree condition variables, 1 deer impact score and 7 measures of the change of resident and middle-distance foliage gleaners (table 3.23.1). There were 5 relationships with variables describing both spring and winter climate change. Table 3.24.1 shows that the thrushes did better where April temperature increased least and where changes in both the amount of rainfall and number of days with rainfall in both April and May where more positive. These results accord with the knowledge that these species benefit from wet conditions in spring due to increased availability of soil invertebrates during breeding attempts. These species also did better where January and March temperatures increased most and where January and February rainfall increased most but where March rainfall decreased most. The latter result is unintuitive, given the positive associations with all other measures of rainfall and may be related to increased amplitudes of patterns local rainfall variation, given the March is the only month of those examined for which rainfall decreased between 1980 and 2004. Over all, the results suggest that the thrushes have benefited from milder winters (which is intuitive since ground frosts reduce the availability of soil invertebrates) and more rainfall in both winter and spring. The few relationships with other woodland characteristics suggest climate change may be one of the most important drivers of their population changes.

Table 3.23.2 shows that the RSPB axis was related to latitude and longitude, 4 field layer, 2 structural, 1 tree condition and 2 deer impact variables, as well as to the abundance of 1 potential nest predator and 5 measures of change of resident and middle-distance foliage gleaners. There were 4 relationships with spring climate change but in contrast to the BTO axis, none with winter climate change. Table 3.24.2 shows that the thrushes did better where April temperatures increased least but where change in the amount of rainfall in April and May and the number of days with rain in May was more positive. This accords with the results for the BTO axis and is intuitive given spring rainfalls effect of increasing the availability of soil invertebrates during the breeding season.

3.4.3.5 Small insectivorous residents

All species included have important positive relationships on the first axis for each dataset (table 3.22.5), which therefore summarises the changes of these species well in each case. Axis 2 for the BTO dataset has a strong positive loading for goldcrest and a moderate one for long-tailed tit. No other species have important loadings so the axis represents a gradient of increasingly positive changes for these two species alone. Axis 2 for the RSPB dataset contrasts the changes of long-tailed tit (strongly negative) and dunnock (weakly negative) with those of robin (strongly positive) and wren (moderately positive).

Axis 1 for the BTO dataset was related to latitude, and 1 field layer and 2 structural variables, as well as to all 8 measures of change of resident and middle-distance foliage gleaners (table 3.23.1). There was 1 relationship with spring and 3 with winter climate change. Table 3.24.1 shows that these species did better where May temperature increased least and where January, February and March temperatures increased most. These results suggest that these species have benefited from milder winters. Axis 2 was related to latitude (table 3.24.1), 3 field layer, 1 structural, 1deer impact and 1 landscape composition variable as well as to 3 measures of change of potential competitor species. There were no relationships with climate change.

For the RSPB dataset, axis 1 was related to latitude and longitude, 3 variables related to woodland structure, 2 to tree condition, 1 measure of deer impacts and 1 physical feature as well as to 6 measures of the changes of potential competitor species (table 3.23.2). There were 2 relationships with spring climate change and 3 with winter climate change. Table 3.24.2 shows that these species did better where May temperatures and the number of days with rain in April increased least and where the number of days with rain in May decreased least. They also did better where January maximum temperatures increased most, where January rainfall increased least and where March rainfall decreased least. There were therefore surprisingly more relationships with changes in rainfall than temperature and these were in different directions for different months making conclusions difficult to draw, although there was some evidence of an effect of winter temperatures as for the BTO dataset. Axis 2 was related to longitude (table 3.24.2), 5 variables describing woodland structure, 5 tree condition variables, 1 measure of landscape composition and 1 physical feature as well as to 2 measures of change in abundance of potential competitor species. There were 5 relationships with spring climate change and 2 with winter climate change. Table 3.2.4.2 shows that the positively loaded species (robin and wren) did best where April temperatures increased least and changes in the amount of rain and number of days with rain in both April and May were more positive, the reverse being true for the negatively loaded species (long-tailed tit and dunnock). The positively loaded species also did better where March maximum temperatures increased least and January rainfall increased most, with the reverse again being true for the negatively loaded species. These results agree with the results for spring climate change in that the positively loaded species have done better in areas with increasing rainfall and the negatively loaded species have done better in areas with increasing temperatures.

Table 3.22 Summary of species loadings on the first two axes of the PCA of change in abundance between 1980s and 2003-04 of species predicted to be affected by climate change at BTO and RSPB sites. Species are listed in ascending order of their loading. See Appendix 2 for species codes.

3.22.1 Resident foliage-gleaners

	BTO		**RSPB**	
Loading	**Axis 1**	**Axis 2**	**Axis 1**	**Axis 2**
	36.96	**13.23**	**21.07**	**15.04**
-0.8 - -0.7		**WILTI**		
-0.7 - -0.6				
-0.6 - -0.5				**BLUTI**
-0.5 - -0.4		**MARTI, NUTHA**		
-0.4 - -0.3				**NUTHA**
-0.3 - -0.2				CHAFF
-0.2 - -0.1		COATI	WILTI	
-0.1 - 0				WILTI
0 - 0.1		GOLDC		GRETI
0.1 - 0.2	WILTI	BLUTI, GRETI		
0.2 - 0.3		CHAFF, LOTTI	COATI, MARTI	GOLDC
0.3 - 0.4			**LOTTI**	
0.4 - 0.5	**GOLDC, NUTHA**		**GOLDC, NUTHA**	**COATI**
0.5 - 0.6	**MARTI**		**BLUTI**	**LOTTI, MARTI**
0.6 - 0.7	**LOTTI, COATI, CHAFF**		**CHAFF**	
0.7 - 0.8	**GRETI**		**GRETI**	
0.8 - 0.9	**BLUTI**			

3.22.2 Middle-distance migrants

	BTO	**RSPB**
Loading	**Axis 1**	**Axis 1**
	76.84	**57.18**
0 - 0.1		
0.1 - 0.2		
0.2 - 0.3		
0.3 - 0.4		
0.4 - 0.5		
0.5 - 0.6		
0.6 - 0.7		
0.7 - 0.8		**BLACA, CHIFF**
0.8 - 0.9	**BLACA, CHIFF**	

Table 3.22.3 Long-distance migrants

	BTO		RSPB	
Loading	**Axis 1**	**Axis 2**	**Axis 1**	**Axis 2**
	20.74	**20.12**	**22.48**	**18.12**
-0.8 - 0.7				**REDST**
-0.7 - 0.6				
-0.6 - -0.5				
-0.5 - -0.4		**TREPI**		
-0.4 - -0.3				**SPOFL**
-0.3 - -0.2	PIEFL			WOOWA, PIEFL
-0.2 - -0.1		SPOFL		TREPI
-0.1 - 0				
0 - 0.1		REDST		
0.1 - 0.2	WILWA	WOOWA		
0.2 - 0.3	GARWA	PIEFL	REDST	
0.3 - 0.4			**SPOFL**	**GARWA**
0.4 - 0.5	**WOOWA**		**PIEFL, WOOWA**	
0.5 - 0.6	**TREPI, SPOFL**		**TREPI, GARWA**	**WILWA**
0.6 - 0.7	**REDST**	**GARWA**	**WILWA**	
0.7 - 0.8				
0.8 - 0.9		**WILWA**		

3.22.4 Thrushes

	BTO	RSPB
Loading	**Axis 1**	**Axis 1**
	49.33	**40.24**
0 - 0.1		
0.1 - 0.2		
0.2 - 0.3		
0.3 - 0.4		**SONTH**
0.4 - 0.5		
0.5 - 0.6	**MISTH**	
0.6 - 0.7		
0.7 - 0.8	**SONTH, BLABI**	**MISTH, BLABI**

3.22.5 Small insectivorous residents

	BTO		RSPB	
Loading	**Axis 1**	**Axis 2**	**Axis 1**	**Axis 2**
	45.11	**20.86**	**28.44**	**24.03**
-0.6 - -0.5				**LOTTI**
-0.5 - -0.4				
-0.4 - -0.3				**DUNNO**
-0.3 - -0.2		DUNNO, WREN, ROBIN		GOLDC
-0.2 - -0.1				
-0.1 - 0				
0 - 0.1				
0.1 - 0.2				
0.2 - 0.3				
0.3 - 0.4	**GOLDC**		**ROBIN**	
0.4 - 0.5			**LOTTI**	**WREN**
0.5 - 0.6	**LOTTI**	**LOTTI**	**DUNNO**	
0.6 - 0.7	**DUNNO**		**GOLDC, WREN**	
0.7 - 0.8	**ROBIN**	**GOLDC**		**ROBIN**
0.8 - 0.9	**WREN**			

Table 3.23 Summary of significant relationships between explanatory variables and site scores on the first two axes of the PCA of change between the 1980s and 2003-04 at a) BTO sites and b) RSPB sites of groups of species predicted to be affected by climate change. The number of variables in each group is shown in brackets after each variable group name. For each PCA axis, the number of significant relationships is shown in bold followed in brackets by the percentage of variables in that group with significant relationships. Column headings refer to PCA axes as follows: ResG1 – resident foliage gleaners axis 1; ResG2 – resident foliage gleaners axis 2; MDMs1 – middle-distance migrants axis 1; LDMs1 – long-distance migrants axis 1; LDMs2 – long-distance migrants axis 2; Thrush1 – thrushes axis 1; SIR1 – small resident foliage gleaners axis 1; SIR2 – small resident foliage gleaners axis 2.

Table 3.23.1 BTO sites

	ResG1	**ResG2**	**MDMs1**	**LDMs1**	**LDMs2**	**Thrush1**	**SIR1**	**SIR2**
Location (2)	**1** (50)	**0**	**1** (50)	**0**	**1** (50)	**1** (50)	**1** (50)	**1** (50)
Field layer (9)	**1** (11)	**0**	**1** (11)	**2** (22)	**2** (22)	**1** (11)	**1** (11)	**3** (33)
Structure (13)	**0**	**3** (23)	**4** (31)	**1** (8)	**3** (23)	**1** (8)	**2** (15)	**1** (8)
Tree condition (7)	**0**	**0**	**1** (14)	**1** (14)	**1** (14)	**2** (29)	**0**	**0**
Deer (3)	**0**	**1** (33)	**1** (33)	**0**	**1** (33)	**1** (33)	**0**	**1** (33)
Landscape (2)	**0**	**0**	**0**	**1** (50)	**0**	**0**	**0**	**1** (50)
Physical features (4)	**1** (25)	**0**	**1** (25)	**1** (25)	**0**	**0**	**0**	**2** (50)
Spring climate change 6)	**1** (17)	**1** (17)	**1** (17)	**0**	**1** (17)	**5** (83)	**1** (17)	**0**
Winter climate change (9)	**4** (44)	**1** (11)	**0**	**1** (11)	**0**	**5** (55)	**3** (33)	**0**
Predation (3)	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Competition (8)	**2** [(66)]	**0**	**4** [(100)]	**5** (63)	**6** (75)	**7** (88)	**8** (100)	**3** (38)

Table 3.23.2 RSPB sites

	ResG1	**ResG2**	**MDMs1**	**LDMs1**	**LDMs2**	**Thrush1**	**SIR1**	**SIR2**
Location (2)	**0**	**1** (50)	**2** (100)	**2** (100)	**2** (100)	**2** (100)	**2** (100)	**1** (50)
Field layer (9)	**2** (22)	**0**	**1** (11)	**4** (44)	**0**	**4** (44)	**0**	**0**
Structure (13)	**3** (23)	**3** (23)	**2** (15)	**4** (31)	**4** (31)	**2** (15)	**3** (23)	**5** (38)
Tree condition (7)	**2** (29)	**0**	**1** (14)	**4** (57)	**0**	**1** (14)	**2** (29)	**5** (71)
Deer (3)	**1** (33)	**0**	**1** (33)	**1** (33)	**1** (33)	**2** (67)	**1** (33)	**0**
Landscape (2)	**0**	**1** (50)	**1** (50)	**2** (100)	**1** (50)	**0**	**0**	**1** (50)
Physical features (4)	**0**	**1** (25)	**0**	**0**	**1** (25)	**0**	**1** (25)	**1** (25)
Spring climate change 6)	**1** (17)	**2** (33)	**3** (50)	**2** (33)	**3** (50)	**4** (67)	**2** (33)	**5** (83)
Winter climate change (9)	**5** (55)	**2** (22)	**2** (22)	**6** (66)	**3** (33)	**0**	**3** (22)	**2** (22)
Predation (3)	**2** (67)	**0**	**1** (33)	**0**	**0**	**1** (33)	**0**	**1** (33)
Competition (8)	**2** [(66)]	**1** [(33)]	**3** [(75)]	**6** (75)	**1** (13)	**5** (63)	**6** (75)	**2** (25)

Table 3.24 Direction and significance of effects of variables on site scores of sites from PCA of change in abundance between the 1980s and 2003-04 at BTO and RSPB sites of species predicted to be affected by climate change. + = positive relationship; - = negative relationship. * = P<0.1; ** P< 0.05; ***= P< 0.01. All effects are calculated from mixed models including region as a random effect and each variable shown as the sole fixed effect. Column headings refer to PCA axes as follows: ResG1 – resident foliage gleaners axis 1; ResG2 – resident foliage gleaners axis 2; MDMs1 – middle-distance migrants axis 1; LDMs1 – long-distance migrants axis 1; LDMs2 – long-distance migrants axis 2; Thrush1 – thrushes axis 1; SIR1 – small resident foliage gleaners axis 1; SIR2 – small resident foliage gleaners axis 2.

Table 3.24.1 BTO

Effect	**ResG1**	**ResG2**	**MDM1**	**LDM1**	**LDM2**	**Thrush1**	**SIR1**	**SIR2**
Location								
Longitude						- ***		
Latitude	+ ***		+ ***	- *	+ **		+ ***	- ***
Field layer								
Bracken			+ **					- **
Bramble	- *					- **		
Herb	+ *			+ **				
Grass				- **	+ ***			
Moss	+ **						+ **	
LeafLitter								
BareGround								+ ***
p1flayer			- *		- ***			+ *
p2flayer	+ *							+ ***
Structure								
Cover05_2					+ *	- ***		
Cover2_4								+ *
Cover4_10								+ *
Horizivisibility								
understpc1						+ *		
understpc2								- **
CanopyCov			- **					
BasalArea			- **					
MaxDBH		- **		- **			- ***	
MaxHeight					- **			
treestructurepc1		+ **	+ **		+ **		+ **	
treestructurepc2	- *						- *	
Dominantsp					*			
Tree condition								
Lichen		- *	+ **	- **	+ ***	+ **		
Ivy								
ShrubDiversity								
DeadTree							+ *	
DeadLimbs						+ *		
GroundWood								+ *
deadwoodpc1						- **		- *

Effect	**ResG1**	**ResG2**	**MDM1**	**LDM1**	**LDM2**	**Thrush1**	**SIR1**	**SIR2**
Deer								
Trackwaysper100m		+ ***						+ ***
DeerPCAAxis1			- ***	+ *	- **	+ **		
DeerPCAAxis2				+ *				
Landscape								
threekmHabPCA1	+ *		- *	+ **				+ **
threekmHabPCA2								
Altitude etc								
Drainage								+ ***
Altitude						+ *		
Contigarea		- *	+ ***	- **				- ***
Tracks	+ **							
Spring CC								
ChApr_temp						- ***		
ChMay_temp	- ***		- ***		- ***		- ***	
ChApr_cmRain						+ ***		
ChMay_cmRain						+ **		
ChgApr_Raindays						+ **		
ChgMay_Raindays		- ***			+ *	+ ***		
Winter CC								
ChJan_minT	+ **							
ChFeb_minT	+ **	+ *						
ChMar_minT	- ***							
ChJan_MaxT	+ *	- **				+ ***	+ **	
ChFeb_MaxT				- **			+ **	
ChMar_MaxT	+ ***					+ **	+ **	
ChJan_cmRain					- *	+ ***		
ChFeb_cmRain						+ **		
ChMar_cmRain						- ***		
Predation								
DreyDensity								
CalGRSWO			- *					
JAY				+ *				
Competition								
BTch	▨	▨	+ ***	+ **	+ ***	+ ***	+ ***	+ **
GTch	▨	▨	+ **	+ ***		+ ***	+ ***	
CHch	▨	▨	+ **	+ ***	+ *		+ ***	+ **
CCch	+ *				+ ***	+ **	+ ***	
BCch	+ ***				+ ***	+ ***	+ ***	- *
resFGch	▨	▨	+ ***	+ ***	+ ***	+ ***	+ ***	+ **
MDMFGch	+ ***				+ ***	+ ***	+ ***	- *
ResMDMFGch	▨	▨		+ ***	+ ***	+ ***	+ ***	+ *

Table 3.24.1 Continued**.**

Table 3.24.2 RSPB

	ResG1	ResG2	MDM1	LDMs1	LDMs2	Thrush1	SIR1	SIR2
Location								
Longitude		+ ***	+ **	- ***	- ***	- ***	- **	- ***
Latitude	+ *		- *	+ ***	+ ***	+ ***	+ ***	
Field Layer								
Bracken			+ *	+ *			+ *	
Bramble			+ ***					- *
Herb	+ **				- *	- *		
Grass				+ *		+ **		
Moss				+ ***				
LeafLitter		- *	- *	- ***		- ***		
BareGround	- **			- **	+ *	- **		+ *
p1flayer	- *			- ***		- ***	- *	
p2flayer								
Structure								
Cover05_2			+ **					
Cover2_4			+ **					- **
Cover4_10		+ *		+ *	- **			
Horizivisibility								
understpc1		- *	- *					+ **
understpc2					+ ***			
CanopyCov				- *	- ***		- *	
BasalArea		- **	- *	- **				+ **
MaxDBH	- **						- *	
MaxHeight	- **			- ***		- ***	- **	- *
treestructurepc1	+ *			+ ***			+ ***	
treestructurepc2	- **	+ **	+ *					- **
Dominantsp			*		***	***		
Tree condition								
Lichen				+ ***		+ ***		+ **
Ivy	- **		- **				- ***	
ShrubDiversity								- **
DeadTree				+ ***	- *			+ ***
DeadLimbs	+ **				- *			+ **
GroundWood				+ **			+ *	
deadwoodpc1	- *			- ***	+ *		- **	- ***
Deer								
Trackwaysper100m			+ *		+ **			
DeerPCAAxis1			+ **	+ ***		+ ***	+ **	
DeerPCAAxis2	- **					- **		
Landscape								
threekmHabPCA1	- *	+ *		- ***	- *			
threekmHabPCA2			- **	+ **				+ **

	ResG1	ResG2	MDM1	LDMs1	LDMs2	Thrush1	SIR1	SIR2
Physical features								
Drainage					+ **			
Altitude		- **					+ ***	+ ***
Contigarea			+ *					
Tracks								
Spring CC								
ChApr_temp		+ *	+ **		- ***	- **		- **
ChMay_temp	- ***			- ***	- ***		- **	
ChApr_cmRain		- ***				+ **		+ ***
ChMay_cmRain			- **			+ **		+ **
ChgApr_Raindays	- *	- ***	- ***	- **			- **	+ ***
ChgMay_Raindays			- *		+ **	+ **	+ **	+ **
Winter ClimCh								
ChJan_minT								
ChFeb_minT	+ **	- *		- ***	- ***			
ChMar_minT	- **						- *	+ *
ChJan_MaxT	+ **	- *	+ *	- ***			+ **	
ChFeb_MaxT		- ***	+ **	- ***	- ***	- *		
ChMar_MaxT	+ ***		+ ***	- ***			+ *	- ***
ChJan_cmRain	- **	- ***			+ *		- **	+ **
ChFeb_cmRain				+ ***	+ ***			
ChMar_cmRain				- ***			+ ***	
Predation								
DreyDensity	+ ***		+ **				+ *	- ***
CalGRSWO	+ **					+ **		
JAY					- *			
Competition								
BTch								+ *
GTch			+ **	+ ***	- ***		+ ***	
CHch			+ **	+ ***		+ ***	+ **	
CCch	+ *							
BCch	+ ***	+ **		+ ***		+ ***	+ ***	- ***
resFGch			+ ***	+ **		+ ***	+ ***	
MDMFGch	+ **			+ ***		+ ***	+ ***	- **
ResMDMFGch				+ ***		+ ***	+ ***	- *

Table 3.2.4.2 Continued.

3.4.4 Hypothesis Four: *That increased levels of nest predation have been responsible for population declines.*

Capsule: There was little evidence to support this hypothesis. There was no evidence from either dataset that the population changes of hole-nesters varied in relation to the densities of potential nest predators. However, there was possible evidence from the RSPB dataset that at least one species of open nester may have declined more where great spotted woodpecker density was higher. This result is supported by results presented in section 3.3.2.

3.4.4.1 Hole nesters

Table 3.25.1 shows that for the BTO dataset, marsh tit and lesser spotted woodpecker have strong positive loadings and pied flycatcher and willow tit moderate positive loadings on axis 1 so this axis represents a gradient of increasingly positive change scores for these species. For the RSPB dataset, axis 1 contrasts the change in abundance of lesser spotted woodpecker (which has a weak negative loading) with the changes of the other three species, especially pied flycatcher which is strongly positively loaded but also the moderately positive marsh tit and weakly positive willow tit. Axis 2 on the RSPB dataset contrasts the changes of the strongly positively loaded willow tit with those of the strongly negatively loaded marsh tit.

Tables 3.26 and 3.27.1 show that the BTO axis was related to latitude, 3 structural and 1 tree condition variable and 2 measures of spring and 4 of winter climate change, as well as to 6 of the 8 variables concerning change in the density of potential competitors. However, there was no relationship with great spotted woodpecker density (or with jay or grey squirrel density) and thus no evidence from this dataset supporting the idea that declines in hole-nesting species may have been due to nest predation from the increased population of great spotted woodpeckers.

The RSPB dataset was related to longitude, 5 structural and 2 tree condition variables, 1 deer impact measure, 2 measures of spring and 3 of winter climate change and to 1 measure of change of resident and middle-distance migrant foliage gleaners (tables 3.26 and 3.27.2). Axis 2 was related to longitude, 3 structural variables and 1 variable relating to each of tree condition and field layer cover. There was no relationship with great spotted woodpecker density (or with jay or grey squirrel density) for either axis so, as for the BTO axis, there is no evidence that nest predation has driven declines in the dependent variable PCA species.

3.4.4.2 Open nesters

Figure 3.25.2 shows that, 5 of the 7 species included for the BTO dataset and 6 of the 7 species included for the RSPB dataset have important positive loadings on axis 1 and this axis therefore represents a gradient of increasingly positive scores for these species. In each case, hawfinch is not importantly loaded which reduces the power of this analysis as hawfinch is a species that has been predicted to suffer high nest predation rates from grey squirrels. It is also one of two species for which Amar *et al.* (2006) showed a negative relationship between change in its populations at individual sites and grey squirrel drey density.

For the BTO dataset, axis 2 contrasts the changes of the moderately negatively loaded chaffinch and wood warbler with those of the moderately positively loaded mistle thrush and hawfinch. The equivalent RSPB dataset contrast the changes of the moderately negatively loaded chaffinch and wood warbler and weakly negatively loaded mistle thrush with the moderately positively loaded hawfinch and weakly positively loaded dunnock and willow warbler and is thus (with the exception of the relationship for mistle thrush) almost equivalent to the BTO axis.

Tables 3.26 and 3.27.1 show that axis 1 for the BTO dataset was related to latitude and 1 variable relating to each of woodland structure, tree condition and spring climate change, as well as to 6 measures of change of potential competitors. Axis 2 was related to 2 measures of woodland structure, 3 measures of tree condition, 1 physical feature and 2 measures of winter climate change. As there were no relationships with grey squirrel or jay density, there was no evidence from the BTO dataset that nest predation had driven declines in these species.

Tables 3.26 and 3.27.2 show that axis 1 for the RSPB dataset was related to latitude and longitude, 5 field layer and 4 structural variables and to 1 measure of deer impact, 2 of landscape composition and 2 of winter climate change, as well as to 3 measures of change in the density of potential competitors. Axis 2 was related to latitude and longitude, 2 field layer and 4 structural variables, 1 measure of spring and 5 of winter climate and to 2 measures of change of potential competitors, as well as to great spotted woodpecker density. This last result suggests that the positively loaded species (hawfinch, dunnock and willow warbler) declined more where great spotted woodpecker abundance was higher, or that the negatively loaded species declined less in these circumstances. These relationships are perhaps unlikely to be related to nest predation, however, since the great spotted woodpecker is likely to be primarily a predator of nests in tree holes. As the most strongly negatively loaded species on this axis, the hawfinch, nests in the canopy near to main branches of trees, it is likely that the woodpeckers opportunistically predate nests of this species so the possibility of an effect cannot be ruled out. It is unlikely that the nests of dunnock or willow warbler are taken by the species, though. Overall, there is no evidence from these results that nest predation by grey squirrels or jays has been important in driving the population declines of these species.

Table 3.25 Summary of species loadings on the first two axes of the PCA of change in abundance between 1980s and 2003-04 of species predicted to be affected by predation at BTO and RSPB sites. Species are listed within a cell in ascending order of their loading. See Appendix 2 for species codes.

Table 3.25.1 Hole nesters

	BTO	**RSPB**	
Loading	**Axis 1**	**Axis 1**	**Axis 2**
	37.85	**29.71**	**26.64**
-0.9 - 0.8			
-0.8 - -0.7			
-0.7 - -0.6			**MARTI**
-0.6 - -0.5			
-0.5 - -0.4			
-0.4 - -0.3		**LESWO**	
-0.3 - -0.2			LESWO
-0.2 - -0.1			
-0.1 - 0			PIEFL
0 - 0.1			
0.1 - 0.2			
0.2 - 0.3			
0.3 - 0.4		**WILTI**	
0.4 - 0.5	**PIEFL**		
0.5 - 0.6	**WILTI**	**MARTI**	
0.6 - 0.7	**LESWO**		
0.7 - 0.8	**MARTI**	**PIEFL**	**WILTI**

Table 3.25.2 Open-nesters

	BTO		RSPB	
Loading	**Axis 1**	**Axis 2**	**Axis 1**	**Axis 2**
	24.51	**18.11**	**25.81**	**16.73**
-0.7 - -0.6				
-0.6 - -0.5		**CHAFF**		**CHAFF**
-0.5 - -0.4		**WOOWA**		**WOOWA**
-0.4 - -0.3				**MISTH**
-0.3 - -0.2		WILWA		
-0.2 - -0.1				
-0.1 - 0	HAWFI			
0 - 0.1				
0.1 - 0.2	WOOWA	GARWA		
0.2 - 0.3		DUNNO	HAWFI	GARWA
0.3 - 0.4	**MISTH**		**DUNNO**	**DUNNO, WILWA**
0.4 - 0.5	**CHAFF**		**WOOWA, MISTH**	**HAWFI**
0.5 - 0.6		**MISTH, HAWFI**	**CHAFF**	
0.6 - 0.7	**DUNNO, WILWA**		**WILWA, GARWA**	
0.7 - 0.8	**GARWA**			

	BTO			RSPB			
	Hole1	**Open1**	**Open2**	**Hole1**	**Hole2**	**Open1**	**Open2**
Location (2)	**1** (50)	**1** (50)	**0**	**1** (50)	**1** (50)	**2** (100)	**2** (100)
Field layer (9)	**0**	**0**	**0**	**0**	**1** (11)	**5** (56)	**2** (22)
Structure (13)	**3** (23)	**1** (8)	**2** (15)	**5** (38)	**3** (23)	**4** (31)	**4** (31)
Tree condition (7)	**1** (14)	**1** (14)	**3** (43)	**2** (29)	**1** (14)	**0**	**0**
Deer (3)	**0**	**0**	**0**	**1** (33)	**0**	**1** (33)	**0**
Landscape (2)	**0**	**0**	**0**	**0**	**0**	**2** (100)	**0**
Physical features (4)	**0**	**0**	**1** (25)	**0**	**0**	**0**	**0**
Spring climate change (6)	**2** (33)	**1** (17)	**0**	**2** (33)	**0**	**0**	**1** (17)
Winter climate change (9)	**4** (44)	**0**	**2** (22)	**3** (33)	**0**	**2** (22)	**5** (55)
Predation (3)	**0**	**0**	**0**	**0**	**0**	**0**	**1** (33)
Competition (8)	**6** (75)	**5** (63)	**0**	**1** (13)	**0**	**3** (38)	**2** (25)

Table 3.26 Summary of significant relationships between explanatory variables and site scores on the first two axes of the PCA of change between the 1980s and 2003-04 at BTO and RSPB sites of declining species predicted to be vulnerable to impacts of increased nest predation. The number of variables in each group is shown in brackets after each variable group name. For each PCA axis, the number of significant relationships is shown in bold followed in brackets by the percentage of variables in that group with significant relationships. Column headings refer to PCA axes as follows: Hole1 – hole nesters axis 1; Hole2 – hole-nesters axis 2; Open1 – Open-nesters axis 1; Open2 – Open-nesters axis2.

Table 3.27 Direction and significance of effects of variables on site scores of sites from PCA of change in abundance between the 1980s and 2003-04 of species predicted to be affected by nest predation and interspecific competition. 1. BTO sites. 2. RSPB sites. + = positive relationship; - = negative relationship. * = P<0.1; ** P< 0.05; ***= P< 0.01. All effects are calculated from mixed models including region as a random effect and each variable shown as the sole fixed effect. Column headings refer to PCA axes as follows: Hole1 – hole nesters axis 1; Hole2 – hole-nesters axis 2; Open1 – Open-nesters axis 1; Open2 – Open-nesters axis2.

Table 3.27.1 BTO sites

Effect	Hole1	Open1	Open2	LDMGs1	LDMGs2
Location					
Longitude					
Latitude	+ ***	+ **			+ ***
Field layer					
Bracken					
Bramble					
Herb					
Grass					
Moss					
LeafLitter				- *	
BareGround					
p1flayer					
p2flayer					
Structure					
Cover05_2			- **		
Cover2_4					
Cover4_10			+ *		
Horizivisibility	+ **				
understpc1					
understpc2			- **		
CanopyCov					
BasalArea	+ **				
MaxDBH		- **		- *	
MaxHeight					
treestructurepc1				+ *	
treestructurepc2					
Dominantsp					
Tree condition					
Lichen	+ ***	+ ***	+ **		+ ***
Ivy					
ShrubDiversity					
DeadTree					
DeadLimbs			+ ***		+ *
GroundWood			+ *		
deadwoodpc1			- ***		

Effect	**Hole1**	**Open1**	**Open2**	**LDMGs1**	**LDMGs2**
Deer					
Trackwaysper100m					
DeerPCAAxis1					
DeerPCAAxis2					
Landscape					
threekmHabPCA1					- **
threekmHabPCA2					
Altitude etc					
Drainage					
Altitude					+ *
Contigarea			+ **	- ***	
Tracks			- *		
Spring CC					
ChApr_temp					
ChMay_temp	- ***	- **			- *
ChApr_cmRain					
ChMay_cmRain				+ *	
ChgApr_Raindays					
ChgMay_Raindays	+ ***			+ **	
Winter CC					
ChJan_minT	+ **				
ChFeb_minT					
ChMar_minT					
ChJan_MaxT	+ ***		+ **		+ **
ChFeb_MaxT	+ **				+ ***
ChMar_MaxT	+ **				+ **
ChJan_cmRain			+ **		- **
ChFeb_cmRain					
ChMar_cmRain					
Predation					
DreyDensity					
CalGRSWO					
JAY					
Competition					
BTch	+ ***	+ ***		+ ***	+ *
GTch	+ **	+ ***		+ ***	
CHch	+ **	▨	▨	+ **	
CCch		+ ***		+ ***	+ ***
BCch		+ ***		+ **	+ **
resFGch	+ ***	▨	▨	+ ***	
MDMFGch	+ **	+ ***		+ **	+ ***
ResMDMFGch	+ ***	▨	▨	+ ***	+ *

Table 3.27.1 Continued**.**

Table 3.27.2 RSPB sites

	Hole1	Hole2	Open1	Open2	LDMGs1	LDMGs2
Location						
Longitude	+ ***	+ **	- ***	- ***	- ***	- ***
Latitude			+ ***	+ **	+ ***	+ ***
Field Layer						
Bracken					+ *	
Bramble	- *	+ **				
Herb			- **	- ***	- **	
Grass				- *		
Moss			+ **		+ ***	
LeafLitter	- *		- ***		- ***	
BareGround			- **			+ *
p1flayer			- ***		- ***	
p2flayer	+ *			- **		
Structure						
Cover05_2		+ *		+ *		
Cover2_4	+ **	+ *				
Cover4_10	+ ***					- **
Horizivisibility						
understpc1	- ***	- **		- **		
understpc2	- **					+ **
CanopyCov			- **		- **	- ***
BasalArea				- *	- *	
MaxDBH		- ***		+ ***		
MaxHeight			- ***		- ***	+ *
treestructurepc1			+ ***		+ ***	
treestructurepc2		- ***		+ ***		+ **
Dominantsp					+ ***	***
Tree condition						
Lichen	+ ***					- **
Ivy	+ *		- *			
ShrubDiversity		+ ***				
DeadTree	+ *					- *
DeadLimbs					+ **	- ***
GroundWood			+ *		- **	
deadwoodpc1	- **		- *			+ *
Deer						
Trackwaysper100m		+ *	+ *		+ ***	
DeerPCAAxis1	+ **		+ ***			
DeerPCAAxis2					- ***	
Landscape						
threekmHabPCA1			- **		+ *	
threekmHabPCA2			+ **			

	Hole1	Hole2	Open1	Open2	LDMGs1	LDMGs2
Physical features						
Drainage				+ *		+ *
Altitude	- *	- *		- *		
Contigarea						
Tracks	- *					
Spring CC						
ChApr_temp		+ *		- **	- *	- ***
ChMay_temp						- ***
ChApr_cmRain						
ChMay_cmRain					- *	
ChgApr_Raindays	- **					
ChgMay_Raindays	- **					+ ***
Winter CC						
ChJan_minT					- **	
ChFeb_minT				- ***	- ***	- ***
ChMar_minT	+ **			+ *	- ***	
ChJan_MaxT	- **			- **	- ***	
ChFeb_MaxT			- ***	- **		- ***
ChMar_MaxT	- **		- *	- **	- *	
ChJan_cmRain						
ChFeb_cmRain			+ ***	+ **	+ ***	+ ***
ChMar_cmRain	- *				+ **	
Predation						
DreyDensity						
CalGRSWO	+ *			- ***		- **
JAY						- **
Competition						
BTch				- **	+ **	- **
GTch			+ **	- ***	+ ***	- ***
CHch			▨	▨		
CCch					+ ***	
BCch	+ ***		+ ***		+ **	- **
resFGch			▨	▨	+ ***	- **
MDMFGch	+ *		+ ***		+ ***	
ResMDMFGch		+ *	▨	▨		- **

Table 3.27.2 Continued**.**

3.4.5 Hypothesis Five: *Competition from residents has been responsible for declines of some migratory species.*

Capsule: There was no evidence from these analyses that the declines of long-distance migrant foliage gleaners were related to the degree of increase of potential resident competitors. However, methodological issues mean that the test of this hypothesis was weak. There was some indirect evidence potentially supporting the hypothesis from sections 3.4.3.1-3.

The competition hypothesis was not tested in analyses of all-species population change due to inclusion of the competitor species in the dependent variable PCAs. There was, however, no evidence of negative relationships between the long-distance migrant species and their resident ecological equivalents from the loadings of the PCAs. Numerous positive relationships between PCAs constructed on data from subsets of species and the changes of resident and middle distance foliage gleaners (sections 3.4.1 to 3.4.4) indicate that to some extent these species underwent more positive changes where other species did, possibly indicating shared response to environmental changes as discussed below.

Table 3.28 shows that for both BTO and RSPB datasets, 4 of the 5 species included in the analysis to test this hypothesis had important positive loadings on axis 1. In each case, willow warbler and garden warbler were the most strongly positively loaded species. For both datasets this axis therefore describes a gradient of increasingly positive change for 4 of the 5 species. For the BTO dataset, the second axis contrasts the change scores of redstart (which is negatively loaded) with that of pied flycatcher and garden warbler. For the RSPB dataset, this axis contrasts less strongly the change scores of willow warbler from redstart, wood warbler and pied flycatcher.

Table 3.29 shows that for the BTO dataset, apart from the competition variables, scores on the first axis were related to only a single physical feature and one spring climate change variable. For the RSPB dataset there were many more significant associations, scores on this axis being related to latitude and longitude, 4 field layer and 5 structural variables, 3 describing tree condition, 2 measures of deer impacts, 1 landscape structure score and 6 measures of winter climate change (but no spring climate change variables). Axis 2 for the BTO axis was again related to only a few variables, namely latitude, single tree condition and landscape variables and 4 measures of winter climate change. The equivalent RSPB axis was related to latitude and longitude, 5 structural and 2 tree condition variables, 1 landscape variable, 3 measures each of spring and winter climate change and the abundance of 2 predator species.

Table 3.27.1 and 3.27.2 show that for both datasets, all of the relationships between potential foliage gleaning competitors and the key axis of variation in change scores of the long distance migrant equivalent were positive, all 8 being significant for the BTO dataset and 6 out of 8 for the RSPB dataset. The significant relationships for the second axes suggest that, for the BTO dataset, garden warbler and pied flycatcher did better and redstart did less well where blackcap and chiffchaff did better. For the RSPB dataset, results for this axis suggest that redstart, wood warbler and pied flycatcher did better and willow warbler did less well where blue tit, great tit and blackcap change scores were higher.

Overall, there was thus no evidence of long distance migrants doing less well where potential competitors had done well. For each dataset, there was some evidence from one axis of a single species doing less well where potential competitors had done better but, given the greater number of species with the opposite loadings on these axes, this result is just as likely to reflect positive relationships between them and the potential competitors. The modelling carried out here is a very weak test of the competition hypothesis as no attempt was made to control for the other factors that influence the abundance and changes of abundance of the species concerned. Given that the species contributing to dependent and independent variables were selected for their ecological similarity, with the exception of their migratory status, it is not surprising there was no evidence of negative associations or that there was evidence of positive associations in their changes. A stronger test would involve controlling for the effects of habitat and other factors (such as climate) that affect their abundance and before looking for residual relationships. Whilst it is very likely that the ecological similarity of these species has resulted in these relationships (i.e. common responses to some resource or environmental change), it should be noted that these results are potentially compatible with the ‘heterospecific attraction’ specific attraction hypotheses proposed by (Mönkkönen *et al.* 1999). This is impossible to assess without an experimental approach.

	BTO		**RSPB**	
Loading	**Axis 1**	**Axis 2**	**Axis 1**	**Axis 2**
	28.09	**24.34**	**28.53**	**24.11**
-0.8 - -0.7				**REDST**
-0.7 - -0.6		**REDST**		
-0.6 - -0.5				**WOOWA**
-0.5 - -0.4				**PIEFL**
-0.4 - -0.3				
-0.3 - -0.2		WOOWA		
-0.2 - -0.1	PIEFL			
-0.1 - 0			REDST	
0 - 0.1				
0.1 - 0.2				GARWA
0.2 - 0.3		WILWA		
0.3 - 0.4	**WOOWA**		**PIEFL**	**WILWA**
0.4 - 0.5	**REDST**	**GARWA**	**WOOWA**	
0.5 - 0.6				
0.6 - 0.7	**GARWA**	**PIEFL**		
0.7 - 0.8	**WILWA**		**GARWA, WILWA**	

Table 3.28 Summary of species loadings on the first two axes of the PCA of change in abundance between 1980s and 2003-04 of long-distance migrant foliage gleaners (species potentially affected by competition from residents) at BTO and RSPB sites. Species are listed in ascending order of their loading. See Appendix 2 for species codes.

	BTO		**RSPB**	
	Axis 1	**Axis 2**	**Axis 1**	**Axis 2**
Location (2)	**0**	**1** (50)	**2** (100)	**2** (100)
Field layer (9)	**0**	**0**	**4** (44)	**0**
Structure (13)	**0**	**0**	**5** (38)	**5** (38)
Tree condition (7)	**0**	**1** (14)	**3** (43)	**2** (29)
Deer (3)	**0**	**0**	**2** (67)	**0**
Landscape (2)	**0**	**1** (50)	**1** (50)	**1** (50)
Physical features (4)	**1** (25)	**0**	**0**	**0**
Spring climate change 6)	**1** (17)	**0**	**0**	**3** (50)
Winter climate change (9)	**0**	**4** (44)	**6** (66)	**3** (33)
Predation (3)	0	**0**	**0**	**2** (67)
Competition (8)	**8** (100)	**3** (38)	**6** (75)	**5** (63)

Table 3.29 Summary of significant relationships between explanatory variables and site scores on the first two axes of the PCA of change between the 1980s and 2003-04 at BTO and RSPB sites of declining species predicted to be vulnerable to effects of competition from resident foliage gleaners. The number of variables in each group is shown in brackets after each variable group name. For each PCA axis, the number of significant relationships is shown in bold followed in brackets by the percentage of variables in that group with significant relationships.

4. DISCUSSION

4.1 Study Design and Statistical Issues

The analyses presented here have found numerous relationships between scores on PCA axes of bird abundance in 2003-04 and population change between the 1980s and 2003-04, although the number of significant relationships varied greatly between dependent variables. The multiple models reported here represent exploratory analyses and it is not surprising, given the number of variables for which effects were examined, that there were many relationships. It is likely that some represent type III errors. Furthermore, as the different characteristics of sites are inter-related and these analyses have not been designed to discriminate statistically between their different effects, it is not possible to reliably judge which are most likely to represent causal relationships. Identification of the most likely causal relationships would require further work, such as inclusion of those variables with significant effects on each dependent variable axis in an information theoretic approach. Nevertheless, these results accurately describe the characteristics of woods that have undergone different degrees of change in bird community structure whilst controlling for the possible effects of spatial autocorrelation of sites within regions. Interpretation of the results so far obtained in the light of knowledge of the ecology of British woods and the ecological processes likely to be operating within the sample studied can provide some insight to which processes are most likely to be operating. One limitation to the degree of inference that can be made is that, due to the availability of data, change in bird communities was related to conditions in 2003-04 rather than to changes in conditions between the 1980s and 2003-04, with the exceptions of climate change and the population changes of some potential competitor species.

In most cases, there were more significant relationships between dependent variable axis scores and potential covariates for the RSPB dataset than the BTO dataset. It is not immediately clear why this is, particularly as in general the RSPB axes summarised a lower percentage of the total variance within the dataset than equivalent axes for the BTO dataset (as shown in each table of species' loadings). Additionally, as the dataset is based on the maximum count from the RWBS dataset for the 1980s and 2003-04, community changes may be more robust for the BTO dataset since more sites were covered in two years in each survey episode, so year-to-year fluctuations in individual species are less important. One possibility is that the sample of woods is larger (RSPB 252 woods, BTO 92 woods). More likely is that there is a greater diversity of sites within the RSPB dataset, since they span a wider geographical area due to the inclusion of sites in Scotland and more sites from the uplands of Wales in particular. Although the RSPB sites cluster into localities, and therefore do not so evenly cover the area they span compared to the BTO sites, these localities were originally studied in part because they exemplified certain types of woodland (such as Welsh upland oak woods or Scottish birch). For this reason, there is a greater contrast between the types of sites within the RSPB dataset, both in the characteristics of the woods and, given the lower amount of variance the axes of the PCAs of change scores explain, presumably also in the patterns of change of bird populations within them. This may give a greater chance of finding relationships between community parameters and potential covariates. Where this has implication for specific results, it has been highlighted within the results sections.

Although the modelling of the effects of potential covariables has been carried out including region as a random factor to take account of the potential lack of independence between sites, PCAs used to create dependent variables are carried out as if sites are independent. There is, therefore, likely a degree of spatial autocorrelation in the axes that arises because the sites are not randomly selected or distributed and this may be especially strong in the case of the RSPB sites as they are clustered into localities.

Other, more specific points may have implications for the results that have been obtained. For instance, the habitat scores used for each wood were the mean of the values for each of ten points, which for some variables are in turn the means of values recorded in each of four subplots at each point. This gives a fair indication of the overall habitat conditions in each wood but information on the variance of the scores or the presence of extreme conditions is lost. This might also be important in determining the suitability of sites for species that require complex habitat structures or multiple habitat components.

4.2 Evidence Regarding Causes of Community Changes

Bearing in mind the issues and caveats that have been outlined above, it is still possible to assess the amount of evidence supporting each of the hypotheses raised to explain woodland bird declines and changes in community structure. This evidence comes mainly from the relationships between the axis scores and covariates. In most cases, declining species did not have important relationships with the axes describing overall community changes so limited inference can be made from these axes regarding the causes of their declines.

There was some evidence from the PCAs of abundance that the density of a number of increasing species was related to the stature of woods, suggesting they may benefit from stand ageing (axis 1 for each dataset, section 3.1), in contrast to a number of declining species. However, shifts on these axes were more often related to winter climate change (section 3.2), which suggests that climatic effects have been more important in determining changes over the period examined than ageing of woods. The second axis and shifts on the second axis for each dataset was more clearly related to habitat characteristics (sections 3.1. and 3.2), suggesting habitat change may have been important for these species. However, it is equally possible that these relationships reflect expansion of populations into different woodland habitats following population changes driven by other factors. The PCAs of change scores for all species (section 3.3) provided clear evidence for the influence of both climate change and habitat, changes described by axis 1 of the BTO dataset most likely related to climate and those described by 2 to habitat, with the reverse being the case for the RSPB dataset. Spatial patterns in these analyses are outlined in the relevant sections and also section 3.5. Although there was clear variation across the areas covered by the two sets of sites, there were differences between the two datasets in the geographical patterns of variation in the change and abundance parameters and it was not possible to identify clear-cut sets of sites undergoing similar changes.

4.2.1 Effects of Deer Grazing

There was little direct evidence that deer grazing had been responsible for population changes of declining species, although patterns of change with respect to habitat characteristics were consistent with those expected to occur as a result of severe deer impacts (section 3.4.1). In particular, the measures of deer impacts we have used may actually be better regarded as measures of deer activity and as such they may be precursors to deer impacts on habitat availability and consequent changes to bird community structure. There was, however, some evidence from the BTO dataset (section 3.3.1) that three increasing species (blackcap, chiffchaff and wren) had increased less where measures of deer impact were higher. It is therefore possible that the declining species that were predicted to suffer from the effects of deer grazing may have been affected but that the effects of this have been masked by other, perhaps wide-scale rather than local, factors. Relationships between the axis of change of ‘deer impact species’ for the RSPB dataset and vegetation characteristics were consistent with the hypothesis. The strong relationships between change of deer impact species and winter climate change found for the RSPB dataset could potentially be indicative of an effect of increasing deer populations (table 3.19.2), although they could equally indicate an effect of competition from increasing resident foliage gleaning birds.

4.2.2 Reduction in Active Management of Woods

There was some evidence supporting the possibility that reduction in active woodland management had caused declines, both from the overall axes of change (section 3.3) and from the axes of change of species thought to be vulnerable to these processes (section 3.4.2). This was particularly the case for the RSPB dataset. However, an important caveat is that this evidence is effectively an association between the population changes of species and habitat characteristics predicted to prevail where management has been reduced. It is not clear, however, whether these population changes have been driven by habitat change or whether the associations between habitat characteristics and population change reflect re-distribution of birds following population changes caused by other factors. Furthermore, in the absence of direct information on the changes in management of individual woodlands, or indeed on change in habitat rather than habitat characteristics in 2003-04, the link between the population declines and a reduction in woodland management is speculative even though the observed results are consistent with this.

4.2.3 Climate Change

There was evidence that all groups of species examined in section 3.4.3 had been affected by climate change. As would be predicted, resident gleaners appear to have benefited from warmer winters (according to both datasets in section 3.4.3.1). Middle distance migrants appear to have benefited in the same way – a result that accords with the findings of Lemoine and Böhning-Gaese (2003) for short-distance migrants. There was some evidence from both datasets that long-distance migrants have done worse where winters have warmed most (section 3.4.3.3), possibly due to interactions with residents. This is discussed below. Thrushes (section 3.4.3.4) did best where spring rainfall increased most (according to both datasets) and where winter temperatures and rainfall increased most (according to the BTO dataset). Surprisingly, evidence was less clear for small resident insectivores but there was evidence from the BTO dataset especially that they had done better where winter temperatures had increased most and spring temperatures had increased least. Overall, there was clear evidence that changes particularly in the increasing species had occurred in parallel to climate change. Note also that there also some positive relationships between winter warming and the changes of some declining hole-nesters according to the BTO dataset (table 3.26.1), suggesting that climate change may have benefited these species and can not be responsible for their population declines. Also, relationships between axis 2 of the PCA of change scores for all species in the RSPB dataset suggest that climate change could be important for some declining species. It should be noted that (as with the possible interaction of long-distance migrants with residents) the effects of climate change could be indirect as they could operate via increasing the abundance of potential nest predators such as grey squirrels or great spotted woodpeckers or through increasing deer densities to a level where habitat impacts from grazing are detrimental.

4.2.4 Nest Predation and Competition between Residents and Migrants

Tests undertaken of the predation (section 3.4.4) and competition (section 3.4.5) hypotheses were weak. This is because the effects of factors simultaneously controlling the abundance of both potential nest predators / potential competitors and those species predicted to have been negatively affected by the interspecific interactions have not been controlled for. Furthermore, it is unclear whether a numerical response would occur on a site-by-site basis even in if either process were affecting the fitness of individuals of declining species. One relationship possibly indicative of an effect of nest predation, however, was that three declining open-nesters declined more where great spotted woodpecker density was higher but only one of these - hawfinch – was considered to be at all vulnerable to this predator. Also, the results for axis 2 of the PCA of change for all species in the RSPB dataset suggested that both hawfinch and lesser spotted woodpecker had declined most where great spotted woodpecker and grey squirrel abundance was higher. Together with the result from Amar *et al.* (2006), which suggested these species were more likely to decline where grey squirrel abundance was higher, these results indicate that nest predation may indeed be a problem for these species.

The presence of overall positive relationships between the changes shown by long-distance migrants and the most likely resident competitors should not be taken as evidence sufficient to reject the hypothesis, given the lack of control of confounding factors within the analysis. Additionally, opposite relationships were found between winter climate change and change of resident and long-distance migrant foliage-gleaners (see above). A similar effect was reported by Lemoine and Böhning-Gaese (2003) who found species richness of resident birds increased and that the species richness of long-distance migrants declined slightly in southern Germany in parallel to warming of winters in southern Germany between 1980 and 1992.

4.3 Conclusions

All conclusions drawn from exploratory analyses of the nature of those reported here must be tentative. This is especially true given as tests of some hypotheses (especially interspecific interactions) were of relatively weak inferential power. However, there was clear evidence overall of relationships between measures of population change and both climate and habitat. There was more evidence that climate change had been responsible for increases than declines, although relationships for long-distance migrants indicated a possible indirect effect via interactions with resident species. Relationships with habitat were potentially consistent with increased deer browsing and reductions in management having driven declines in some species and in this respect the findings agree with those of Amar *et al.* (2006) based on analysis of species level patterns of change using the same data. Overall, results suggest that declining residents may possibly be affected by interspecific interactions in some cases but there is little evidence for an effect of climate change. Declining long-distance migrants may be affected by habitat change and possibly by the indirect effects of winter climate change. The results are also consistent with them being negatively affected by events on the wintering grounds outside of Europe, resulting in changes in habitat associations accompanying changes in the size of breeding populations through preferential occupation of optimal sites by a reduced population.

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APPENDIX 1 Species Loadings from the PCAs of BTO and RSPB Data

The two axes with the strongest loading are shown in each case, except where the second axis was not used in analysis of covariates (see section 2.4.3). See section 2.4.2 for details of CANOCO procedure used to perform PCAs. In each column, species are shown in ascending order of their loading on the relevant axis.

a) Abundance in 2003-4

BTO				**RSPB**			
Species	**Axis 1**	**Species**	**Axis 2**	**Species**	**Axis 1**	**Species**	**Axis 2**
TREPI	-0.2267	BLACA	-0.4779	WILWA	-0.7777	CHIFF	-0.3854
SISKI	-0.1764	CHIFF	-0.4546	TREPI	-0.6792	DUNNO	-0.3088
GARWA	-0.1282	DUNNO	-0.3586	REDPO	-0.3866	WILTI	-0.1638
HAWFI	-0.1056	LOTTI	-0.3229	CHAFF	-0.3439	MARTI	-0.1424
REDST	-0.0434	BULLF	-0.2976	REDST	-0.1633	BLACA	-0.0634
WOOWA	-0.03	GREWO	-0.2415	WOOWA	-0.1182	ROBIN	-0.03
PIEFL	0.0019	GRSWO	-0.2021	SPOFL	0.0189	BLABI	-0.0199
LESWO	0.0195	WREN	-0.1965	PIEFL	0.0276	JAY	0.0261
REDPO	0.0244	JAY	-0.1952	COATI	0.0554	SONTH	0.0751
WILTI	0.0952	NUTHA	-0.1757	LOTTI	0.0693	REDPO	0.0955
GREWO	0.1956	MAGPI	-0.1719	MISTH	0.0825	LESWO	0.0998
MAGPI	0.2269	WILTI	-0.1641	GARWA	0.0967	WILWA	0.1041
JACKD	0.2287	CHAFF	-0.1507	LESWO	0.097	WREN	0.1221
JAY	0.2426	JACKD	-0.1354	HAWFI	0.1093	HAWFI	0.1275
WILWA	0.2869	SPOFL	-0.111	WILTI	0.1456	GOLDC	0.1788
GRSWO	0.3042	ROBIN	-0.091	DUNNO	0.3236	LOTTI	0.1829
MARTI	0.3541	BLABI	-0.0859	TREEC	0.3553	GARWA	0.2127
BULLF	0.3939	GARWA	-0.059	WREN	0.3788	COATI	0.2154
DUNNO	0.4109	GRETI	-0.007	GRETI	0.4311	GRETI	0.2268
SPOFL	0.425	REDPO	0.0713	GOLDC	0.4442	TREPI	0.2456
MISTH	0.4848	SISKI	0.1022	SONTH	0.5089	CHAFF	0.2619
LOTTI	0.5382	BLUTI	0.1789	JAY	0.5109	SPOFL	0.2949
COATI	0.5398	HAWFI	0.1898	ROBIN	0.5742	NUTHA	0.3553
NUTHA	0.5536	SONTH	0.2037	BLUTI	0.5853	BLUTI	0.4914
CHIFF	0.5651	LESWO	0.2066	MARTI	0.5871	TREEC	0.5547
TREEC	0.6195	GOLDC	0.2524	NUTHA	0.5974	MISTH	0.5877
BLACA	0.6533	TREPI	0.2918	BLACA	0.6819	WOOWA	0.6032
GOLDC	0.6775	PIEFL	0.3184	CHIFF	0.6839	PIEFL	0.6623
GRETI	0.6849	WOOWA	0.3322	BLABI	0.7911	REDST	0.7339
CHAFF	0.7225	WILWA	0.3382				
WREN	0.7317	REDST	0.3589				
ROBIN	0.7462	COATI	0.5571				
SONTH	0.7986	TREEC	0.6559				
BLABI	0.8557	MARTI	0.7265				
BLUTI	0.883	MISTH	0.7328				

b) Change in abundance between 1980s and 2003-04

BTO				**RSPB**			
Species	**Axis 1**	**Species**	**Axis 2**	**Species**	**Axis 1**	**Species**	**Axis 2**
TREPI	0.0218	CHIFF	-0.6035	WILTI	-0.0275	HAWFI	-0.5229
HAWFI	0.038	BLACA	-0.4493	REDST	0.0788	GARWA	-0.3761
SISKI	0.1062	WREN	-0.3753	HAWFI	0.088	LESWO	-0.3633
REDPO	0.1081	DUNNO	-0.2634	TREPI	0.0942	WILWA	-0.3293
WILTI	0.1102	WILWA	-0.2529	JAY	0.1066	REDPO	-0.3068
WOOWA	0.1199	GARWA	-0.2469	COATI	0.1154	BLABI	-0.287
REDST	0.137	SISKI	-0.2345	REDPO	0.1192	ROBIN	-0.2588
GREWO	0.1689	ROBIN	-0.2297	MARTI	0.1251	JAY	-0.1835
MAGPI	0.2699	WILTI	-0.1275	SPOFL	0.1348	SONTH	-0.1645
PIEFL	0.3222	PIEFL	-0.1182	CHIFF	0.1533	DUNNO	-0.1186
LESWO	0.3388	MAGPI	-0.0829	PIEFL	0.1744	MISTH	-0.0684
SONTH	0.3529	BLABI	-0.0778	LOTTI	0.2401	WREN	-0.0628
MISTH	0.3572	GREWO	-0.0178	LESWO	0.243	BLUTI	-0.0141
WILWA	0.3659	LOTTI	0.0042	DUNNO	0.2696	SPOFL	-0.0083
SPOFL	0.3716	CHAFF	0.0174	SONTH	0.2967	WILTI	0.0022
GARWA	0.3869	JAY	0.0237	TREEC	0.3243	CHAFF	0.0039
GOLDC	0.3883	GRETI	0.0463	NUTHA	0.3282	GOLDC	0.0948
JAY	0.4192	BLUTI	0.0786	ROBIN	0.3718	COATI	0.1056
NUTHA	0.4247	BULLF	0.1081	GOLDC	0.3859	WOOWA	0.1274
BULLF	0.4445	GRSWO	0.1277	MISTH	0.3957	TREPI	0.1277
CHIFF	0.445	MISTH	0.1376	WOOWA	0.4012	NUTHA	0.1332
JACKD	0.4595	COATI	0.1751	WILWA	0.4231	PIEFL	0.1791
GRSWO	0.4605	NUTHA	0.1777	BLUTI	0.4565	BLACA	0.2079
LOTTI	0.4943	MARTI	0.2146	GRETI	0.4781	CHIFF	0.2888
TREEC	0.5136	JACKD	0.2158	GARWA	0.4836	LOTTI	0.3259
CHAFF	0.5271	LESWO	0.2321	BLABI	0.4853	REDST	0.3672
MARTI	0.5302	SONTH	0.2537	WREN	0.501	TREEC	0.4267
BLACA	0.5698	HAWFI	0.2594	BLACA	0.5733	MARTI	0.4486
BLABI	0.573	GOLDC	0.266	CHAFF	0.6008	GRETI	0.5014
COATI	0.6028	REDST	0.2676				
ROBIN	0.607	TREEC	0.2952				
DUNNO	0.6294	WOOWA	0.3681				
WREN	0.7129	TREPI	0.3735				
GRETI	0.7221	REDPO	0.4221				
BLUTI	0.7307	SPOFL	0.5459				

c) Change in abundance (1980s to 2003-04), declining species vulnerable to impacts of deer grazing

BTO				RSPB			
Species	**Axis 1**	**Species**	**Axis 2**	**Species**	**Axis 1**	**Species**	**Axis 2**
BULLF	0.5548	WILWA	-0.5906	DUNNO	0.5738	WILWA	-0.3424
WILWA	0.6218	GARWA	-0.2471	WILWA	0.7513	GARWA	-0.2783
DUNNO	0.6951	DUNNO	0.2496	GARWA	0.7625	DUNNO	0.8181
GARWA	0.7391	BULLF	0.6785				

d) Change in abundance (1980s to 2003-04), declining species vulnerable to impacts of reduction in active management including

BTO				RSPB			
Species	**Axis 1**	**Species**	**Axis 2**	**Species**	**Axis 1**	**Species**	**Axis 2**
WILTI	0.1994	WILWA	-0.4982	PIEFL	0.157	DUNNO	-0.4569
PIEFL	0.3807	GARWA	-0.3968	WILTI	0.2065	GARWA	-0.0527
WILWA	0.5536	DUNNO	0.1465	DUNNO	0.5235	WILWA	0.0439
BULLF	0.5655	BULLF	0.1632	GARWA	0.7569	WILTI	0.632
GARWA	0.6746	PIEFL	0.5899	WILWA	0.76	PIEFL	0.7345
DUNNO	0.7313	WILTI	0.5993				

e) Change in abundance (1980s to 2003-04), long-distance migrants

BTO				RSPB			
Species	**Axis 1**	**Species**	**Axis 2**	**Species**	**Axis 1**	**Species**	**Axis 2**
PIEFL	-0.2497	TREPI	-0.4791	REDST	0.2027	REDST	-0.7555
WILWA	0.1559	SPOFL	-0.1535	SPOFL	0.35	SPOFL	-0.3601
GARWA	0.2678	REDST	0.042	PIEFL	0.4	PIEFL	-0.2414
WOOWA	0.4979	WOOWA	0.1326	WOOWA	0.4338	WOOWA	-0.2334
TREPI	0.5076	PIEFL	0.2389	TREPI	0.5359	TREPI	-0.1755
SPOFL	0.5927	GARWA	0.648	GARWA	0.5914	GARWA	0.3959
REDST	0.6606	WILWA	0.8116	WILWA	0.6517	WILWA	0.517

f) Change in abundance (1980s to 2003-04), middle-distance migrants

BTO		RSPB	
Species	**Axis 1**	**Species**	**Axis 1**
BLACA	0.8766	BLACA	0.7562
CHIFF	0.8766	CHIFF	0.7562

g) Change in abundance (1980s to 2003-04), resident foliage gleaners

BTO				RSPB			
Species	**Axis 1**	**Species**	**Axis 2**	**Species**	**Axis 1**	**Species**	**Axis 2**
WILTI	0.1221	WILTI	-0.7628	WILTI	-0.1427	BLUTI	-0.5165
GOLDC	0.461	MARTI	-0.4638	COATI	0.2286	NUTHA	-0.3855
NUTHA	0.4901	NUTHA	-0.4102	MARTI	0.2788	CHAFF	-0.2485
MARTI	0.5836	COATI	-0.1029	LOTTI	0.3784	WILTI	-0.022
LOTTI	0.6222	GOLDC	0.0638	GOLDC	0.4588	GRETI	0.0605
COATI	0.6486	BLUTI	0.1385	NUTHA	0.4819	GOLDC	0.2017
CHAFF	0.655	GRETI	0.1508	BLUTI	0.5284	COATI	0.4222
GRETI	0.7716	CHAFF	0.2905	CHAFF	0.6098	LOTTI	0.5645
BLUTI	0.8284	LOTTI	0.2906	GRETI	0.7133	MARTI	0.5784

h) Change in abundance (1980s to 2003-04), for thrushes

BTO		RSPB	
Species	**Axis 1**	**Species**	**Axis 1**
MISTH	0.5884	SONTH	0.3958
SONTH	0.7353	MISTH	0.7145
BLABI	0.7702	BLABI	0.7348

i) Change in abundance (1980s to 2003-04), small resident insectivores

BTO				RSPB			
Species	**Axis 1**	**Species**	**Axis 2**	**Species**	**Axis 1**	**Species**	**Axis 2**
GOLDC	0.3848	DUNNO	-0.2875	ROBIN	0.3925	LOTTI	-0.5898
LOTTI	0.551	WREN	-0.2529	LOTTI	0.4015	DUNNO	-0.3054
DUNNO	0.6781	ROBIN	-0.217	DUNNO	0.5446	GOLDC	-0.2581
ROBIN	0.7885	LOTTI	0.5264	GOLDC	0.6133	WREN	0.4257
WREN	0.8499	GOLDC	0.7564	WREN	0.6588	ROBIN	0.7159

j) Change in abundance (1980s to 2003-04), declining hole-nesters

BTO				RSPB			
Species	**Axis 1**	**Species**	**Axis 2**	**Species**	**Axis 1**	**Species**	**Axis 2**
PIEFL	0.4999	PIEFL	-0.8231	LESWO	-0.3219	MARTI	-0.6301
WILTI	0.5532	WILTI	0.0535	WILTI	0.3845	LESWO	-0.2398
LESWO	0.6424	MARTI	0.1053	MARTI	0.5858	PIEFL	-0.0111
MARTI	0.7385	LESWO	0.4734	PIEFL	0.7706	WILTI	0.7815

k) Change in abundance (1980s to 2003-04), declining open-nesters

BTO				RSPB			
Species	**Axis 1**	**Species**	**Axis 2**	**Species**	**Axis 1**	**Species**	**Axis 2**
HAWFI	-0.0437	CHAFF	-0.5356	HAWFI	0.2531	CHAFF	-0.5066
WOOWA	0.1259	WOOWA	-0.4479	DUNNO	0.3777	WOOWA	-0.4508
MISTH	0.3277	WILWA	-0.2224	WOOWA	0.4217	MISTH	-0.3962
CHAFF	0.4158	GARWA	0.1098	MISTH	0.4859	GARWA	0.2794
DUNNO	0.6537	DUNNO	0.2927	CHAFF	0.5755	WILWA	0.3611
WILWA	0.6694	MISTH	0.5517	WILWA	0.6277	DUNNO	0.3845
GARWA	0.7365	HAWFI	0.5732	GARWA	0.6791	HAWFI	0.4448

l) Change in abundance (1980s to 2003-04), long-distance migrant foliage gleaners

BTO				RSPB			
Species	**Axis 1**	**Species**	**Axis 2**	**Species**	**Axis 1**	**Species**	**Axis 2**
PIEFL	-0.1238	REDST	-0.646	REDST	-0.0716	REDST	-0.7247
WOOWA	0.3583	WOOWA	-0.2752	PIEFL	0.3486	WOOWA	-0.5697
REDST	0.4792	WILWA	0.2795	WOOWA	0.4234	PIEFL	-0.4809
GARWA	0.6741	GARWA	0.4169	GARWA	0.7331	GARWA	0.1586
WILWA	0.7593	PIEFL	0.6872	WILWA	0.7637	WILWA	0.3152

APPENDIX 2 Scientific Names and Codes Used for Species Mentioned in the Text

Birds

Common name	Code	Scientific name
Bullfinch	BULLF	*Pyrrhula pyrrhula*
Chaffinch	CHAFF	*Fringilla coelebs*
Chiffchaff	CHIFF	*Phylloscopus collybita*
Coal tit	COATI	*Periarus ater*
Dunnock	DUNNO	*Prunella modularis*
Garden warbler	GARWA	*Sylvia borin*
Goldcrest	GOLDC	*Regulus regulus*
Great tit	GRETI	*Parus major*
Green woodpecker	GREWO	*Picus viridis*
Great spotted woodpecker	GRSWO	*Dendrocopos major*
Hawfinch	HAWFI	*Coccothraustes coccothraustes*
Jackdaw	JACKD	*Corvus monedula*
Jay	JAY	*Garrulus glandarius*
Lesser spotted woodpecker	LESWO	*Dendrocopos minor*
Long-tailed tit	LOTTI	*Aegithalos caudatus*
Marsh tit	MARTI	*Poecile palustris*
Mistle thrush	MISTH	*Turdus viscivorus*
Nuthatch	NUTHA	*Sitta europaea*
Pheasant	PHEAS	*Phasianus colchicus*
Pied flycatcher	PIEFL	*Ficedula hypoleuca*
Lesser redpoll	REDPO	*Carduelis cabaret*
Redstart	REDST	*Phoenicurus phoenicurus*
Robin	ROBIN	*Erithacus rubecula*
Siskin	SISKI	*Carduelis spinus*
Song thrush	SONTH	*Turdus philomelos*
Spotted flycatcher	SPOFL	*Muscicapa striata*
Treecreeper	TREEC	*Certhia familiaris*
Tree pipit	TREPI	*Anthus trivialis*
Willow tit	WILTI	*Poecile montanus*
Willow warbler	WILWA	*Phylloscopus trochilus*
Wood warbler	WOOWA	*Phylloscopus sibilatrix*
Wren	WREN	*Troglodytes troglodytes*

Mammals

Grey squirrel	*Sciurus carolinensis*

Plants

Ash	*Fraxinus excelsior*
Beech	*Fagus sylvatica*
Birch	*Betula* sp.
Bracken	*Pteridium aquilinum*
Bramble	*Rubus fruticosus*
Oak	*Quercus* sp.