Impact of climate change on communities: revealing species' contribution

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Abstract

1. Although climate is known to play an important role in structuring biological communities, high-resolution analyses of recent climatic impacts on multiple components of diversity are still sparse. Additionally, there is a lack of knowledge about which species drive community response to environmental change.

2. We used a long-term breeding bird data set that encompasses a large latitudinal and altitudinal range to model the effect of temperature on spatial and temporal patterns in alpha and beta diversity. We also established a novel framework for identifying species-specific contributions to these macroecological patterns, hence combining two different approaches for identifying climatic impacts.

3. Alpha diversity increased over time, whilst beta diversity declined; both diversity metrics showed a significant relationship with recent temperature anomalies. By partitioning beta diversity, we showed that the decline was predominately driven by changes in species turnover rather than nestedness suggesting a process of replacement by more common species.

4. Using jackknife analyses we identified how individual species influenced the modelled relationships of diversity with temperature and time. Influential species tended to be habitat generalists with moderate to large distributions.

5. We demonstrate that different facets of avian diversity can respond rapidly to temperature anomalies and as a result have undergone significant changes in the last decade. In general, it appears that warming temperatures are driving compositional homogenization of temperate bird communities via range expansion of common generalist species.

Key-words: alpha diversity, beta diversity, birds, homogenization, nestedness, turnover

Introduction

It is well established that range boundaries fluctuate over time (MacArthur 1972). Although expansions and contractions can occur on longer timescales without any directional change in the environment (Kirkpatrick & Barton 1997), short-term fluctuations are often explained by abiotic or biotic environmental changes, i.e. variation in the niche components (Brown & Lomolino 1998). Species range shifts and their relationship to abiotic trends are now receiving increased interest due to recent climate change (Parmesan & Yohe 2003; Hickling *et al*. 2006; Thomas 2010; Chen *et al*. 2011). In the same vein, the search is on to understand the mechanisms and processes

that shape the distribution of biodiversity along environmental gradients (Meynard *et al*. 2011). While the importance of climate for structuring large-scale diversity patterns is well known (Gaston 1996; Hawkins *et al*. 2003; Willig, Kaufman & Stevens 2003; Currie *et al*. 2004), the relationship between species-specific response to environmental changes and the resulting changes in local communities has hardly been investigated.

To date, many macroecological studies have focused on patterns in diversity of local sites (alpha diversity) often measured with species richness. For instance, it is well established that species richness decreases with latitude and increases with temperature (Turner, Lennon & Lawrenson 1988; Rosenzweig 1995; Lennon, Greenwood & Turner 2000). In temperate regions, warming is therefore expected to lead to an increase in richness (Lennon,

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Greenwood & Turner 2000; Hawkins *et al.* 2003), which has been confirmed in plant, butterfly, fish and bird communities (H-Acevedo & Currie 2003; Klanderud & Birks 2003; Lemoine & Böhning-Gaese 2003; Menéndez *et al.* 2006; Hiddink & ter Hofstede 2008; La Sorte *et al.* 2009; Davey *et al.* 2012). Beyond alpha diversity, the difference in species composition between sites (beta diversity) and the diversity of the regional species pool (gamma diversity) play important roles in structuring community richness and composition across scales (Magurran 2004). However, few studies have tracked temporal changes in spatial beta diversity (Magurran *et al.* 2010).

Predicting net changes in diversity is scale dependent. For example, local richness increases may not result in gains at the regional level (Sax & Gaines 2003). Similarly, the relationship between species richness and turnover changes with scale (Lennon *et al.* 2001), as does the power of environmental variables to explain diversity patterns (Koleff & Gaston 2002). However, at local scales the environment is expected to be influential (Koleff & Gaston 2002), predominately through relationships with common rather than rare species (Jetz & Rahbek 2002; Lennon *et al.* 2004; Gaston *et al.* 2007). To date, increases in alpha diversity at local scales have generally been attributed to generalist species (Klanderud & Birks 2003; Menéndez *et al.* 2006; Britton *et al.* 2009; Davey *et al.* 2012). If a warming climate promotes the expansion of a few 'winning' species then communities will become increasingly homogenized (McKinney & Lockwood 1999), a process that should be reflected in decreasing beta diversity.

More recently there has been an effort to use indices that represent functional aspects of communities to examine the impact of environmental change. For example, the community temperature index (CTI) reflects the relative composition of high- versus low- temperature dwellers in local communities (Devictor *et al.* 2008). A Europe-wide cross-taxon analysis of CTI showed consistent northward shifts of bird and butterfly communities, reflecting the changing distribution of species with a preference for high temperatures (Devictor *et al.* 2012). Although functional indices can provide more information on the changes in community composition, which and why individual species contribute to these observed changes is still poorly understood (Lennon *et al.* 2004).

The combination of macroecology and a high-resolution long-term data set, encompassing variable environmental conditions, provides a powerful tool for identifying climatic impacts (Kerr, Kharouba & Currie 2007). However, we currently lack information linking individual species range shifts to changes in community patterns. Utilizing the Swedish nationwide bird monitoring scheme, we investigate how avian alpha and beta diversity have changed in response to temperature during the last 13 years while accounting for land-cover differences between sites. We also assess the contribution of individual species to those changes. Sweden

covers a large latitudinal and climatic range and has experienced recent temperature increases. Additionally, many bird species meet their northern range limits within Sweden, providing us with an opportunity to track large-scale distribution shifts with a single homogenous dataset.

Materials and Methods

SURVEY DATA

We analysed data from the fixed route scheme of the Swedish Breeding Bird Survey (BBS), an annual monitoring scheme that started in 1996. The scheme consists of 716 routes systematically located throughout Sweden in a 25- km grid. This layout ensures that all major habitats are proportionally represented. At the centre of each grid cell the survey takes place over eight 1-km transects arranged in a square. The surveys are conducted once a year during the breeding season of most birds, between 15 May and 10 June (in the south) to between 15 June and 5 July (in the north). The survey starts at 4 am, timed to coincide with the greatest singing activity. The observer walks at 30–40 min per km and records all bird seen and heard. If obstructions prevent the surveyor from following the line, deviations of up to 200 m are allowed. The surveys are carried out by a combination of experienced volunteers and professional surveyors. We used data from 1998 to 2010, the period over which we obtained a representative coverage across Sweden. The number of routes surveyed in this period has varied between 166 (1998) and 584 (2008), with more than 400 routes surveyed in 8 of the 13 years.

MEASURES OF COMMUNITY DIVERSITY

Alpha diversity was calculated for each site and year, as species richness (S): the number of species observed. Beta diversity was calculated using the Sørensen dissimilarity index (β_{sor}) (Koleff, Gaston & Lennon 2003). Annual pairwise β_{sor} values were calculated between each focal route and each adjacent route also surveyed in the same year. The final value attributed to the focal route was the average of up to eight pairwise β_{sor} values in a given year (mean number of pairs: 4.74 ± 0.03) (Lennon *et al.* 2001). Note that in our case, β_{sor} is a measure of singularity as it measures the mean dissimilarity of pairs of routes rather than the heterogeneity of whole neighbourhoods (Jurasinski *et al.* 2012). Following the work of Baselga (2010) we partitioned the Sørensen index into two additive components: nestedness and turnover. Turnover was measured using the Simpson dissimilarity index (β_{sim}), which measures differences in composition between sites while controlling for differences due to richness (Lennon *et al.* 2001). The nestedness dissimilarity index (β_{nes}), which reflects the dissimilarity of communities as a result of ordered species loss, is then defined as β_{sor} - β_{sim} (Baselga 2010).

To further examine community dynamics, we modelled the matching components used to calculate beta diversity, *a* (continuity) the average number of common species between squares, *b* (gain) the average number of species present in the neighbouring squares that are not in the focal square, and *c* (loss) the average number of species present in the focal square, but not in the neighbouring sites (Koleff, Gaston & Lennon 2003; Gaston *et al.* 2007).

LAND COVER AND CLIMATE DATA

Land cover data were obtained from the Corine Land Cover Map 2006 (CLC2006, EEA 2007). To define habitat we clipped the CLC2006 using a 200 m buffer around each transect. The buffer distance was chosen as a compromise between the likely maximum boundary for bird detections and the fact that observers can deviate up to 200 m from the exact route. Corine land cover classes were further aggregated into the following categories (new aggregate category and constituent Corine Habitat Codes are shown): Arable (AR) 12,19,20; Bare ground (BA) 31,32; Broadleaved woodland (BL) 23; Coniferous Forest (CF) 24; Coastal (CO) 30, 42–44; Moors and Heathland (MO) 27; Natural Grassland (NG) 26; Shrub and Sclerophyllous vegetation (SH) 28,29; Urban (UR) 2–11; Water (WA) 40,41; Wetlands (WE) 35,36. The habitat for each transect was defined as the dominant aggregate class. We also derived a measure of habitat diversity (Hab$_{div}$) for each transect using the *vegan* package in R (Oksanen *et al.* 2011) to calculate a Shannon diversity index using the percentage land cover for each habitat class within each buffer zone. This index was used to control for patterns in community composition due to habitat heterogeneity.

Mean monthly temperatures were obtained from the Swedish Meteorological and Hydrological Institute (SMHI) gridded data set. Data from approximately 300 weather stations around Sweden have been interpolated to a 4×4 km grid, using geo-statistic interpolation (Johansson 2000). We selected the interpolated point nearest to each site resulting in 716 virtual weather sites spread evenly over the country.

We defined breeding season temperature (T) as the average of the mean monthly temperatures from April to the end of June, calculated each year (1998–2010) for each site. Because diversity measures have been shown to be highly correlated with broad temperature gradients (e.g. Turner, Lennon & Lawrenson 1988; Rosenzweig 1995) we included in our model a 'baseline' temperature value (T$_{base}$) (Fig. 1). For each site this was calculated as the average breeding season temperature for the 10 years prior to the start of the bird survey. T$_{base}$ was used to explain any variation in communities attributable to broad spatial climatic gradients as opposed to recent climate changes. To examine the effect of recent temperature we calculated the difference between the
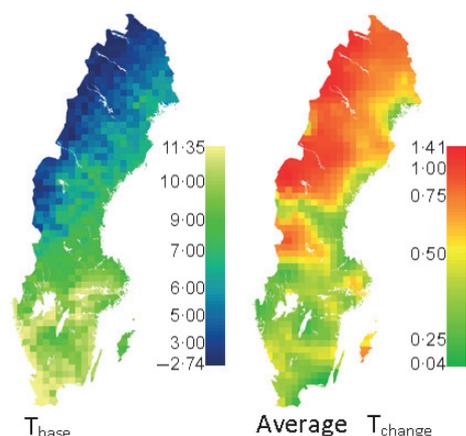
current breeding season temperature and the baseline (T-T$_{base}$ =T$_{change}$). Because the T$_{change}$ variable showed a strong positive temporal trend, we detrended it by running a simple linear regression of T$_{change}$ = Year and used the residuals in the final analyses. We interpret these residuals as temperature anomalies (T$_{anom}$) as they represent local increase or decrease in temperature compared to the baseline, but independent of any temporal trend. Using a detrended climate variable allowed us to examine the response of communities to temperature change independent of any processes that may also drive linear temporal trends. Since it is likely that the temporal trend will also account for some community response to temperature, our approach for detecting climatic impact on diversity is conservative.

STATISTICAL ANALYSES

Generalized additive models (GAMs) were used to model the spatial and temporal structure of bird communities (response variables: S, β$_{sor}$, β$_{sim}$, β$_{nes}$, *a*, *b*, *c*) and to examine the effects of historical temperature gradients and recent temperature anomalies. The GAMs were constructed using version 1·7–9. of the mgcv package (Wood 2006) in the statistical program R (R Development Core Team. 2011). We used generalized cross validation (GCV) optimization to select the degrees of freedom for each term automatically and included a gamma penalty of 1·4 to reduce the likelihood of over fitting the data (Wood 2006). As we wanted to account for possible spatial structure in our variables, we controlled for the nonlinear effect of the coordinates (latitude and longitude) using a smoothing function (Beale *et al.* 2010). The model variables were determined *a priori* as either important determinants of bird communities (e.g. Habitat: Devictor *et al.* 2008; Filippi-Codaccioni *et al.* 2010) or as the focus of hypothesis testing, so no model selection was undertaken. The dominant land cover class in Sweden, Coniferous Forest (CF), was set as the intercept. The model took the form:

g(diversity) = β_0 + s(lat, long) + year + habitat + hab$_{div}$ + T$_{base}$ + T$_{anom.}$

Where *g(diversity)* is the link function, diversity one of the community components (S, β$_{sor}$, β$_{sim}$, β$_{nes}$, *a*, *b*, *c*), β_0 is the intercept and *s* is a thin plate spline (Wood 2006). We examined diagnostic plots to check the model assumptions and to determine the best distribution family for each dependent variable. For all variables specifying a normal distribution ensured the best fit to the data and adherence to the assumptions for GAM models. We tested for spatial autocorrelation in the residuals of the GAMs using Moran's I correlograms. These showed positive autocorrelation in the residuals for beta diversity. Therefore, we also constructed simultaneous autoregressive error models (SAR$_{err}$) using the *spdep* library in R (Bivand 2011). In these models, the spatial error term is predefined from a neighbourhood matrix and autocorrelation in the dependent variable estimated, then parameters are estimated using a generalized least squares framework (Beale *et al.* 2010). We used first order neighbours with equal weighting (Kissling & Carl 2008; Melo, Rangel & Diniz-Filho 2009). For the SAR$_{err}$ models we carried out cross-validation by examining the fit of the models to a randomly selected 50% of the data (Appendix S1).

The parameter estimates and significance values from both the SAR$_{err}$ and GAM models showed high agreement. Therefore, we present the full model results from the SAR$_{err}$ models, but use the GAMs to construct spatially explicit predictive maps. We used the fitted GAM models to predict diversity values for each

Fig. 1. Values for T$_{base}$, the mean April–June temperature (ºC) for Sweden from 1987 to 1997 and average T$_{change}$: an average of the difference between T$_{base}$ and the mean April–June temperature for the years 1998–2010.

25- km grid cell square in Sweden for 1998 and 2010. To map the change in the predicted values we simply subtracted the predicted values for 1998 from those for 2010. Full GAM results are provided in Appendix S1.

Estimating species contribution with a species jackknife

We ran a jackknife analysis to investigate how individual species contributed to the modelled community responses. We removed each species one by one from the data set and re-calculated alpha diversity (S) and the Simpson dissimilarity index (β_{sim}) for each site and year. We used β_{sim} as this measure is independent from S. We re-ran our SAR_{err} models and examined the coefficients for 'T_{anom}' and 'Year' to assess the influence each species had on the global model. These coefficients allowed us to identify species that were responding to recent temperature in a way that also influenced the observed temporal trend in diversity for the whole assemblage. To estimate the relative species-specific impact, we calculated the percentage difference between the global model coefficient and the jackknife coefficient for each species. A positive difference indicated that a species had contributed towards the trend of the global model, whereas a negative difference suggested that a species did not support the overall trend. To obtain a measure of total influence for a given species (Sp_{inf}), we calculated the cumulative percentage difference by adding together the contribution values for 'T_{anom}' and 'Year' for each species.

Species trait analyses

We examined the relationship between Sp_{inf} and a small number of functional traits and population characteristics. We used a species temperature index (STI) calculated as the average breeding season temperature of the species European distribution (Devictor *et al.* 2008). We measured habitat specialization using the species specialization index (SSI), calculated as the coefficient of variation (standard deviation and/or mean) of a species density across habitats (Julliard *et al.* 2006). To examine whether or not common species were more likely to drive changes in trends we used the mean average annual percentage occupancy of surveyed squares as a proxy for distribution size. Finally, we used the log-linear population trend from 1998 to 2010 (Lindström, Green & Ottvall 2011). We carried out linear regressions between each Sp_{inf} score and the four different characteristics. We only included species when the Sp_{inf} score was greater than zero (S : 152 species; β_{sim} : 92 species).

Results

SPATIAL STRUCTURE OF SWEDISH BIRD COMMUNITIES

The alpha and beta diversity of Swedish bird communities showed a clear spatial pattern (Fig. 2). Alpha diversity was highest in the south of the country and generally declined towards the north (latitudinal gradient) and northwest (altitudinal gradient), although it remained high along the eastern coastline. This distribution likely reflects different ecotones across Sweden as highlighted by the habitat coefficients (Table 1). For example, areas of high richness correlate well with farmland habitats, while areas of moderate diversity appear to cover areas of managed coniferous forest (the central part of southernmost Sweden, and the central area of northern Sweden). Finally, the mountainous,

Table 1. Results of the simultaneous auto-regressive models (SARs) used to examine the influence of year, habitat and temperature on diversity indices of Swedish bird communities. Parameter estimates, standard errors and *P*-values are shown. Habitat coefficients are in reference to 'Coniferous Forest' habitat (CF), which is the most abundant land cover category in Sweden

Model terms	Species Richness (S) Pseudo $R^2 = 0.62$			Sørensen pairwise dissimilarity (β_{sor}) Pseudo $R^2 = 0.52$			Simpson pairwise dissimilarity (β_{sim}) Pseudo $R^2 = 0.45$			Nestedness dissimilarity (β_{nes}) Pseudo $R^2 = 0.13$		
	Coef	S.E	*P*	Coef	S.E	*P*	Coef	S.E	*P*	Coef	S.E	*P*
(Intercept)	−469·935	73·339	<0·001	6·599	0·593	<0·001	4·284	0·661	<0·001	2·310	0·469	<0·001
Year	0·237	0·037	<0·001	−0·003	0·0003	<0·001	−0·002	0·0003	<0·001	−0·001	0·0002	<0·001
T_{base}	3·408	0·111	<0·001	−0·016	0·002	<0·001	−0·010	0·002	<0·001	−0·005	0·001	<0·001
T_{anom}	0·492	0·176	0·005	−0·008	0·001	<0·001	−0·008	0·002	<0·001	0·001	0·001	NS
Arable (AR)	4·854	0·477	<0·001	0·006	0·004	NS	0·005	0·004	NS	0·000	0·003	NS
Bare (BA)	−0·273	1·383	NS	0·061	0·011	<0·001	0·058	0·013	<0·001	0·006	0·009	NS
Broadleaved forest (BL)	−2·103	0·627	<0·001	−0·010	0·005	0·035	−0·002	0·006	NS	−0·009	0·004	0·022
Coastal (CO)	−1·327	0·789	NS	0·087	0·006	<0·001	0·085	0·007	<0·001	0·002	0·005	NS
Moors & Heathland (MO)	0·864	0·796	NS	0·010	0·007	NS	0·013	0·007	NS	−0·002	0·005	NS
Natural Grasslands (NG)	−9·480	4·756	0·046	0·076	0·036	0·036	0·077	0·040	NS	0·001	0·029	NS
Shrub (SH)	−2·190	0·623	<0·001	−0·006	0·005	NS	0·000	0·005	NS	−0·006	0·004	NS
Urban (UR)	−3·812	1·565	0·014	0·040	0·012	0·001	0·044	0·014	0·001	−0·006	0·010	NS
Water (WA)	−5·415	0·563	<0·001	0·056	0·004	<0·001	0·052	0·005	<0·001	0·004	0·003	NS
Wetland (WE)	−0·323	0·676	NS	−0·001	0·005	NS	0·007	0·006	NS	−0·008	0·004	NS
Hab_{div}	10·735	0·330	<0·001	−0·011	0·003	<0·001	−0·010	0·003	<0·001	−0·001	0·002	NS
	N = 4784			N = 4683			N = 4683			N = 4683		

tundra regions of Sweden are the most species poor (Fig. 2). Habitat heterogeneity had a significant positive effect on alpha diversity (Table 1). In contrast, beta diversity (β_{sor}) increased with the latitudinal and altitudinal gradient, with southern Sweden shown to be highly homogenous (Fig. 2). Coastal areas in the north of Sweden appeared to be one of the few areas where high alpha and beta diversity values were coincidental. Patterns in β_{sor} were mirrored in species turnover (β_{sim}) (Fig. 2; Table 1). By contrast, nestedness dissimilarity (β_{nes}) showed no strong latitudinal or altitudinal trends, although the highest β_{nes} values did coincide with areas of high β_{sor} in the mountains and along the northern coastline (Fig. 2).

TEMPORAL AND TEMPERATURE EFFECTS

Both alpha and beta diversity showed significant temporal trends. Species richness increased over time, while β_{sor}, decreased. Of the partitioned components, β_{sim} showed a steeper temporal decline than β_{nes} (Table 1). The variables measuring recent detrended temperature changes (T_{anom}) and the underlying temperature gradient (T_{base}) were significantly different from zero in all models ($P < 0.05$, Table 1) with the exception of β_{nes} that showed no association with T_{anom}. Alpha diversity increased while β_{sor} and β_{sim} decreased with T_{base} and T_{anom} (Table 1). It is likely that the temporal trend also accounted for some of the response to temperature.

There was large spatial variation in the magnitude of the changes (Fig. 2), but these did not necessarily coincide with the areas experiencing the greatest temperature change (Fig. 1). Although the largest absolute gains in alpha diversity occurred in the north east of Sweden, along the coast and the border with Finland, the highest percentage gains were in the mountains, demonstrating the relative importance of gaining species in a low richness region. The spatial structure of change in β_{sor} was similar to species richness, with areas undergoing the greatest losses of β_{sor} coinciding with areas of the greatest alpha diversity gains (Fig. 2), providing evidence for the link between these processes. Of the partitioned components of beta diversity, turnover (β_{sim}) appeared to drive the pattern in β_{sor} Losses of β_{nes} appeared to be greatest where beta diversity was already low, for example, the southern tip of Sweden (Fig. 2).

Matching components

Of the three matching components, continuity (*a*), gain (*b*) and loss (*c*), only continuity showed a significant temporal trend and relationship with T_{anom} (Table 2). Mapping component *a*, demonstrated the close positive relationship with species richness (Fig. 2). These results suggest that changes in β_{sor} and β_{sim} are primarily driven by an increase in the number of species in common between adjacent sites (*a*) rather than a loss of unique species (*b*, *c*).

SPECIES CONTRIBUTION TO COMMUNITY CHANGE

As expected, the majority of species had little effect on the 'Year' and 'T_{anom}' coefficient values, with a small number of species apparently contributing to the modelled trends in alpha and beta diversity (Appendix S2). There was high congruence between the 15 most influential species for both indices (Table 3), with Crane, Crested tit, Cuckoo, Dunnock, Garden warbler, Great spotted woodpecker, Green sandpiper, Mistle thrush, Spotted flycatcher and Wren all appearing on both lists (see Table 3 for scientific names).

Distribution size had a significant positive effect on Sp_{inf} (S: $b = 0.06 \pm 0.006$, adj-$R^2 = 0.35$, $P < 0.001$; β_{sim}: $b = 0.05 \pm 0.008$, adj-$R^2 = 0.25$, $P < 0.001$). Habitat specialization also influenced Sp_{inf}, with habitat generalists (low SSI score) more likely to influence the model (S: $b = -0.014 \pm 0.002$, adj-$R^2 = 0.22$, $P < 0.001$; β_{sim}: $b = -0.016 \pm 0.003$, adj-$R^2 = 0.22$, $P < 0.001$). The majority of the most influential species have shown significant positive population trends since 1998 (Table 3, Lindström, Green & Ottvall 2011). However, although population trend had a significant positive effect, the effect magnitude was negligible (S: $b = 0.001 \pm 0.0004$, adj-$R^2 = 0.03$, $P < 0.05$; β_{sim}: $b = 0.001 \pm 0.0005$, adj-$R^2 = 0.04$, $P < 0.05$). The STI of each species had no significant effect on Sp_{inf}.

Discussion

Spatial patterns in the diversity of Swedish birds conformed to the well-established latitudinal gradient in species richness (Turner, Lennon & Lawrenson 1988; Rosenzweig 1995; Lennon, Greenwood & Turner 2000) and provided more evidence for an altitudinal gradient in beta diversity (Gaston *et al.* 2007; Melo, Rangel & Diniz-Filho 2009). Over time, there was evidence for a positive trend in alpha diversity and a negative trend in beta diversity. Both the underlying temperature gradient (T_{base}) and recent temperature anomalies (T_{anom}) contributed to these patterns by showing a positive correlation with alpha diversity and a negative correlation with beta diversity (Table 1). A number of studies, including our own, have now demonstrated a relationship between increasing temperatures over time and species richness of plant, butterfly, fish and bird communities (Klanderud & Birks 2003; Lemoine & Böhning-Gaese 2003; Menéndez *et al.* 2006; Hiddink & ter Hofstede 2008; La Sorte *et al.* 2009; Davey *et al.* 2012). These richness increases have been attributed to generalist species expanding their distributions (Menéndez *et al.* 2006; Davey *et al.* 2012; Le Viol *et al.* 2012) with the expectation that this would result in taxonomic homogenization (McKinney & Lockwood 1999) and decreased beta diversity. This process has been demonstrated in plant communities where warming temperature have resulted in both increases in alpha diversity and declines in beta diversity (Britton *et al.* 2009; Bühler
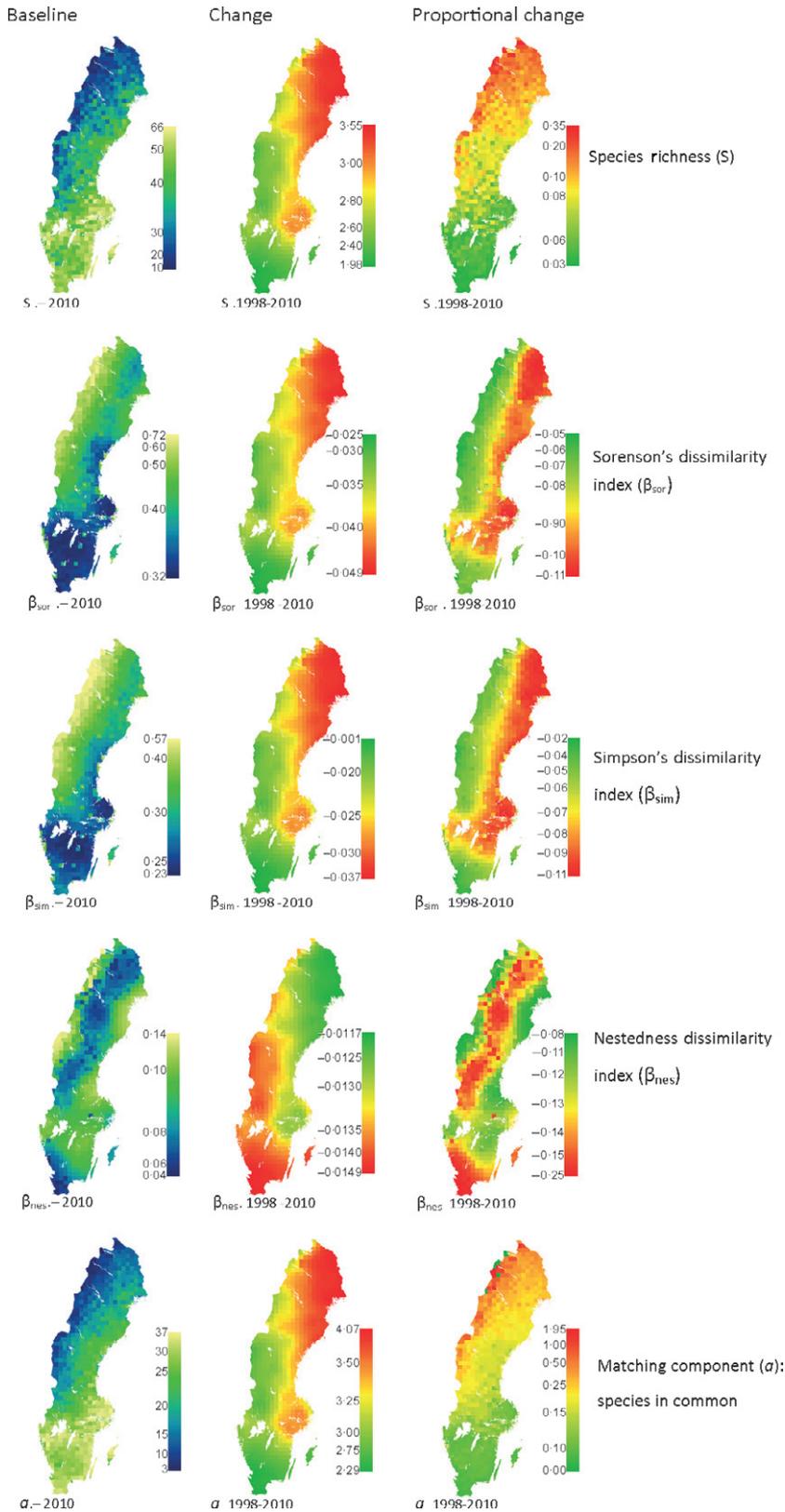
Fig. 2. Maps showing the predicted values from the Generalized Additive Models for alpha and beta diversity, the beta diversity components and the matching component *a*. Figures to the far left show the modelled values for 2010 to illustrate the spatial structure of the variables. The maps in the middle column show the difference in predicted values from 1998 to 2010. The maps on the right express the change in value from 1998 to 2010 as a percentage. Scale bars are based on geometric intervals.

& Roth 2011). To our knowledge, we provide the first evidence of this pattern in bird communities, although it should be noted that while La Sorte & Boecklen (2005) found consistent increases in avian species richness, species turnover showed no trend in their study.

To examine the underlying processes shaping broad patterns and change in beta diversity we partitioned the index into several components. Patterns of beta diversity were primarily attributable to species turnover (β_{sim}) rather than nestedness (β_{nes}). In other words, differences

Table 2. Results of the simultaneous auto-regressive models (SARs) used to examine the influence of year, habitat and temperature on matching components of Swedish bird communities. Parameter estimates, standard errors and *P*-values are shown. Habitat coefficients are in reference to 'Coniferous Forest' habitat (CF), which is the most abundant land cover category in Sweden

Model terms	Continuity (*a*)			Gain (*b*)			Loss (*c*)		
	Pseudo $R^2 = 0.76$			Pseudo $R^2 = 0.27$			Pseudo $R^2 = 0.27$		
	Coef	S.E	*P*	Coef	S.E	*P*	Coef	S.E	*P*
(Intercept)	−527·809	38·129	<0·001	51·814	41·836	NS	−28·386	38·771	NS
Year	0·269	0·019	<0·001	−0·019	0·021	NS	0·019	0·019	NS
T_{base}	1·065	0·118	<0·001	0·184	0·108	NS	0·595	0·088	<0·001
T_{anom}	0·546	0·090	<0·001	−0·099	0·099	NS	-0·101	0·092	NS
Arable (AR)	1·411	0·234	<0·001	0·938	0·260	<0·001	0·865	0·242	<0·001
Bare (BA)	−0·578	0·731	NS	−0·505	0·804	NS	2·928	0·744	<0·001
Broadleaved forest (BL)	−0·132	0·315	NS	−0·542	0·349	NS	−0·172	0·324	NS
Coastal (CO)	−3·330	0·395	<0·001	3·709	0·436	<0·001	3·418	0·405	<0·001
Moors & Heathland (MO)	−0·056	0·422	NS	−0·596	0·464	NS	1·027	0·428	0·016
Natural Grasslands (NG)	−4·655	2·292	0·042	−2·712	2·550	NS	2·206	2·377	NS
Shrub (SH)	−0·300	0·310	NS	−0·850	0·344	0·013	−0·134	0·320	NS
Urban (UR)	−1·243	0·775	NS	−0·499	0·861	NS	2·078	0·802	0·009
Water (WA)	−3·140	0·278	<0·001	0·818	0·308	0·008	0·702	0·286	0·014
Wetland (WE)	−0·133	0·329	NS	−0·376	0·368	NS	0·342	0·344	NS
Hab_{div}	2·988	0·161	<0·001	1·110	0·179	<0·001	0·762	0·167	<0·001
	N = 4683			N = 4683			N = 4683		

in species assemblages between sites were not driven by differences in species richness only (i.e. species loss and/or gain), but by true changes in species composition (i.e. replacement) between the sites (Baselga 2010). Similarly it appeared that the observed decrease in beta diversity was due to a decrease in turnover between sites, species compositions became more similar and not simply because of richness increases. Nestedness is a consequence of any factor that promotes a non-random process of species loss (Gaston & Blackburn 2000), with glaciation a likely explanation for patterns in Europe (Baselga 2010; Leprieur *et al*. 2011). Our results suggest that what we see are changes due to recent processes rather than slow spatial dynamics (i.e. re-colonization from the last glaciation). However, we believe that our ability to disentangle these processes is scale dependent. For instance, although historical processes might be visible at larger scales, the localized scale of our analysis may prevent us from detecting such processes.

To examine the mechanisms behind changes in beta diversity we modelled the matching components used to calculate the indices. Increasing species richness will generally increase the number of species that two sites have in common (component *a*) (Koleff & Gaston 2002). Accordingly, we found that the negative temporal trend was predominately driven by an increase in the continuity component (*a*), rather than to decreases in the unique components (*b*,*c*) (Table 2). There are two mechanisms by which component *a* could increase: 1) species already present in Sweden expand their distributions; 2) new species invade and become established. Since 1998, a small number of new bird species have entered Sweden, but only one (*Phalacrocorax aristotelis*) has been observed in

the fixed route scheme and only on a single site. Therefore, we can infer that changes in diversity indices must reflect changes in the distribution of species already present within Sweden. Species' distributions may show a number of different responses to changing climate, for example, they may remain static, expand, contract or shift (Maggini *et al*. 2011). Several studies of vertebrate species have found evidence for range expansions but less evidence for contractions or complete shifts (Thomas & Lennon 1999; La Sorte 2006; Moritz *et al*. 2008). We found a trend in the continuity component (*a*) and species richness, but no trend in *b* or *c*, suggesting that changes in Swedish bird communities are currently being driven by range expansions rather than shifts and contractions. This may be because many of these species do not meet their southern range margin in Sweden. The greatest gains in richness and component (*a*) were mostly concentrated in mountainous areas (Fig. 2), suggesting that these habitats are easily colonized by expanding species and have the potential to provide some refuge for species shifting north. However, the double blow of reduced habitat suitability and increased competition may also mean that the current residents of these areas come under increasing pressure in future (Crick 2004).

Recent work has demonstrated that habitat and climatic niches are inter-related, and unlikely to change independently (Barnagaud *et al*. 2012). For example, Wilson *et al*. (2007) found that although species richness gradients shifted upwards in elevation, low-elevation species failed to colonize the mountains because of their habitat requirements. Our results showed some spatial mismatches between changes in temperature and diversity suggesting that temperature was not the sole cause of the

temporal trend (Figs 1 & 2). This is likely due to the importance of other environmental variables such as habitat and land use changes, which have also been reported to increase richness and homogenization (Devictor & Robert 2009; Clavero & Brotons 2010; Filippi-Codaccioni *et al.* 2010). Our results suggested that managed habitats, such as the forested and agricultural areas of Sweden had high alpha but low beta diversity. While we might expect this to be due in part to the homogeneity of managed habitats, we found that higher habitat diversity was related to decreased beta diversity (Table 1). Again, the results may be influenced by the relative importance of different processes at different spatial scales (Lennon *et al.* 2001) and future work would benefit from a fine-scale analysis of the importance of habitat heterogeneity for shaping communities.

Within Sweden there are strong geographical habitat and climatic gradients, this can make it difficult to separate effects of recent temperature while controlling for confounding variables that are likely to explain a certain amount of variation in the variables of interest. However, we took a conservative approach for detecting climatic impacts by including habitat, a baseline temperature value, and by using a detrended variable to measure recent temperature change. We are therefore confident that our results represent an underestimate rather than overestimate of the climatic impact. However, variation between sites in temperature trends will result in temperature anomalies being serially correlated. Consequently, an exploratory analysis using breeding season temperature of the previous year gave similar results, although the models explained less variance. Additionally, it is likely that no single climatic variable explains the response of all breeding bird species, and responses may show different lag periods (La Sorte & Jetz 2012; Lindström *et al.* 2012). Therefore, although we are confident that there is a relationship between temperature and diversity, we cannot be entirely sure of the mechanism. One potential explanation is that in warmer springs migrants may 'over shoot' their typical breeding sites (Otterlind 1954) leading to an apparent northward shift in distributions. However, although the jackknife analyses did suggest a predominance of migrants were driving community trends, several resident species were also influential. Additionally the representation of migrants did not necessarily exceed that expected by chance given that 73% of birds breeding in Sweden are migrants (Ottvall *et al.* 2009). Alternatively, increasing abundance as a result of warmer temperatures may have made species more detectable. However, we found that changes were most often detected for common species, and since our indices are based on presence and/or absence, changes in detectability are less likely to have affected these results. Note, however, that such conclusions may not be applicable across taxa as birds, being highly mobile organisms may be more equipped to respond to climate change than other groups.

The spatial description of alpha and beta diversity patterns has utility for conservation planning (Devictor *et al.* 2010; Mokany *et al.* 2011). However, while a macroecological approach can provide evidence that changes in distribution have occurred, it lacks the detail required for species-specific management. In this article we have established a framework by which macroecological and species approaches can be used together. To our knowledge, this is the first time that species have been ranked in terms of their response to temperature and ability to influence community diversity patterns. The most influential species (Table 3) lack unifying physical traits. However, a functional approach showed that habitat generalists with large distributions were more likely to influence community trends. We might have expected habitat specialists, with restricted ranges to be particularly vulnerable to climate change (McKinney & Lockwood 1999; Gaston & Blackburn 2002; Julliard, Jiguet & Couvet 2003), however, the jackknife showed that these species did not have a large influence on community patterns. The richness patterns of rare species and their association with environmental variables have been shown to be difficult to predict (Lennon *et al.* 2011). Additionally, previous studies have shown that common rather than rare species contribute more to spatial patterns in richness (Lennon *et al.* 2004; Vázquez & Gaston 2004; La Sorte 2006; Pearman, Guisan & Zimmermann 2010), beta diversity (Gaston *et al.* 2007) and species-energy relationships (Evans, Greenwood & Gaston 2005). Our results show that common species are also driving patterns in diversity-temperature relationships. Therefore, diversity indices based on all species in a community, may not be suitable for monitoring climatic impacts for vulnerable species. It should be noted that the most common species in terms of distribution (e.g. willow warbler) had little influence on diversity trends. These species have no boundaries within the geographical data set so we are unable to reliably assess their climatic niche (Lennon *et al.* 2004, 2011).

The consequences of expansions by common and generalist species are that these species also possess "common" functional traits. Therefore, an increase in common species in local communities is likely driving a functional as well as taxonomic homogenization. This process, discussed in Clavel, Julliard & Devictor (2011) has not yet been investigated empirically but we provide a framework to do so. Via our community and species analyses we can identify 1) change in community composition; 2) how and where these changes are related to climate changes (easily extendable to habitat and land-use changes); 3) what species are responsible for these changes; and 4) species-specific characteristics that influence community changes. Identifying the specific species and traits that drive community changes should allow a greater understanding of the processes of climate change impacts, allowing better conservation recommendations.

Table 3. The results of the jackknife analyses showing the percentage difference between the coefficient from the global mode and that for a model run without the named species. A positive value indicates that the species contributed to the trend of the global model. The linear population trend, expressed as a percentage change from the baseline year of 1998 is shown ($P < 0.05$(*), $P < 0.01$(**), $P < 0.001$ (***)) (Lindström, Green & Ottvall 2011). *Loxia sp.* represents *Loxia curvirostra* and *Loxia pytyopsittacus*. Only the 15 most influential species are shown. Full results are provided in Appendix S2

	% Difference 'T$_{anom}$'	% Difference 'Year'	Total% difference	Population trend	% Occupancy
Species Richness					
Crossbill *Loxia species*	5·81	12·78	18·59	11·8 ***	60
Wren *Troglodytes troglodytes*	7·41	3·37	10·78	3·6 ***	52
Crane *Grus grus*	4·00	5·89	9·89	6·8 ***	41
Spotted flycatcher *Muscicapa striata*	4·66	3·55	8·21	3·4 ***	53
Nuthatch *Sitta europaea*	2·74	4·50	7·24	5·2 ***	30
Cuckoo *Cuculus canorus*	3·42	3·29	6·71	2·4 ***	82
Green sandpiper *Tringa ochropus*	2·06	4·36	6·42	3·5 ***	42
Mistle thrush *Turdus viscivorus*	1·68	4·72	6·40	6·4 ***	44
Blackbird *Turdus merula*	1·94	4·44	6·38	2·9 ***	66
Fieldfare *Turdus pilaris*	8·40	-2·43	5·97	-2·1 ***	60
Garden warbler *Sylvia borin*	4·51	1·11	5·61	1·4 ***	66
Great spotted woodpecker *Dendrocopos major*	0·89	4·54	5·43	4·3 ***	66
Dunnock *Prunella modularis*	-0·83	6·17	5·33	3·8 ***	60
Redstart *Phoenicurus phoenicurus*	1·92	3·23	5·14	1·9 ***	58
Crested tit *Parus cristatus*	1·92	3·14	5·07	3·4 ***	30
Beta Diversity					
Cuckoo *Cuculus canorus*	4·48	7·72	12·21	2·4 ***	82
Pied wagtail *Motacilla alba*	5·09	3·31	8·40	1·7 ***	58
Garden warbler *Sylvia borin*	4·36	3·85	8·21	1·4 ***	66
Green sandpiper *Tringa ochropus*	0·46	7·25	7·71	3·5 ***	42
Crested tit *Parus cristatus*	3·29	3·72	7·01	3·4 ***	30
Mistle thrush *Turdus viscivorus*	0·70	6·09	6·79	6·4 ***	44
Spotted flycatcher *Muscicapa striata*	1·36	5·41	6·78	3·4 ***	53
Dunnock *Prunella modularis*	-3·24	9·87	6·63	3·8 ***	60
Buzzard *Buteo buteo*	3·26	3·31	6·57	1·2 NS	27
Lesser whitethroat *Sylvia curruca*	3·04	3·27	6·32	3·4 ***	51
Greenshank *Tringa nebularia*	4·58	1·55	6·14	-0·5 NS	23
Whooper swan *Cygnus cygnus*	3·43	2·06	5·48	3·5 **	16
Wren *Troglodytes troglodytes*	3·78	1·33	5·11	3·6 ***	52
Crane *Grus grus*	2·77	2·12	4·89	6·8 ***	41
Great spotted woodpecker *Dendrocopos major*	-2·21	6·69	4·48	4·3 ***	66

Conclusions

We have demonstrated that Swedish bird communities can respond rapidly to temperature anomalies and as such have undergone significant changes in the last decade. Alpha and beta diversity have shown contrasting trends, with an increase in species richness occurring concurrently with a decline in species turnover. We provide a framework for identifying species-specific contributions to these macroecological patterns, hence combining two different approaches for identifying climatic impacts. The changes in community indices can be attributed to common species becoming increasingly common, likely due to climate related range expansions, although habitat and land use changes are also likely to have contributed. However, we were unable to detect changes due to rarer range-restricted species, either because they have not occurred yet or, more likely, these responses are swamped by those of more common species. Despite this, our results still provide strong evidence that increasing temperatures have driven a compositional homogenization of Swedish bird communities, a trend likely to continue under future climate change scenarios.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Additional model results.

Appendix S2. Species influence scores.