



Regional variation in climate change winners and losers highlights the rapid loss of cold-dwelling species

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ABSTRACT

Aims Climate change is known to drive both the reshuffling of whole assemblages and range shifts of individual species. Less is known about how local colonizations and extinctions of individual species contribute to changes at the community level. Our aim was to estimate the contribution of individual species to a change in community composition attributed to climate change and to relate these species-specific contributions to species' commonness, climatic niche characteristics and life history traits most likely to influence species sensitivity to climate change.

Location Sweden.

Methods Focussing on birds, we analysed changes from 1998 to 2012 in the Community Temperature Index (CTI), a measure of the average climatic niche of a community. Using a jackknife approach we assessed the contribution of individual species to the temporal trend in CTI in four different regions across Sweden, controlling for habitat distribution. We further tested whether species contribution was related to population trends and rarity to identify species most vulnerable to climate change.

Results Community Temperature Index had increased over time with the greatest gains occurring in the north of the country, reflecting the larger temperature increases in this area. Changes in the regional CTI were driven both by warm-dwelling species colonizing new sites and by extirpations of cold-dwelling species. Furthermore, the community changes were influenced by both rare and common species. At the same time, the distribution changes of a large number of species were seemingly unaffected by climate change.

Main conclusions Both range expansion and contractions contributed to the relative increase of warm-dwelling species in Swedish bird communities. We successfully identified the climatic impacts on some of Sweden's rarest species, including cold-dwelling species in the mountainous north. Our approach may be an efficient tool to use when characterizing the impacts of climate change on species and communities.

Keywords

avian ecology, climate change, community temperature index, macroecology.

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INTRODUCTION

Geographic patterns in communities are driven by differences in the distributions of individual species (Lennon *et al.*, 2004). Changes in these patterns therefore reflect underlying processes of colonization and extinction and can

be used to assess the impact of environmental change (i.e. abiotic and biotic changes) on whole communities. Recent changes in climate have impacted community composition across a number of taxa (Menéndez *et al.*, 2006; Lemoine *et al.*, 2007; La Sorte *et al.*, 2009; Davey *et al.*, 2012; De Frenne *et al.*, 2013). These changes reflect underlying shifts

in the distributions of individual species, but at the level of the community it is impossible to discern to what extent these changes are driven by climate warming ‘winners’ expanding or by ‘losers’ contracting. Explicitly linking changes in community patterns with the range-shifts of individual species is a crucial next step.

An important factor to take into account when studying the effect of climate change on individual species is its commonness, not least because this may influence the statistical power of analyses (Godet *et al.*, 2015). Climate driven increases in species richness have been attributed to expansions in the ranges of common, generalist species (Menéndez *et al.*, 2006; Britton *et al.*, 2009; Davey *et al.*, 2012), a pattern confirmed by linking species contributions to temporal declines in beta diversity (Davey *et al.*, 2013). Additionally, those studies that have examined shifts in species range margins have found greater evidence for range expansions (Thomas, 2010). However, spatial patterns in species richness are shaped more by common species than rare ones (Lennon *et al.*, 2004) and range expansions are easier to detect than range contractions (Thomas *et al.*, 2006). Therefore, identifying climatic impacts on vulnerable, range-restricted species has been difficult (Thomas *et al.*, 2006). Furthermore, using traditional diversity indices and/or range-margin studies to identify climate change impacts on rarer species remains problematic due to data scarcity, resulting in low statistical power. This a concern as many rare species, especially those with specific habitat requirements, are likely to be particularly vulnerable to climate change due to their restricted ranges (Calosi *et al.*, 2008).

The balance between warm and cold-dwelling species can be reflected by the community temperature index (CTI), which measures the average temperature niche of a community (Devictor *et al.*, 2008). CTI is calculated as the average species temperature index (STI) of all species present at a site during each survey, where STI is the average temperature of each species’ breeding distribution (Devictor *et al.*, 2008, 2012). Increases in CTI have been demonstrated for birds, butterflies and plants, parallel to climate warming (Devictor *et al.*, 2008, 2012; Kampichler *et al.*, 2012; Lindström *et al.*, 2013; Roth *et al.*, 2014; Gaüzère *et al.*, 2015). Increases may be driven via colonisations by warm-dwelling species and/or extirpations of cold-dwelling species, but the relative importance of these two processes to community dynamics is poorly known (but see Princé & Zuckerberg, 2014). Moreover, CTI has generally been estimated for a given area (typically at national scale) while ignoring geographic variation in responses – for example caused by differences in landscape structure and composition (Clavero *et al.*, 2011). Although the CTI method has been adopted as an indicator of climate change impact on biodiversity at the European level (Zisenis, 2010), how species contribute to the dynamics of CTI in space and time remains to be described.

In this paper, we addressed two main objectives. We first estimated the contribution of individual species to climate driven changes in community composition. We then

related species-specific contributions to species’ commonness and climatic niche characteristics. We focused on Swedish bird communities, where CTI values at local and national scales have been found to track summer temperature changes with 1–3 years lag (Lindström *et al.*, 2013). We then estimated the influence of habitat and climate variables on CTI trend. By identifying the contribution of individual species to changes in CTI we describe how species-specific distribution changes were responsible for changes in the index and how this information can be used to inform conservation action.

METHODS

Bird data

We used extensive monitoring data for birds collected from the Fixed route scheme of the Swedish Breeding Bird Survey (BBS) from the years 1998–2012. The Fixed route scheme was initiated in 1996 (Lindström *et al.* 2007) and consists of 716 plots systematically located throughout Sweden in a 25 km grid (for survey details see Appendix S1). The grid covers the latitudinal range of 55–69°N (approximately 1500 km). We also used the national population trends that are calculated using these data (Lindström & Green, 2013).

Community temperature index

For each species we calculated its STI as the average April–August temperature over the period 1961–2008 for its European distribution (following Lindström *et al.*, 2013). Distributions were defined by the European bird atlas (Hagemeijer & Blair, 1997) and climate data came from the Worldclim database (Hijmans *et al.*, 2005). To examine colonisations and extinction processes, we calculated CTI based on presence/absence as the average STI across all species present in a community (see Appendix S1 for further details). Species were classified as warm-dwellers if their STI fell above average CTI (calculated using all years), cold-dwellers if their STI was below average CTI. For completeness, we also calculated a CTI based on abundance data (CTI_{ab}), i.e. the average STI of all individual birds found in a survey, which by definition gives more weight to abundant species.

Habitat and climate data

Land cover data were obtained from the Corine Land Cover Map 2006 (CLC2006; EEA 2007) and used to calculate percentage cover of each habitat class (see Appendix S1). Temperature data were obtained from the Swedish Meteorological and Hydrological Institute (SMHI) (see Appendix S1). Breeding season temperature was defined as the average of the mean monthly values from April until August. We calculated the long-term mean as the average temperature at each site over the period 1961–1990 (T_{61-90}) and the recent temperature trend for each site as the mean

annual change in breeding season temperature 1998–2012 (T_{change}). Sweden shows strong latitudinal and altitudinal gradients in temperature which are closely matched by CTI (Fig. 1a,b). There have also been distinct geographical trends in warming across Sweden with much greater increases in the north of the country (Fig. 1c), and since CTI has been shown to track changing temperatures we would expect rates of community change and each individual species contribution to those changes to also differ geographically. Therefore, we used the T_{change} variable to divide Sweden into four regions showing different climatic trends (Fig. 1c) (see Appendix S1).

Modelling

To visualize our data we first calculated the mean annual change in observed CTI values at each site. For sites that were not sampled in consecutive years, annual change was calculated by dividing the difference in CTI by the number of years elapsed between surveys. We then used Inverse Distance Weighting (IDW) interpolation methods in ArcMap 9.3 to produce maps of CTI change (Fig. 1d). IDW is a type of moving average, which weights data points in the neighbourhood on their proximity to the focal site.

We used Generalized Additive Mixed Models (GAMMs) to model the national and regional temporal trends in CTI. The national model included the covariate *Year* while the regional model included the covariates, *Year* and *Region* as well as a *Year:Region* interaction term in order to obtain estimates of the temporal trend in each region. The southernmost region (Region 1) was set as the reference (Fig. 1c). We used a Gaussian error structure with an identity link. This model had to account for the fact that neighbouring sites were more similar in terms of CTI and environmental variables than distant sites. Moreover, when analysing time-series, data on two consecutive years were more similar than other pairs. A detailed and explicit integration of both spatial and temporal autocorrelation was not feasible in the same model. We therefore first accounted for spatial autocorrelation by fitting the plot's geographical coordinates using a smoothing function (2-dimensional thin plate regression splines) as a trend-surface of CTI (Dormann *et al.*, 2007) according to the methods of Wood (2006). We then ensured that the temporal autocorrelation of values from the same site through time was accounted for by defining the model's error term correlation structure as a 1st order autoregressive function with *Year* nested within *Site* (Pinheiro & Bates, 2000). We finally took into account the uncontrolled variability between sites (observers, habitat, regional species pool and bioclimatic region) by allowing for the random variation of the intercept of each site by adding *Site* as a random effect (Monnet *et al.*, 2014). Finally, environmental covariates (the 11 CORINE habitat classes and T_{61-90}) were tested for inclusion to help account for the influence of temperature gradients and land use. The GAMMs were constructed using version 1.7-9. of the *MGCV* package (Wood, 2006) in the sta-

tistical 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 fit the models using restricted maximum likelihood (REML) (Wood, 2006).

Identifying species' contribution to CTI

We used a jackknifing approach to identify how individual species contributed to the modelled community response. To do this we removed each species one by one (with replacement) from the dataset and re-calculated CTI for each site and year and re-ran our national and regional models. For each removed species we estimated the relative contribution to the *Year* trend both nationally and in each region by calculating the difference between the coefficient of the 'all species model' and the coefficient for 'CTI minus species *x* model'. A positive difference indicated that a species had contributed towards the trend of the global model, i.e. when the species was removed the coefficient of the *Year* trend decreased (Davey *et al.*, 2013). Note that, for a given species, a contribution depends on two dimensions. One is the difference between its specific STI and the average STI of the rest of the assemblage (the 'originality' of the individual species' STI). The other dimension is the trend in the relative occurrence (or abundance) of the species, i.e. how different is the individual species' trend compared with that of the community.

To investigate how species contribution to CTI was related to species rarity, each species was given a commonness rank according to its population size in Sweden (Ottosson *et al.*, 2012), from the most abundant species (1 – Willow Warbler *Phylloscopus trochilus*, 13 million pairs) to the rarest one (251 – Kentish Plover *Charadrius alexandrinus*, 1 pair).

Population trends and CTI contribution

Niche-tracking theory suggests that in a warming climate, warm-dwelling species should increase their populations and vice versa (Jiguet *et al.*, 2010). If all species are tracking climate warming then all species should contribute to an increase in CTI over-time. However, the documented heterogeneity in species-level contributions to CTI, where even negative contributions occur, suggests that many species are not showing distribution changes that would be predicted given their observed temperature niche (Princé & Zuckerman, 2014). To examine this we investigated the relationship between STI and long-term population trend for two groups, those species contributing as investigated to the CTI and those showing negative contributions. For those species contributing positively towards the increase in CTI we would expect a relationship between their climatic preference and their population trend. For example, we would expect warm-dwelling species to have positive population trends and cold-dwelling species to show negative population trends. Those species that did not contribute to the CTI are less likely to

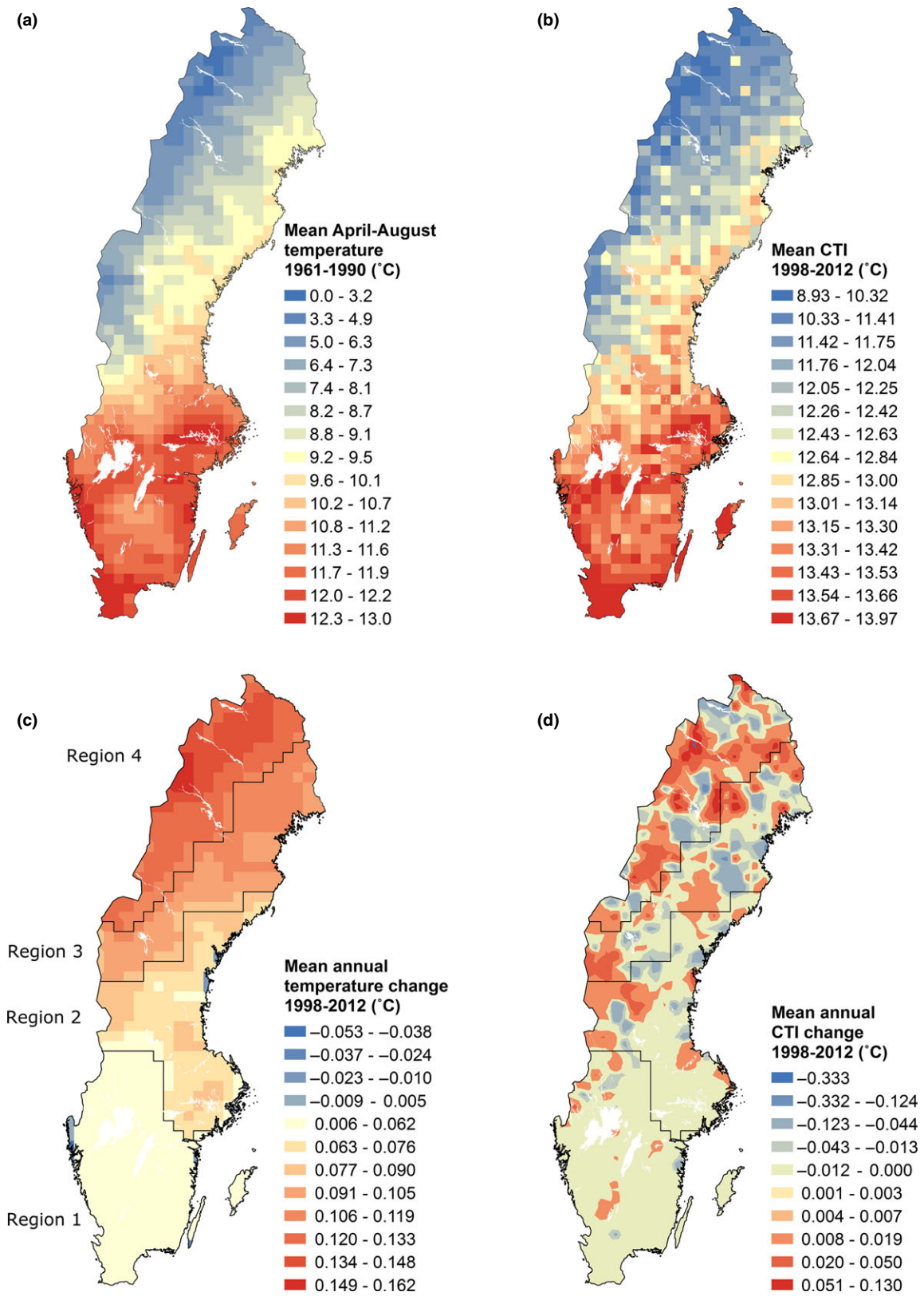


Figure 1 Patterns in climate and CTI across Sweden (a) Mean April-August temperature from 1961 to 1990, (b) Mean observed CTI values from 1998 to 2012, (c) Mean annual change in April – August temperature (1998–2012), and (d) Mean observed annual change in the CTI (1998–2012) interpolated using Inverse Distance Weighting.

have a strong sensitivity to climate, and therefore, we would expect temperature not to have a strong influence on their population trend. To test this we used the species contribution value from the national model for CTI to separate the two groups of species. For each group we ran a linear model of the relationship between species' STI and their log-linear population trends obtained from the Swedish Breeding Bird Annual Report (Lindström & Green, 2013).

Species' traits and CTI contribution

To examine the influence of different traits on species' contributions to the national trend in CTI we fit linear models using phylogenetic generalized least squares (PGLS) in the CAPER package (Orme, 2012) in R (R Development Core Team, 2011), using a phylogenetic tree for European birds provided by Roquet *et al.* (2015). We examined the relationship between species' contribution score for both warm-dwelling and cold-dwelling species for a number of functional traits likely to influence species' sensitivity to climate change. To investigate the influence of life history we examined adult mass, longevity, number of clutches and clutch size all obtained from the AnAge online database (De Magalhães & Costa, 2009). Migratory status was classified as 'resident': no movement or movement within Sweden only, 'short-distance migrant': movements within Europe, 'long-distance migrant': movements outside of Europe (Ottvall *et al.*, 2009). When trait information was not available the species was excluded from the analysis.

RESULTS

Nationally, the CTI showed a significant increase over time (Table S1). However, this general increase masked important regional variations (Fig 1d). The best fit regional model for CTI, retained the baseline temperature variable (T_{61-90}) and six land-cover classes and had an adjusted R-sq of 0.87 (Table 1). Out of the land-cover classes, Urban, Arable, Broadleaved, Coniferous, Coastal and Bare were retained as significant predictors. CTI showed a positive correlation with Arable, Broadleaved, Coniferous and Urban land-cover, and a negative correlation with Bare and Coastal. Annual increases in CTI were greatest towards the North of the country, particularly in Region 4 which is predominately mountainous, while in regions 1 and 2 where temperature was relatively stable from 1998 to 2012, there was no significant change in CTI (Fig. 1 c,d, Table 1). The corresponding results for the abundance-based CTI_{ab} were similar, although the rate of increase was highest in Region 3 and Region 1, 2 and 4 were also statistically significant (Table S4–6). The temporal and spatial patterns of CTI change suggests that the Swedish avifauna has responded to climate warming during the period considered.

We used the jackknifing approach to assess the contribution that each individual species made to the CTI trend both nationally and in each region. We found that for the national

Table 1 Results from the GAMM examining how temporal trends in presence/absence-based CTI varied by regions.

| Parametric coefficients | | | | |
|--|----------|-----------|---------|----------|
| CTI ~ s(X, Y) + T_{61-90} + Year*Region + Urban % + Arable % + Broadleaved % + Coniferous % + Coastal % + Bare % | | | | |
| | Estimate | SE | t-value | P(> t) |
| (Intercept) | 7.7750 | 2.5380 | 3.0640 | 0.0022 |
| T_{61-90} | 0.2109 | 0.0166 | 12.7040 | < 0.0001 |
| Year | 0.0015 | 0.0013 | 1.2000 | 0.23025 |
| Region 2 | 0.4508 | 3.9630 | 0.1140 | 0.90943 |
| Region 3 | -13.0400 | 4.5030 | -2.8950 | 0.00381 |
| Region 4 | -26.2400 | 4.8070 | -5.4600 | < 0.0001 |
| Bare % | -1.0500 | 0.2285 | -4.5940 | < 0.0001 |
| Urban % | 1.6860 | 0.2587 | 6.5190 | < 0.0001 |
| Arable % | 0.8614 | 0.0949 | 9.0790 | < 0.0001 |
| Broadleaved % | 0.9080 | 0.0988 | 9.1900 | < 0.0001 |
| Coniferous % | 0.4613 | 0.0547 | 8.4280 | < 0.0001 |
| Coastal % | -0.2515 | 0.1017 | -2.4740 | 0.01341 |
| Year: region 2 | -0.0002 | 0.0020 | -0.1060 | 0.91522 |
| Year: region 3 | 0.0065 | 0.0022 | 2.9140 | 0.00358 |
| Year: region 4 | 0.0132 | 0.0024 | 5.5080 | < 0.0001 |
| Smooth terms | | | | |
| | e d.f. | Ref. d.f. | F | P-value |
| s(X, Y) | 15.98 | 15.98 | 11.46 | < 0.0001 |

model 121 out of 247 species contributed positively to CTI (Table S2). These 121 species all showed distribution changes in the direction expected by climatic niche theory. However, this also suggests that more than half of all species did not contribute to the trend (Table S2). The jackknife analysis of the regional model allowed us to identify spatial variation in species' contributions. We found that changes in CTI were driven both by colonising species with a STI higher than the regional average (warm-dwelling species) and extirpating species with a STI lower than the regional average (cold-dwelling species) (Fig. 2, Table 2, Table S3). Cold-dwelling species with shrinking distributions and warm-temperature dwelling species with expanding distributions made approximately equal contributions to community warming in regions with a significant temporal trend (Fig. 2). For CTI_{ab} only Region 3 had a greater rate of increase overtime compared to the other regions (Table S6). Similarly a corresponding mix of warm- and cold dwelling species was found in the analysis of CTI_{ab} (Table S7, S8).

Amongst those species that did support the positive trend in CTI, contributions were skewed towards a smaller number of species that had a particularly large effect (Fig. 3, Table 2, Table S2, Table S3). Relatively scarce and declining montane and boreal species were amongst the top contributors to the increase in CTI. For example, Snow bunting, Siberian tit and Ptarmigan were the 3rd, 6th and 16th most influential species in Region 4 (Table 2). These species have STI's 4–6 °C lower than the regional average (11.6 °C) and likely contribute strongly to an increase in CTI via local extirpations. Among

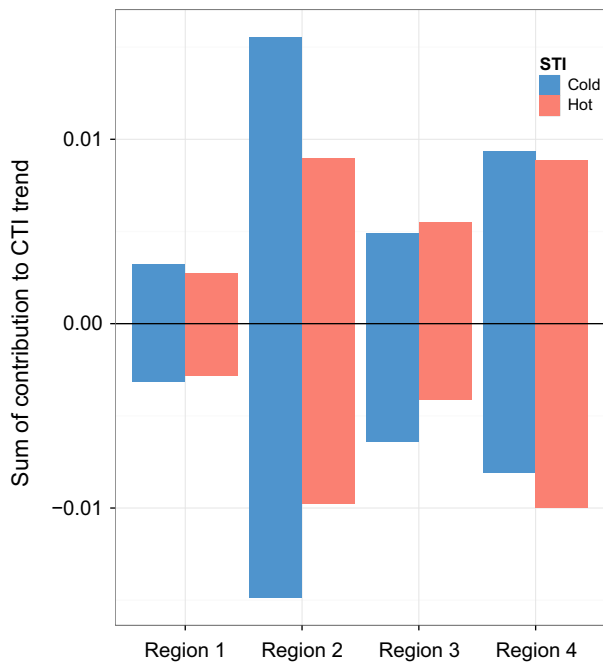


Figure 2 Contributions to the trend in the CTI by region. The contributions of each individual species were summed in each region separately for species with an STI lower (shown in blue) or higher (shown in pink) than the regional average. Contributions were summed separately for those species that contributed towards the observed positive trend (contributions > 0) and those that did not contribute towards the positive trend (contributions < 0).

the 20 species in each region contributing most to the positive trend in CTI (Table 2), the average national commonness ranks were 53, 61, 71 and 88, in regions 1–4, respectively. Between four and nine species in each region had ranks higher than 100. The highest rank in each region was 178, 202, 174 and 209, respectively, including species breeding in Sweden with only 500–3000 pairs. Our approach therefore allowed us to identify distribution changes of uncommon species that otherwise would have been difficult to detect. For CTI_{ab} the lists of species having the largest positive effect were similar (Table S8). In the four regions, 11, 8, 11 and 11 of the 20 most influential species were the same as in the presence/absence-based CTI (Table 2, Table S8).

Those species contributing most to the CTI trend showed a significant relationship between their climatic preferences and their population trend, i.e. those species with high STI were increasing and those with low STI were declining (Fig. 4) ($\beta = 0.83 \pm 0.13$, $t = 6.1$, d.f. = 87, $P < 0.001$). We term these groups of species as ‘climatically sensitive’. Species that did not contribute to the positive CTI trend showed no significant relationship between STI and population trend (Fig. 4) ($\beta = -0.19 \pm 0.18$, $t = -1.1$, d.f. = 95, $P = 0.28$).

Phylogenetic generalized least squares (PGLS) analysis showed that several traits influenced species’ contributions. For warm-dwelling species, those with shorter life spans were significantly more likely to drive increases in CTI, although

the effect sizes were small (Table S9). For cold-dwelling species, those long-lived appeared to be most affected by rising temperatures and therefore contributed significantly more to increases in CTI. Cold-dwelling migrants tended to contribute less than resident species, with short-distant migrants doing the best overall (Table S8).

DISCUSSION

It has been shown that CTI varies over time in parallel to temperature change, suggesting that changes in CTI are indeed driven by climate (Devictor *et al.*, 2008; Lindström *et al.*, 2013). Here, we show that after accounting for spatial gradients in habitat composition and temperature, CTI also changes in relation to the spatial variation in temperature change, with larger increases in areas with greater temperature increases. This strengthens the argument that changes in community composition we see are at least partly responses to climate change.

But how biologically important are these changes, such as the rate of CTI change we find for Sweden [0.005 °C/year (Table S1)] or northern-most Sweden (Region 4: 0.015 °C/year [Table 1])? The average local CTI in Sweden declines from approximately 14 °C in the south to 9 °C in the north, over a distance of 1500 km (Fig. 1b). This translates to an average decrease in CTI of 0.0033 °C for each kilometre you move north in Sweden. At the current rate of change, the national CTI has increased by 0.05 °C in 10 years, equivalent to a northward movement in Sweden of a given community CTI of approximately 150 km (0.05 °C divided by 0.0033 °C per km; cf. Devictor *et al.*, 2008; Lindström *et al.*, 2013). Alternatively, if the CTI change in Region 4 (northern-most Sweden) continues at a rate of 0.015 °C per year, it will only take 50 years until Region 4 has the same CTI as that of Region 3 today. Several forest species, e.g. Chaffinch, Robin and Blackbird, who’s northern range limits largely coincide with the border between Regions 3 and 4 (Ottosson *et al.*, 2012), may well advance quickly into the birch forests of Region 4. In parallel, species which have their highest densities in montane birch forest, like Willow Grouse and Brambling, may largely retreat from Region 3.

However, for species such as coniferous forest specialists, the rate at which these changes will take place will depend on the extent of parallel habitat changes. Region 3 mainly consists of taiga forest and Region 4 of montane birch forest and tundra. Therefore, drastic habitat change would be required before bird species with strong habitat preferences could shift from Region 3 to 4. A change from tundra and birch forest to taiga is likely to take much longer than 50 years, since vegetation does not respond to temperature as fast as birds (Svenning *et al.*, 2008; Kissling *et al.*, 2010; Bertrand *et al.*, 2011). Note however that in our analyses, although we included a coarse description of habitat composition we did not have data available to account for habitat change through time. A central challenge thus remains in the investigation of the synergy of climate vs. land-use changes.

Table 2 The top 20 species contributing to the positive Year trend in CTI. Species in pink have an STI above the regional average. Species in blue have an STI below the regional average.

| Non-significant Year trend | | | Significant Year trend | | | Significant Year trend | | | Significant Year trend | | | | | | |
|----------------------------|------------------------------|--------------------------|------------------------------|--------------------------|------------------------------|--------------------------|------------------------------|---------|------------------------------|---------|------------------------------|---------|------------------------------|---------|------------------------------|
| South | | | Region 2 | | | Region 3 | | | Region 4 | | | North | | | |
| Species | % Contribution to Year trend | Species | % Contribution to Year trend | Species | % Contribution to Year trend | Species | % Contribution to Year trend | Species | % Contribution to Year trend | Species | % Contribution to Year trend | Species | % Contribution to Year trend | Species | % Contribution to Year trend |
| Redwing | 51.4 | Brambling | 66 | Blackbird | 18.7 | Long tailed skua | 13 | | | | | | | | |
| Nuthatch | 27.4 | Blackbird | 49.4 | Greenshank | 15 | Great tit | 10.9 | | | | | | | | |
| Fieldfare | 23.1 | Common redpoll | 36.6 | Rough legged buzzard | 14.6 | Snow bunting | 9.7 | | | | | | | | |
| Herring gull | 18.9 | Rustic bunting | 35.9 | Great tit | 13.2 | Red grouse | 7.5 | | | | | | | | |
| Spotted flycatcher | 16.4 | Crane | 31 | Rustic bunting | 12.5 | Lapland bunting | 7 | | | | | | | | |
| Goldcrest | 14.8 | Mistle thrush | 28.4 | Common redpoll | 11.8 | Siberian tit | 6.6 | | | | | | | | |
| Great black backed gull | 14.3 | Crossbill | 25.7 | Brambling | 8.6 | Great-spotted woodpecker | 5.8 | | | | | | | | |
| Blue tit | 11.6 | Wren | 22.5 | Mistle thrush | 7.2 | Whimbrel | 5 | | | | | | | | |
| Long tailed tit | 10.6 | Crested tit | 21.5 | Crane | 7.1 | Rustic bunting | 5 | | | | | | | | |
| Jackdaw | 9.6 | Jay | 17.9 | Merlin | 6.4 | Robin | 4.6 | | | | | | | | |
| Great-spotted woodpecker | 8.7 | Green woodpecker | 17.5 | Great-spotted woodpecker | 6.4 | Waxwing | 4.5 | | | | | | | | |
| Mistle thrush | 7.9 | Wood sandpiper | 16.8 | Wryneck | 4.6 | Greenshank | 4.4 | | | | | | | | |
| Common redpoll | 7.3 | Bean goose | 16.7 | Spotted redshank | 4.6 | Chaffinch | 4.4 | | | | | | | | |
| Blackcap | 6.9 | Great-spotted woodpecker | 16.6 | Wigeon | 4.1 | Crane | 4.4 | | | | | | | | |
| Cuckoo | 6.6 | Blackcap | 13.8 | Lesser whitethroat | 4 | Black throated diver | 4 | | | | | | | | |
| Brambling | 6.2 | Woodpigeon | 13.6 | Ptarmigan | 3.7 | Ptarmigan | 3.6 | | | | | | | | |
| Willow warbler | 6.2 | Red backed shrike | 12.3 | Duncock | 3.5 | Song thrush | 3.3 | | | | | | | | |
| Greenshank | 6 | Redstart | 12.3 | Red grouse | 3.4 | White tailed eagle | 3.2 | | | | | | | | |
| Hobby | 6 | Goldfinch | 11.9 | Greenfinch | 3.3 | Jack snipe | 3 | | | | | | | | |
| Chiffchaff | 6 | Goosander | 11.9 | Siberian tit | 3.2 | Spotted redshank | 2.8 | | | | | | | | |
| Average CTI | 13.5 | | 13.1 | | 12.4 | | 11.6 | | | | | | | | |
| Year Trend | 0.0015 | | 0.0013 | | 0.0081 | | 0.0148 | | | | | | | | |

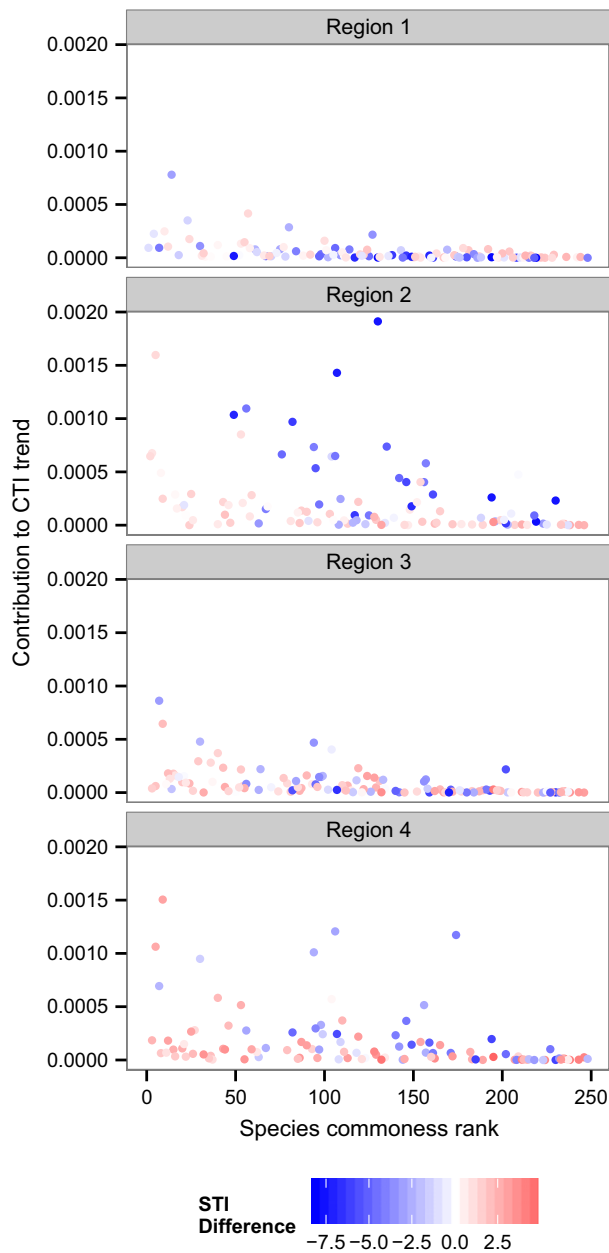


Figure 3 Positive contributions to CTI vs. commonness rank in each region. Colour represents the difference between each species' STI and the baseline CTI of each region, hence blue dots represent relatively cold-dwelling species and red dots warm-dwelling species for a given region. Not least in regions 2 and 4, relatively uncommon birds (low commonness rank) contribute to changes in CTI.

This would for instance reveal the extent to which specific species are more sensitive to one or the other pressure and in what direction. Our results, however, clearly show that rapid changes in community composition do take place and that they are largely proportional to the rate of climate change (Lindström *et al.*, 2013; Gaüzère *et al.*, 2015).

By examining the contributions of individual species to overall community change as reflected by CTI, we show that

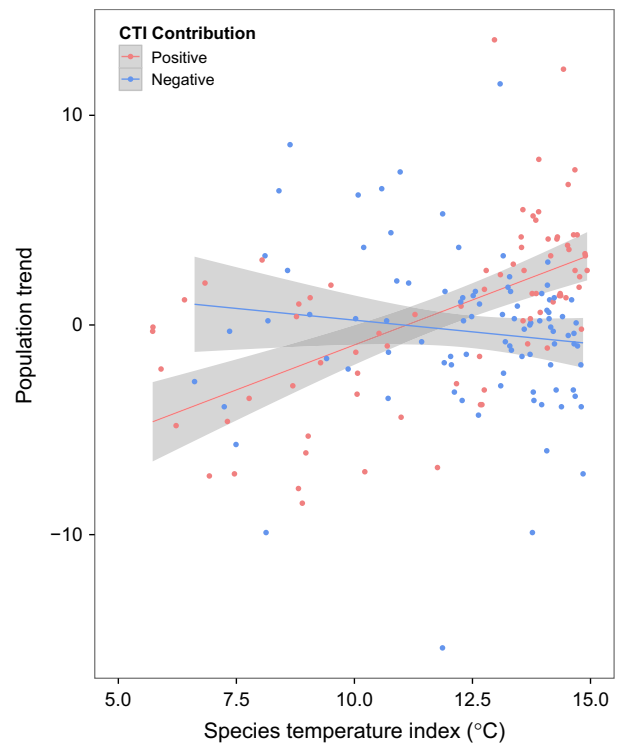


Figure 4 The relationship between the long-term Swedish population trend (% change per year) for a species and its STI. Species that contributed to the positive trend in CTI (as expected by climatic niche-tracking) are shown in pink while those with a negative contribution to CTI change are shown in blue.

both range-contractions of cold-dwelling species and expansions of warm-dwelling species have occurred over a 15 year period of increasing temperatures. The results show that just over half of all Swedish bird species were either expanding or contracting their distributions in line with expectations given their observed climatic niche (Table S2). A previous study conducted on individual species' range shifts, found that only around 20% of species demonstrated tracking of temperature changes (Tayleur *et al.*, 2015). However, the latter analysis only included the 101 most common birds in Sweden, since the statistical methods employed needed a minimum amount of data for each species. Using an analysis of species' contributions to CTI changes therefore provides an alternative to detecting the responses of both common and rare species to temperature changes. The interest of estimating species-specific contribution is that it reflects changes in the 'representativeness' of each species in terms of both their climatic niche (STI) and relative occurrence (or abundance). For instance two species with a similar STI can contribute more or less to the trend in CTI depending on their representativeness in local communities. Thus, a common species might be a weaker contributor than a rare species if the latter is colonizing many sites rapidly. Similarly, the contribution of two species with a similar commonness and trend will depend on how different their STI is from the CTI. A closer

examination of how contributions are distributed amongst species or linked to particular traits is therefore a way to shed light on community dynamics in response to climate change.

Our trait-analyses suggest that species-longevity may play an important role in how species respond to climate change. For warm-dwelling species those with shorter life spans were more likely to be contributing to CTI increases, perhaps as rapid regeneration times allow a greater ability to respond to warming temperatures. At the European scale, CTI in butterflies changed faster in relation to warming temperatures than CTI in birds, possibly because of the shorter generation time in butterflies (Devictor *et al.*, 2012). For cold-dwelling species, the opposite was true, with species with longer life spans contributing more to increase in CTI via their shrinking distributions. Migratory strategy also affected cold-dwelling species contributions to CTI. Residents fared worst and short-distant migrants seemed to cope best with climate warming. Short-distance migrants overall have had the most favourable population trends in Sweden in recent times (Ottvall *et al.*, 2009). Many short-distance migrants are known to be sensitive to winter severity (Saether *et al.* 2004), and it is likely that the generally milder winters in Europe in recent years have been beneficial to these species (Ottvall *et al.*, 2009).

We did not account for imperfect detection of individuals/species in our analyses, a factor that may bias conclusions (Banks-Leite *et al.*, 2014; Kellner & Swihart, 2014). Correcting for imperfect detection in a scheme with several hundred different observers counting 250 different species, many of which occur in many different habitats (and probably have habitat-specific detectability probabilities) is no easy task. Accounting for imperfect detectability relies on the possibility to apply specific corrections to appropriate schemes [e.g. distance sampling, or capture-recapture models, (Williams *et al.*, 2002)]. Given the limited resources available, the Swedish BBS scheme has put its effort in maximizing the number of sites, at the cost of less detailed knowledge for each site. Both factors are important for drawing relevant conclusions on large-scale multi-species data sets like ours (Banks-Leite *et al.*, 2014). We cannot exclude that imperfect detection has influenced our results to some degree, but to be an important factor behind our results, species detectability would have needed to change *directionally* over time and space, in a way systematically related to STI and coinciding with temperature changes.

Spatial variation in species' contribution

Examining species' contributions to changes in CTI proved to be an efficient way of gaining insight into temperature impacts. In particular, our results provide further evidence for the vulnerability of species located in mountainous and northerly regions. In the Fennoscandian mountains, a recent and geographically widespread decline in abundance has been reported in most bird species typical for this Subarctic–

Arctic region (Lehikoinen *et al.*, 2014; Virkkala & Lehikoinen, 2014). Likewise, for the whole of Finland, species with a northern distribution have been doing especially poorly in 1986–2012 (Laaksonen & Lehikoinen 2013).

In southern Sweden the temporal trend in CTI was not significant because the positive contributions were overwhelmed by the negative contributions of other less climatically sensitive species (Fig 2). Approximately half of the bird species in the South did not contribute to the recent (small) increases in CTI. When we split the species into those contributing and those that weren't, only those that contributed showed a significant relationship between their long-term population trend and their climatic niche. While some of these non-contributing species may be long-lived and not yet showing population-level responses to climate change (Bart *et al.*, 2010), we clearly need a better understanding of the factors driving their demography. Species showing long-term population declines that appear insensitive to temperature change should be priorities for further investigation so that conservation effort can be better targeted.

The variation in species' response between regions may provide insight into other factors influencing populations. For example, while the variation between regions in the identity of the top contributors is partly due to the geographic distributions of the species (Table 2), this may also be due to key habitat or management differences between regions. Identifying why some species are top contributors in some regions but not in others may highlight other influences driving their population response.

Identifying climate change impacts on rarer species

A general problem when determining the impact of climate change on species distributions is the difficulty in capturing changes in rarer species, which may also be most vulnerable. Monitoring rare species is often impaired by the lack of data and low detectability so that true changes in abundance or occurrence are more difficult to estimate. The relevance of estimating species-specific contributions in CTI has recently been underlined (Princé & Zuckerberg, 2014). Here, we demonstrate that this method allowed us to detect impacts on rare species, for which population or distribution trends cannot be calculated with certainty from standard monitoring schemes e.g. Bean Goose, Rough-legged Buzzard, Merlin & Siberian Tit. Previous work has highlighted that common species contribute most both to geographic patterns of species richness (Lennon *et al.*, 2011), and spatio-temporal changes in species richness (Davey *et al.*, 2013). However, unlike species richness, CTI is a trait-weighted index: when a species with a more extreme STI value colonises or is lost from a site there will be a greater influence on CTI than the gain or loss of a species with an STI closer to the community average. By accounting for species-specific sensitivity from the beginning, this framework provides an opportunity for identifying climate change impacts on rarer species and processes of range contractions as well as expansions.

Alternative direct and indirect drivers of changes in CTI

While CTI appears to be a good proxy for monitoring community response to climate change, habitat change and its interactive effect with temperature may also influence the index (Clavero *et al.*, 2011; Barnagaud *et al.*, 2012, 2013; Kampichler *et al.*, 2012). In addition to this, the influence of changing temperatures is likely to come through changes in biotic interactions such as prey availability, disease and competition (Ockendon *et al.*, 2014). It is therefore challenging to disentangle the relative importance of different factors on species and community dynamics. Data on fine-scale changes in habitat in Sweden were not available to us, but the predominant patterns in land-use have changed relatively little, especially at the scale of the analysis. For example, the total area of farmland in Sweden has within the study period declined from around 8 to 7.4% of total land area, with a slight shift towards more ley and less crop (Anon, 2013). However, most of the typical farmland birds in Sweden have a large proportion of their national populations outside farmland (in clear-cuts and on mires; Stjernman *et al.* 2013), and the effect of the habitat changes in farmland on CTI are therefore likely to be small.

Conservation implications of CTI

The CTI has been adopted as an indicator of climate change at national (e.g. Sweden and France) and European level. While indicators are useful for conveying messages to policy makers, they are less informative to conservation practitioners unless more specific results can be derived. Previous work on CTI has found that warming of communities has lagged behind changes in temperature (Devictor *et al.*, 2008, 2012; Lindström *et al.*, 2013). If there were no constraints on dispersal, then we would expect a change in CTI to perfectly match climate change. But in the real world plant communities, and therefore bird-habitats, react and change more slowly to climate change (Svenning *et al.*, 2008; Kissling *et al.*, 2010; Bertrand *et al.*, 2011) and species on top of mountains have nowhere to shift to. By examining the complexity behind the changes in CTI, our work shows that increases and even stable measures of CTI reflect a complex dynamic of individual distributions. Linking the change at the indicator level to changes in species' distributions is an important step towards recommending management interventions.

Our results also suggest that a lag in CTI may be due to species showing less sensitivity to climate change than expected, or no sensitivity at all (Fig. 4). This has important implications for interpreting trends in the CTI indicator as there may be species at risk, whose signal is overwhelmed by others in the community that are less sensitive to climate. The inclusion of 'insensitive' species may also influence interpretation of the climate change indicator of the Pan-European Common Bird Monitoring Scheme (Gregory *et al.*, 2009). In this other indi-

cator, population trends of species predicted to expand and those expected to contract under climate change are compiled into composite indicators. Along the same lines, the otherwise important task of projecting future species distributions based on the assumption that species will respond fully to climate change according to their present climatic niche (e.g. Huntley *et al.*, 2007; Barbet-Massin *et al.*, 2012), may over-estimate the responses of some species.

Our approach, examining spatial variation in species-contribution, could be used to examine a number of other management related questions. One example is whether protected areas or specific landscape structures (fragmented, human dominated) can mitigate species' sensitivity to climate change. This may allow better spatial prioritisation for species conservation action. Over time, examining species contributions to the community before and after a specific conservation planning could also be used to evaluate the efficacy of the intervention. This approach is therefore aligned with the recent call to adopt a more dynamic approach to macroecology (Fisher *et al.*, 2010; Mokany *et al.*, 2012). Indeed while diversity patterns are clearly constrained by large scale and rather constant gradient in environmental variables (Gaston, 2000), the rapid reshuffling of community composition and the fluctuation of the trend in particular species must be studied in conjunction with rapid changes in environmental variables in space and time. In this context, our methods can be used for any community weighted mean and could provide insight into the traits driving community response.

ACKNOWLEDGEMENTS

We dedicate this paper to our colleague and co-author Niclas Jonzén who died on 9 May 2015 after a long illness. We are most grateful to the surveyors of the Fixed Routes and to Marcus Flarup at SMHI for helping us with climate data. The Swedish BBS is supported by grants from the Swedish Environmental Protection Agency and the County Administrative Boards of Sweden 'Läansstyrelsen' and carried out within the framework of the Centre for Animal Movement Research (CAnMove, Linnaeus grant 349-2007-8690). CMT was supported by the strategic research environment Biodiversity and Ecosystem Services in a Changing Climate (BECC). HGS was supported by a grant from Formas. VD was supported by the 'Fondation pour la Recherche sur la Biodiversité' (FRB, project PHYBIO).

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SUPPORTING INFORMATION

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

Appendix S1 Additional methodological information.

Figure S1. Mean observed annual change in the abundance based CTI_{ab} for 1998–2012 (cf. the species presence/absence based CTI in Fig. 1).

Table S1 Results from the GAMM estimating the national trend in the presence-based Community Temperature Index (CTI).

Table S2 The contribution (see Methods) of different species to the national trend in presence-based CTI.

Table S3 The contribution (see Methods) of different species to the regional trend in presence-based CTI.

Table S4 Results from the model estimating the national trend in the abundance-based Community Temperature Index (CTI_{ab}).

Table S5 The contribution (see Methods) of different species to the national trend in abundance-based CTI (CTI_{ab}).

Table S6 Results from the GAMM estimating the regional trend in the abundance-based CTI (CTI_{ab}).

Table S7 The contribution (see Methods) of different species to the regional trend in abundance-based CTI (CTI_{ab}).

Table S8 The top 20 species contributing to the positive Year trend in (CTI_{ab}).

Table S9 Results from the Phylogenetic Generalized Least Squares analysis of the relationship between species' contribution to the national trend in CTI vs. life history traits.

BIOSKETCH

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Editor: Guy Midgley