Rapid changes in bird community composition at multiple temporal and spatial scales in response to recent climate change

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Although climate change is acknowledged to affect population dynamics and species distribution, details of how community composition is affected are still lacking. We investigate whether ongoing changes in bird community composition can be explained by contemporary changes in summer temperatures, using four independent long-term bird census schemes from Sweden (up to 57 yr); two at the national scale and two at local scales. The change in bird community composition was represented by a community temperature index (CTI) that reflects the balance in abundance between low- and high-temperature dwelling species. In all schemes, CTI tracked patterns of temperature increase, stability or decrease remarkably well, with a lag period of 1–3 yr. This response was similar at both the national and local scale. However, the communities did not respond fast enough to cope with temperature increase, suggesting that community composition lags behind changes in temperature. The change in CTI was caused mainly by changes in species' relative abundances, and less so by changes in species composition. We conclude that ongoing changes in bird community structure are driven to a large extent by contemporary changes in climate and that CTI can be used as a simple indicator for how bird communities respond.

Research on how biodiversity is affected by climate change has focused on latitudinal or altitudinal shifts in species-specific distributions, and on changes in species' phenology (Parmesan 2006). Climate change also affects species' abundance and thereby community composition, through changed interactions with the abiotic and biotic environment (Brown et al. 2001, Ahola et al. 2007, Jiguet et al. 2010a, Kissling et al. 2010, Davey et al. 2012). To understand how climate change may affect biodiversity in the future, there is a clear need for studies that document whether and how the compositions of species assemblages are affected by contemporary climate change (Gilman et al. 2010).

Whereas the adaptive or demographic response to climate change can be quantified precisely for a given species (Both and Visser 2005, Charmantier et al. 2008), there is a shortage of knowledge about how the composition of species assemblages respond to spatial and short-term change in climate (Lavergne et al. 2010, but see Devictor et al. 2008, 2012, Bertrand et al. 2011). In particular, the delay with which climate change is followed by adjustments of species abundance within local communities is unclear. Biodiversity responses may occur with a time lag, depending on both the characteristic of species and the environment (Hill et al. 1999, Menéndez et al. 2006, Devictor et al. 2008). In addition, changes in community composition

may differ between scales (Van Turnhout et al. 2007). For instance, while habitat composition and species interactions may be important to explain community composition at local scales, biogeographical history and climatic gradients also contribute to shape community composition at larger scales (Reif et al. 2010).

Ideally, assessing changes in community composition in response to climate change should integrate all these potential sources of variation in species abundances across many species. In practice, data on the influence of climatic conditions on community structure are often lacking, changes in species interactions are difficult to monitor between many species, and only a few proxies are available to characterize life-history traits likely to be associated with species' responses to climatic changes (Both and Visser 2005, Jiguet et al. 2010a).

An alternative method to estimate the response of communities to climate change is to assess the change in the realized adjustment of abundances of species dependent on relatively warm versus cold temperatures (Devictor et al. 2008). Using the average temperature of the species distribution, one can estimate a species temperature index (STI) that reflects the long-term dependence of a species to temperature distribution. Then by averaging the STI values of individuals present in an assemblage, any species

assemblage can be characterized by its relative composition of individuals belonging to species dependent on warm (i.e. those with high STI) versus cold (those with low STI) climate. This average, known as a community temperature index (CTI), reflects the composition of the community in terms of species' dependence to temperature and has been used to explain recent changes in community structure of both birds and butterflies (Devictor et al. 2008, 2012, Godet et al. 2011).

In the three studies where CTI has been analysed in relation to changing temperature (for breeding birds Devictor et al. 2008, 2012, for wintering birds Godet et al. 2011), temperature (and CTI) has increased in a rather linear fashion. Although such a relative increase in abundance of individuals with high STI values could be expected when temperatures increase, conclusions are still based on mere correlations.

We therefore set out to do some new types of analyses to deepen the understanding of the relationship between temperature and CTI. First, we assess the short-term time lag between temperature changes and community response. Does a warm summer lead to an increase in CTI in the next few years? This has to our knowledge not been addressed before. Second, should such a lag exist, we would expect long-term trends in CTI to increase, be unchanged, or decrease, in periods of more consistent increasing, constant, or decreasing temperatures (Fig. 1). Third, the effect of climate change on community composition has primarily been studied either at large spatial scales (Devictor et al. 2008, 2012, Davey et al. 2012) or at local scales (Buse et al. 1999, Kerbiriou et al. 2009), and there is a need for studies comparing a given biodiversity response to climate change across scales.

A related fourth question is how the rate of change in CTI corresponds to the rate of change in temperature (Devictor et al. 2008, Loarie et al. 2009). CTI would be expected to change at the same rate as temperature if species were exclusively influenced by change in temperature, and if species could respond instantaneously and linearly to temperature. This is obviously not the case for most species, since, for example, factors other than climate affects bird numbers and thereby community composition (Clavero et al. 2011). But comparing the velocity of change in CTI and temperature can reveal to what extent communities do track climate change (Devictor et al. 2008, 2012).

We address these four issues by analysing four independent and complementary long-term datasets from Sweden (up to 57 yr); two at the national scale covering 1500 km of latitude, and two at the local scale, at sites 1150 km apart.

Material and methods

Bird communities at the national scale

There are two national breeding bird surveys running in Sweden (Lindström et al. 2010). The Old scheme started in 1975 and consists of plots where both date and location were selected freely by the observers. Each plot includes 20 different survey points and was surveyed once a year within ± 5 d of the first year's survey date. Ninety % of the
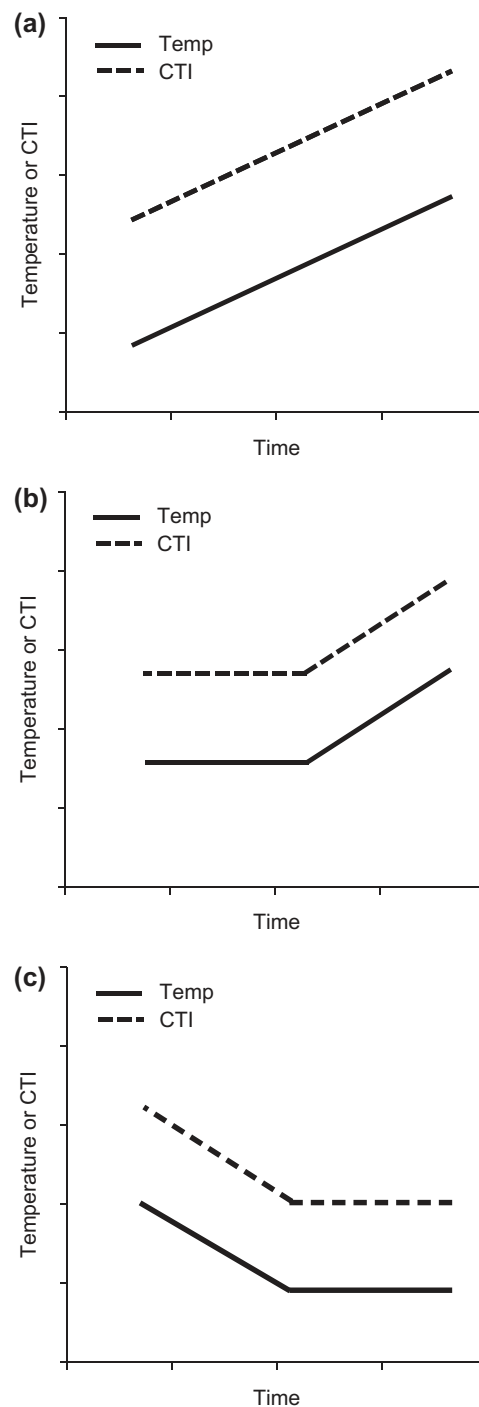

Figure 1. Some hypothetical examples of how CTI (community temperature index) should change over longer time-periods (decades), if being affected by summer temperature, e.g. that species with a high STI (species temperature index) become relatively more common in years following warm summers, and species with low STI become relatively more common in years following cold summers. (a) The three previous studies of trends in CTI all basically look like this, where both CTI and temperature have increased more or less linearly over a long time period (Devictor et al. 2008, 2012, Godet et al. 2011). (b, c) If CTI would remain stable in periods of stable temperature, and decline in periods of declining temperature, this would give additional support to the conclusion that changes in CTI indeed are driven by temperature changes. Temperature normally varies much between years (more than CTI) and the graphs therefore represent long-term averages.

plots were carried out between 2 May and 21 June. The survey dates became significantly earlier over the study period (linear regression, $r^2 = 0.0037$, $p < 0.001$), but the total change in average date was only 3 d over 34 yr. The Old scheme plots are observer-specific and end when the observer stops surveying it. More than 1100 plots have been monitored, between 1 and 35 yr per plot (Fig. 2a).

The New scheme was launched in 1996 and covers 716 plots systematically spread over Sweden in a 25 km grid (Fig. 2b). This distribution ensures a representative coverage of all widespread habitats in Sweden. At each plot a 8 km line transect is surveyed. In contrast to the Old scheme, the plots are fixed over the years, whereas the observer may change. The first two years of survey (1996–1997) were excluded because only few plots were surveyed. Between 165 (1998) and 585 (2008) of the 716 plots were counted yearly (average 353 plots yr^{-1}). The censuses were carried out from mid May (southernmost Sweden) to early July (northernmost Sweden), with no significant average temporal trend in survey dates (linear regression, $r^2 = 0.00065$, $p = 0.09$). Numerically the change corresponded to plots being surveyed on average 0.9 d earlier in 11 yr. In both schemes, all birds seen and heard during a census were recorded. Of the ca 250 breeding species in Sweden, 239 and 244 were reported in the two schemes, respectively.

Bird communities at the local scale

In the schemes described above, the local bird communities of the plots are represented by mere snap-shots through yearly censuses. In contrast, two data sets were available to us where the local bird communities have been recorded very thoroughly by yearly territory mapping. In addition, they provide us with even longer time series (57 and 47 yr, respectively) than in the national schemes. These two datasets were taken as two independent local scale replicates of changes in CTI and temperature to assess potential differences between national and local trends.

A 13 ha broadleaf deciduous wood near Lund in southernmost Sweden (Fågelsångsdalen, literal translation 'Birdsong Valley', 55°43′N, 13°20′E, Fig. 2b), was surveyed by territory mapping (ten visits on average per year) annually between 1953 and 2009 (Enemar et al. 1994, Svensson et al. 2010). The study area has several grazed glades and is surrounded by arable land. A 9 km^2 area of subalpine birch forest near Ammarnäs, Swedish Lapland (65°58′N, 16°00′E, Fig. 2b) was surveyed by line transects and territory mapping (ten visits per year) 1963–2009 (Enemar et al. 2004, Paulson unpubl.). The forest is situated on a south-facing mountain slope, between 540 and 720 m a.s.l. The two sites are 1150 km apart. Only relatively small changes in the local habitat are reported to having occurred
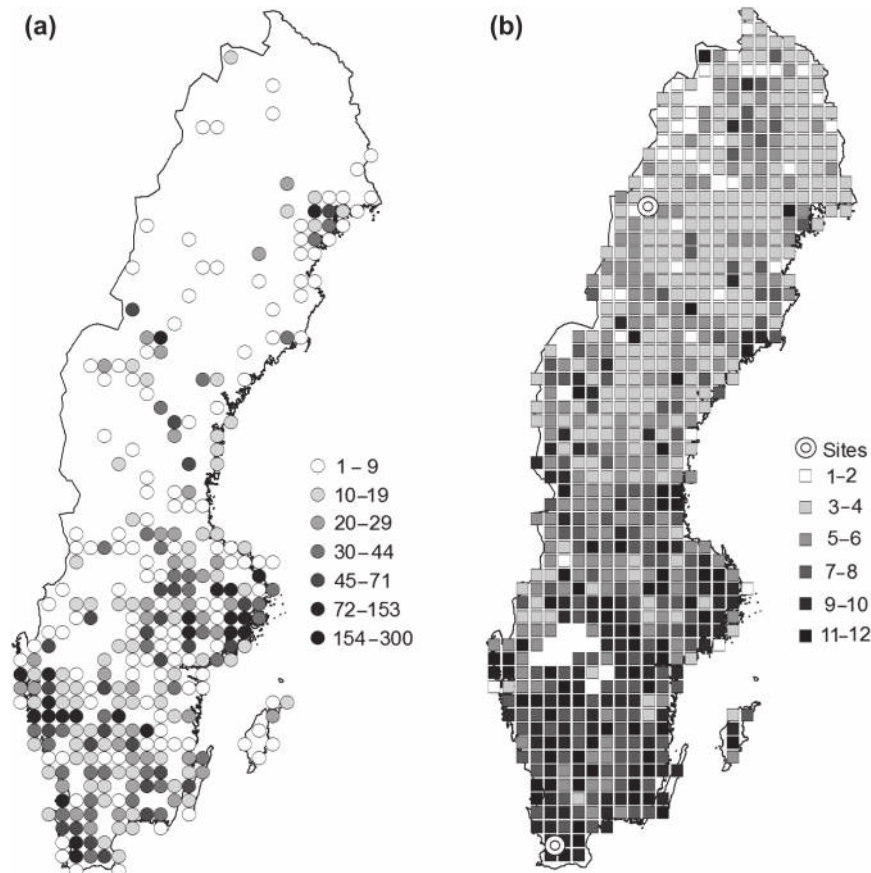

Figure 2. The distribution of survey plots in the old (a) and new (b) breeding bird monitoring schemes in Sweden. For the Old scheme, covering 1975–2009, the number of censuses carried out per 25 km square is shown (in total 7601 censuses of 1098 unique plots). For the New scheme is shown the number of times each plot (one per 25 km square) was surveyed in 1998–2009 (in total 4422 censuses of 716 unique plots). Map (b) also shows the location of the two individual study sites, Birdsong Valley in the south and Ammarnäs in the north (double circles).

throughout the study periods. The two datasets include 41 and 54 species, respectively.

Species and community temperature index

For each species, we calculated a species temperature index (STI), being the mean temperature within the breeding range of the species. The European breeding range was determined by the European atlas of birds, and the temperature was taken from the worldclim database (we used the average April–August temperature averaged over the period 1961–2008) (Hagemeijer and Blair 1997, Devictor et al. 2008). The STI of a given species is used as a proxy for the temperature preference of that species. Besides, the short and long-term species responses to climate change have been shown to be related to their STI (Jiguet et al. 2006, 2010b).

To calculate species' STI, we followed Devictor et al. (2008) and averaged the temperature of the European distribution of each species, ignoring finer intra-species variations in thermal tolerance and variation in temperature within species ranges. Individual STI values will differ depending on from which part of the breeding range and during which time window it is calculated, but this is not a problem because what matters in the CTI approach is the way species are distributed along a gradient of STI, not their individual STI. We calculated STIs using alternative geographic ranges and time-windows, demonstrating that although the individual STIs are all different, the ordering of species within each STI set is always highly similar (Supplementary material Appendix 1). Accordingly, for each of these STIs, the resulting CTI is expected to increase following temperature change. That is why the rate of change in CTI will be more informative than the actual values of STI and CTI themselves.

The CTI of a given plot is calculated as the average STI of all species recorded in the plot weighted by their local abundances (Devictor et al. 2008, Godet et al. 2011). We also calculated a presence-only CTI, which is the average STI of all species, not weighted by each species' abundance. This makes it possible to see whether a change in CTI is caused mainly by changes in abundance or species turnover.

Temperature data

Interpolated monthly average temperature data for 1961–2009 was received from the Swedish Meteorological and Hydrological Inst. (SMHI). Data from all weather stations around Sweden (approximately 300 stations spread evenly over the country) have been interpolated to a 4×4 km grid of virtual weather stations, using geo-statistic interpolation (Johansson 2000). For the national analyses we selected the virtual site nearest to each New scheme plot, resulting in 716 virtual weather sites spread evenly over the country. For each site we calculated a yearly T_{summer} as the average of the April to August mean temperature. For Ammarnäs, data from the nearest virtual site (within 2 km) was used. However, for Birdsong Valley interpolated data was not available for the whole time series. We therefore used data

from the weather station in nearby Lund. For the period 1961–2009, these data were highly correlated to those of the nearest virtual site ($r^2 = 0.99$).

Data analysis

We first analyse how CTI and temperature have changed over time in the four different datasets. After that we analyse if there is a significant short-term lag in the response of CTI to temperature and visualize how this affects long-term trends of CTI. Finally we investigate how the general rate of change in CTI has matched the change in temperature, measured in the apparent speed of northward shift of a given temperature regime and community composition.

To remove most of the spatial dependency of temperature values induced by interpolation of gridded temperature data we produced nation-wide spatial and temporal trends of T_{summer} from the gridded interpolated data. We averaged temperature values each year and used simple regressions on mean values to estimate the temporal trend in temperature in Sweden. To estimate spatial trend in temperature we averaged temperature values in 10 latitudinal bands of equal size. In these models, the standard errors of mean values were taken as weights.

We accounted for the multi-site time-series structure of the national monitoring schemes by using linear mixed models to estimate changes in CTI. In these models, CTI was the dependent variable and time considered as a predictor. We also accounted for both spatial and temporal autocorrelation as follows. First, we included random intercepts and slopes in the mixed models (Schielzeth and Forstmeier 2009) as well as a first-order autoregressive covariance (if this improved model fit as judged by the Akaike information criterion AIC). The inclusion of autoregressive covariance improved model fit for the Old scheme ($\Delta AIC > 9$), but only marginally for the New scheme ($\Delta AIC \leq 2$). It did not affect results qualitatively. We report results for the best-fitting models. To test if there were non-linear effects of time, we added the quadratic effect of time in random slopes quadratic models. All models included latitude to account for and estimate geographic trends.

Second, to ensure that our results were not affected by spatial autocorrelation we calculated the trend for CTI over time at each site separately and modeled the spatial covariance between these trends. When calculating the trends we did not include autoregressive covariances, because of the short duration of many individual time-series. However, estimates of trends will not be biased. We tested several spatial covariance structures (Gaussian, spherical, exponential, power) and selected the spherical as it was supported by models having the lowest AIC (with one exception listed below). We tested if the intercept (estimating mean trend over time) differed from zero while weighing the analyses for the degrees of freedom used to estimate the trend in each point. Analyses were fitted with REML using SAS Proc Mixed and the significance of fixed factors were tested with F-tests using Kenward–Rogers approximation for denominator degrees of freedom.

When analysing single-site time-series (Birdsong Valley, Ammarnäs), and when we used national averages to analyse

lag-effects of temperature, we accounted for serial auto-correlation using the Yule–Walker method with backward elimination (SAS Proc Autoreg). All time-series included significant positive first-order autocorrelations, except that for Ammarnäs which instead included significant positive higher order autocorrelations. All reported results are from models accounting for the serial autocorrelation.

For illustrative purposes, we also performed analyses with time as a factor and estimated least square means for CTI each year (Fig. 3). Since T_{summer} may vary dramatically between years we follow SMHI in adding decade-long running averages when illustrating temperature trends. We used a period of nine years, centred round the fifth year. For comparison, this was done also for CTI. The nine-year averages were not included in any analyses.

From the temporal and spatial trends in T_{summer} and CTI of the national schemes, we calculated the apparent speed at which a given temperature regime, or CTI, move over the Earth's surface. Indeed, for both T_{summer} and CTI, the ratio of the temporal (°C yr^{-1}) and spatial (°C km^{-1}) trend provides a proxy for the velocity of their spatial shift (km yr^{-1}, Devictor et al. 2008, Loarie et al.

Figure 3. The average temperature in April–August (T_{summer}, °C) and community temperature index (CTI, °C) in Sweden, as recorded in two different national bird monitoring schemes. (a) The Old scheme of free choice point counts, covering mainly southern Sweden (Fig. 2a). (b) The New scheme of systematic line transects, covering all of Sweden (Fig. 2b). The solid (T_{summer}) and stippled (CTI) lines denote nine-year running averages (see also Fig. 4).

2009). The standard error of the shift was estimated from the approximation of the variance of a ratio (Raj 1964).

We tested for lags of temperature effects in all four datasets, by relating CTI to temperature one to four years earlier. For the short New scheme time series, only lag periods of 1 and 2 yr were meaningful to analyse. Analyses at the national level were based on yearly means. In none of the datasets were T_{summer} significantly correlated between years, i.e. a warm summer was not systematically followed by a warm summer the subsequent 1–4 yr. All averages and trends are presented with their SE.

Results

Changes in temperature and community composition at the national scale

We found that the average T_{summer} in Sweden increased over time by 0.04 ± 0.01°C yr^{-1} during 1975–2009 ($t_{33} = 3.5$, p = 0.001, Fig. 3). Although T_{summer} tended to increase also in the shorter period 1998–2009 (Fig. 3), the trend was not significant in this period, at least partly caused by the exceptionally warm year 2002 (slope 0.091 ± 0.07°C yr^{-1}, $t_{10} = 1.28$, p = 0.22). Moreover, the average T_{summer} was decreasing from south to north by 0.0046 ± 0.0006°C km^{-1} (p < 0.001).

The CTI in the Old scheme increased with on average 0.0031 ± 0.00061 SE °C yr^{-1} ($F_{1,461} = 26.0$, p < 0.001, Fig. 3a), which is equal to a 0.11°C increase in CTI over 35 yr. The increase over time was confirmed by an analy-sis of trends (intercept = $0.0097 + 0.0015$, $t_{48.8} = 6.4$, p < 0.001) while accounting for spatial autocorrelation which improved model fit ($\Delta AIC = 4.7$). There was a significant quadratic effect of time (linear effect 0.0015 ± 0.00066, $F_{1,423} = 5.3$, p = 0.022, quadratic effect 0.0003 ± 0.00005, $F_{1,310} = 33.1$, p < 0.001), showing that CTI increased in an accelerating way, similar to the apparent trend of temperature (Fig. 3a).

The CTI in the New scheme increased with on average 0.0096 ± 0.0013°C yr^{-1} ($F_{1,468} = 54.8$, p < 0.001, Fig. 3b), which is equal to a 0.11°C increase in CTI over 12 yr. The increase over time was confirmed by an analysis of trends (intercept = 0.0092, $t_{126} = 6.2$, p < 0.001), while accounting for spatial autocorrelation which improved model fit ($\Delta AIC = 4.7$). There was no significant quadratic effect of time (linear effect 0.011 ± 0.0014, $F_{1,323} = 56.8$, p < 0.001, quadratic effect -0.0007 ± 0.0004, $F_{1,392} = 3.3$, p = 0.071). In both schemes the average bird community in Sweden clearly changed over time towards more warmth-loving birds.

At the spatial scale, the average CTI in 1975–2009 in the Old scheme decreased from south to north with 0.0010 ± 0.000042°C km^{-1} ($F_{1,1031} = 636.5$, p < 0.001, Devictor et al. 2008). This result was only marginally affected by accounting for a quadratic effect of time (results not shown). The corresponding figure for the New scheme in 1998–2009 was 0.0022 ± 0.000060 SE °C km^{-1} ($F_{1,703} = 1380.9$, p < 0.001).

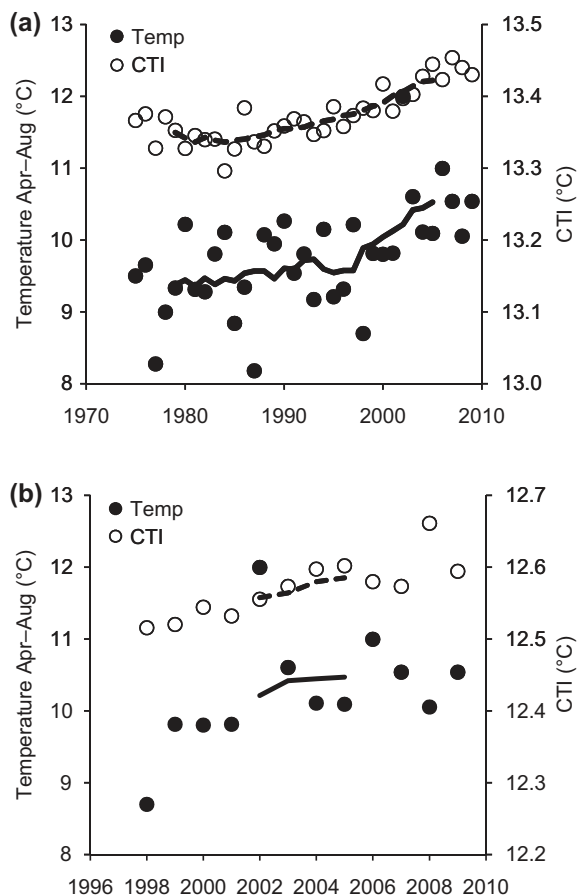In the Old scheme, the change in CTI was mainly caused by changes in abundance, since there was no change over

time when CTI was calculated from presence-absence only ($F_{1,328} = 1.4$, $p = 0.24$). However, in the New scheme, the change in CTI was partly dependent on changes in the occurrence of species, as shown by a significant positive change in the CTI when based on presence-absence only ($b = 0.0062 \pm 0.0013$, $F_{1,468} = 21.3$, $p < 0.001$). When analysing slopes, the result was partly dependent on the choice of covariance structure, being either a tendency (power structure, ΔAIC $= 16.5$, $b = 0.0076 \pm 0.0039$, $t_{5.3} = 1.96$, $p = 0.10$) or significant (spherical structure, ΔAIC $= 16.8$, $b = 0.0085 \pm 0.0040$, $t_{20.4} = 2.13$, $p = 0.045$), suggesting that the change in CTI was indeed partly caused by changes in presence/absence of species.

Changes in temperature and community composition at the local scale

At Birdsong Valley, T_{summer} increased substantially over time, from about 13°C in 1953 to 15°C in 2009 (slope 0.030 ± 0.0053°C yr^{-1}, $t_{55} = 5.7$, $p < 0.001$, Fig. 4a). The CTI changed in parallel, from about 13.7 to 14.1°C (slope 0.0057 ± 0.00074°C yr^{-1}, $t_{1,54} = 7.8$, $p < 0.001$; Fig. 4a). When taking only presence-absence into account, there was a tendency for a decline in CTI over time ($b = -0.0020 \pm 0.0010$°C yr^{-1}, $t_{54} = 1.9$, $p = 0.056$).

In Ammarnäs, T_{summer} showed no obvious trend up to year 2000, after which the average temperature clearly increased, but overall there was a significant increase in temperature (slope 0.022 ± 0.0084°C yr^{-1}, $t_{45} = 2.6$, $p = 0.012$, Fig. 4b). Over the same period, CTI was on average stable over time (slope -0.0018 ± 0.0035°C yr^{-1}, $t_{1,44} = 0.52$, $p = 0.61$; Fig. 4b). Also when taking only presence-absence into account, there was no significant trend in CTI over time ($b = 0.0023 + 0.0037$°C yr^{-1}, $t_{44} = 0.63$, $p = 0.53$). The seemingly cyclic appearance of CTI is driven by brambling *Fringilla montifringilla* abundance, which in turn depends on the cyclic outbreaks of *Epirrita* caterpillars (Enemar et al. 2004). Excluding the brambling from the analysis reduced the variation in CTI, but did not affect the results qualitatively.

The time lag in bird community response to temperature change

In all schemes, the temperature one to three years earlier best predicted CTI in a given year (Table 1). Accordingly, the long-term pattern of CTI seemed to match closely the direction and strength of long-term average temperature changes (Fig. 3–4).

The spatial shift in temperature and community composition

In 1975–2009, the average northward velocity of a given temperature regime in Sweden was 8.7 km yr^{-1} (0.040°C yr^{-1} divided by 0.0046°C km^{-1}). This is equivalent to a total northward shift of 296 ± 27 km over 35 yr. In the same period, the northward velocity of a given CTI in the Old scheme was 3.1 km yr^{-1} (0.0031°C yr^{-1} divided

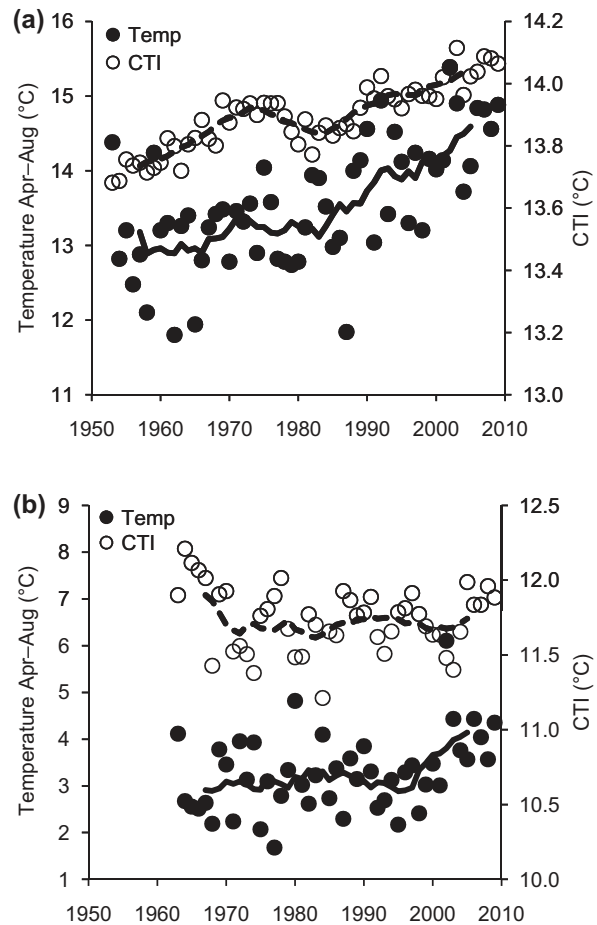Figure 4. The average temperature in April–August (T_{summer}, °C) and community temperature index (CTI, °C) at two long-term study sites of passerine bird communities in Sweden. (a) Birdsong Valley, outside Lund, south Sweden, 1953–2009 (bird data from Enemar et al. 1994, Svensson et al. 2010). (b) Ammarnäs, Swedish Lapland, 1967–2009 (bird data from Enemar et al. 2004, this study). The solid (T_{summer}) and stippled (CTI) lines denote nine year running averages.

by 0.0010°C km^{-1}). This is equal to a northward shift of 105 ± 7 km over 35 yr. Accordingly, temperature shifted 191 ± 34 km more to the north than the bird communities. The corresponding calculations for the New scheme in 1998–2009 was a northward shift in temperature of 218 ± 170 km, and in CTI of 48 ± 7 km. CTI lagged behind temperature with 170 ± 176 km. Clearly, whereas the average Swedish bird community has moved northward in recent time, the shift is not as fast as the temperature shift.

Discussion

The composition of Swedish bird communities seems to rapidly and closely track changes in summer temperatures. In all time-series, there was a significant 1–3 yr lag between summer temperature and CTI. Further, in all four time-series, CTI tracked periods of temperature increase, stability or decrease remarkably well. For example, CTI did not

Table 1. The lagged effects of temperature on CTI in the four datasets. The time-series of the New scheme was too short for a meaningful analysis of a 3 or 4 yr lag.

lag (yr)	New scheme (1998–2009)			Old scheme (1975–2009)			Birdsong Valley (1953–2009)			Ammarnäs (1963–2009)		
	estimate	t	p	estimate	t	p	estimate	t	p	estimate	t	p
1	0.006	0.43	0.67	0.008	1.43	0.16	0.030	2.45	**0.018**	−0.051	1.70	0.097
2	0.028	2.40	**0.049**	0.012	1.91	0.068	0.042	3.48	**0.001**	0.041	1.34	0.19
3				0.016	2.71	**0.012**	0.022	1.92	0.061	0.080	2.45	**0.019**
4				−0.003	0.62	0.55	0.008	0.77	0.44	−0.001	0.04	0.97

change much in periods with fairly stable temperatures, as in the Old scheme in 1975–1995 and Ammarnäs in 1963–2000. At Birdsong Valley, CTI even dropped for about a decade in the 1970s, coinciding with a general decrease in summer temperatures. From the early 1990s and onwards, there were overall strong increases in both summer temperatures and CTI in Sweden. This corroborates the pattern in France and Europe the same period (Devictor et al. 2008, 2012).

Changes in bird community composition

In at least two of the time series (Old scheme, Birdsong Valley), the increase in CTI was mainly explained by the relative changes in abundance of different species. For example, at Birdsong Valley (Enemar et al. 1994, Svensson et al. 2010), where CTI increased over 57 yr, the STI of the five common species increasing most in numbers range 13.9–14.6°C. For the three common species that declined most in numbers the STI range 12.5–13.3°C. Clearly, birds with a high STI gradually replaced birds with low STI.

Recent published analyses corroborate such a pattern. The European population trends of 110 species in 1980–2005 were more favourable in species with higher STI, than in species with a lower STI (Jiguet et al. 2010b). Further, among 62 common European species in France, the Netherlands and Sweden in 1989–2008, populations within each species' breeding distribution were doing gradually and linearly better towards the cold end of their thermal niche (Jiguet et al. 2010a). Both patterns lead to an increase in CTI over time at a given site.

A change in CTI can also be caused by a shift in local or regional species composition (presence-absence) beyond changes in abundances. In the New scheme, there was a significant effect of species turnover, a pattern that was found also in France (Devictor et al. 2008). At the national scale, species turnover in Sweden is low. In 1850–1970 new breeding species entered the Nordic countries (incl. Sweden) at a rate of 2.8 species per decade (balanced by an extinction rate of 0.6 species per decade, Järvinen and Ulfstrand 1980). Roughly the same rate of immigration has continued up to present. The new and disappearing species in Sweden during our sampling period have only rarely been counted in the Swedish schemes (Lindström et al. 2010), and therefore can not have affected CTI. Instead there must have been species turnover at many individual sites around Sweden, reflecting distribution range changes of species already present in the country.

Species turnover did not significantly explain the increase in CTI in the Old scheme. Many of the analysed species have a distribution pattern that roughly coincides with the distribution of the Old scheme plots (the southern half of Sweden and along the east coast of northern Sweden). This gives little opportunity for detecting range shifts. In contrast, the New scheme covers the inland part of northern Sweden better (Fig. 3). The analysis by Jiguet et al. (2010a, based on the Old scheme) revealed that in Sweden, populations furthest away from the thermal maximum of each species' breeding distribution ('northern populations') were generally doing better than populations nearer this thermal maximum ('southern populations'). Accordingly, there is a much larger potential for the New scheme to pick up range shifts towards the north, than for the Old scheme. In nearby Finland, at latitudes comparable to northern Sweden, southern species have increased in numbers and northern species decreased, in parallel to climate warming (Virkkala and Rajasärkkä 2011). At neither of our two local sites did species turnover significantly affect CTI.

Note that the Swedish trend in CTI integrates all site-specific changes in community composition. This approach represents the contribution of all species to community changes over large areas. Interestingly, this approach is also valuable to test the change in community composition of assemblages of migratory birds in their wintering areas (Godet et al. 2011). Some species will be more affected than others in a given assemblage depending on other factors than temperature. For instance, a given species monitored at sites located at the species' range margins will have different population dynamics than at sites located at the core species' range (Guo et al. 2005). However, following temperature increase, one still expects the local relative composition of species with low versus high STI to be affected. The site-specific changes in CTI can then be analyzed either at focal sites or averaged across sites while accounting for between-site variability (e.g. in Sweden). Alternatively, one may test whether the trend in CTI changes along particular gradients (latitude, habitat, disturbance, conservation effort). For instance, the difference in CTI between the southern (Birdsong Valley) and northern sites (Ammarnäs) is increasing over time (Fig. 4), reflecting an increase in the dissimilarity of northern and southern communities' composition and with this possibly also a disequilibrium with climate (see more below). The spatial variation of the temporal trend in CTI, and the detailed contribution of each species to this change, deserves further investigation.

Drivers of climate-related changes in bird community composition

The bird communities responded to short-term changes in summer temperature with a lag of 1–3 yr. It is known that summer temperature can affect population size change between years (Enemar et al. 2004, Saether et al. 2004, Jiguet et al. 2006). If mainly local demographic processes are at play, we would expect that species with high STI in warm summers have relatively higher reproductive success, higher between-year survival, and/or higher local recruitment in coming years, than species with lower STI. This remains to be investigated.

In addition to species-specific differences in local survival and recruitment, there could also be differential emigration and immigration, either through adults changing their breeding sites between years, or first-time breeders moving away from their birth sites. For example, in years following warm summers, there might be relatively more immigrants of species that prefer higher temperatures. Reside et al. (2010) found that the presence of wide-spread but resident Australian bird species were better predicted by models based on weather variables rather than by climate-based models. This suggests that even resident species can show rapid distributional responses to short term changes in weather (Julliard et al. 2003, Jiguet et al. 2011).

Lag in bird community response to climate change

At the community level, we found a difference between temperature increase and the rate of change in CTI. We interpreted this difference as a 'lag' while other authors have named this difference a 'debt' (Devictor et al. 2012). But obviously, the difference between change in CTI and changes in temperature may at the species and individual level be more or less mitigated by local adaptation and plasticity, or put in other words, cause more or less real trouble for the individuals of different species. Our results do not tell which species are tracking climate change fast enough, but rather that communities do not adjust their composition as expected by temperature increase. Accordingly, this approach does not replace more species-specific studies or experimental investigations on how local populations are able to adapt (Visser 2008, Charmantier et al. 2008) or suffer from climate change (Both et al. 2006, Sherry et al. 2007).

Although the bird communities in Sweden (this study), France (Devictor et al. 2008) and larger parts of Europe (Devictor et al. 2012) have matched recent temperature changes well in a qualitative way, the quantitative match is poorer. In France, the average bird community moved 91 km northward over 17 yr, at the same time as temperature profiles moved 273 km northwards. In Europe, the average bird community moved 37 km northward over 18 yr, at the same time as temperature profiles moved 249 km northwards. Accordingly, CTI lagged behind temperature by 182 and 212 km respectively, which is equivalent to a lag increasing by about 10–12 km yr^{-1}. In Sweden, the corresponding lag rate was 15.4 km yr^{-1} in the New scheme and 5.6 km yr^{-1} in the Old scheme (the latter includes a long initial period of rather stable temperatures). The lag

rates have thus been fairly similar in recent years. Overall we can conclude that present day changes in CTI are not fast enough to track the recent rate of increase in summer temperatures.

The reason for this lag, and its effect on individual fitness and bird population abundance, are not yet clear. The actual movement needed to track temperature change, 10–15 km yr^{-1}, should not be a problem per se for the highly mobile birds. Instead, this lagged response may be caused by breeding and natal site tenacity (Greenwood and Harvey 1982), or the inability to detect and respond to small temperature changes. In addition, many species are dependent on particular vegetation and habitat types, and vegetation does not respond to temperature as fast as birds (Svenning et al. 2008, Kissling et al. 2010, Bertrand et al. 2011).

In the longest time series, Birdsong Valley, T$_{summer}$ increased about 2°C in 57 yr. CTI increased with about 0.4°C. The bird community in 2009 thus experienced about 1.6°C higher temperatures, in relation to CTI, than the community in 1953. However, in Ammarnäs, there is currently an 8°C difference between T$_{summer}$ and CTI. Since many species involved are present at both sites, there is at the species level evidently a great capacity to cope with dramatically different temperatures. This could suggest that the changes in T$_{summer}$ may not yet have too dramatic effects. On the other hand, local adaptations and responses to different temperature conditions in passerine birds may be strong and have a genetic base (Wikelski et al. 2003, Broggi et al. 2005, Visser et al. 2011), suggesting that temperature differences may indeed affect fitness.

Overall, our results show that community changes follow temperature change and that this change is occurring at a lower velocity than temperature change. But to what extent species are 'suffering' remains to be tested with species-by-species approaches. Indeed the fact that CTI does not change at the same rate as temperature can result from species being highly tolerant to change in temperature. They simply do not need to track climate change. Alternatively, species would benefit from tracking temperature more closely, but cannot adjust their distribution because they face other constraints (e.g. local adaptation to other variables, dispersal limitations, changes in the breeding success, and/or survival, specialization to particular habitats or resources). This difference between 'true' lag (or debt) and 'apparent' lag (or debt) could be disentangled with field data providing evidence for change in species' fitness.

Conclusions

Our study adds additional support to recent findings that ongoing changes in bird community structure are driven to a large extent by contemporary changes in climate and that CTI can work as a simple indicator for the qualitative and quantitative response of birds to climate change at different spatial scales. The finding of a community change with a lower velocity than the contemporary temperature change suggest further studies to detail the mechanism behind this, in order to be able to predict future community changes in the face of climate change.

References

Ahola, M. et al. 2007. Climate change can alter competitive relationships between resident and migratory birds. – J. Anim. Ecol. 76: 1045–1052.

Bertrand, R. et al. 2011. Changes in plant community composition lag behind climate warming in lowland forests. – Nature 479: 517–520.

Both, C. and Visser, M. E. 2005. The effect of climate change on the correlation between avian life-history traits. – Global Change Biol. 11: 1606–1613.

Both, C. et al. 2006. Climate change and population declines in a long distance migratory bird. – Nature 441: 81–83.

Broggi, J. et al. 2005. Local adaptation to winter conditions in a passerine spreading north: a common-garden approach. – Evolution 59: 1600–1603.

Brown, J. H. et al. 2001. Complex species interactions and the dynamics of ecological systems: long-term experiments. – Science 293: 643–650.

Buse, B. A. et al. 1999. Effects of elevated temperature on multispecies interactions: the case of pedunculate oak, winter moth and tits. – Funct. Ecol. (Suppl. 1) 13: 74–82.

Charmantier, A. et al. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. – Science 320: 800–803.

Clavero, M. et al. 2011. Climate change or land use dynamics: do we know what climate change indicators indicate? – PLoS One 6: e18581.

Davey, C. M. et al. 2012. Rise of the generalists: evidence for climate driven homogenization in avian communities. – Global Ecol. Biogeogr. 21: 568–578.

Devictor, V. et al. 2008. Birds are tracking climate warming, but not fast enough. – Proc. R. Soc. B 275: 2743–2748.

Devictor, V. et al. 2012. Differences in the climatic debts of birds and butterflies at a continental scale. – Nat. Clim. Change 2: 121–124.

Enemar, A. et al. 1994. Dynamics of a passerine bird community in a small deciduous wood, S Sweden, during 40 years. – Ornis Svecica 4: 65–104.

Enemar, A. et al. 2004. The 37-year dynamics of a subalpine passerine bird community, with special regards to the influence of environmental temperature and *Epirrita autumnata* cycles. – Ornis Svecica 14: 63–106.

Gilman, S. E. et al. 2010. A framework for community interactions under climate change. – Trends Ecol. Evol. 25: 325–331.

Godet, L. et al. 2011. Waders in winter: long-term changes of migratory bird assemblages facing climate change. – Biol. Lett. 7: 714–717.

Greenwood, P. J. and Harvey, P. H. 1982. The natal and breeding dispersal of birds. – Annu. Rev. Ecol. Syst. 13: 1–21.

Guo, Q. et al. 2005. Spatial-temporal population dynamics across species range: from centre to margin. – Oikos 108: 47–57.

Hagemeijer, W. J. M. and Blair, M. J. 1997. The EBCC atlas of European breeding birds: their distribution and abundance. – Poyser.

Hill, J. K. et al. 1999. Climate and habitat availability determine 20th century changes in a butterfly's range margin. – Proc. R. Soc. B 266: 1197–1999.

Järvinen, O. and Ulfstrand, S. 1980. Species turnover of a continental bird fauna: northern Europe, 1850–1970. – Oecologia 46: 186–195.

Jiguet, F. et al. 2006. Thermal range predicts bird population resilience to extreme high temperatures. – Ecol. Lett. 9: 1321–1330.

Jiguet, F. et al. 2010a. Bird population trends are linearly affected by climate change along species thermal ranges. – Proc. R. Soc. B 277: 3601–3608.

Jiguet, F. et al. 2010b. Population trends of European common birds are predicted by characteristics of their climatic niche. – Global Change Biol. 16: 497–505.

Jiguet, F. et al. 2011. Community responses to extreme climatic conditions. – Curr. Zool. 57: 406–413.

Johansson, B. 2000. Areal precipitation and temperature in the Swedish mountains. An evaluation from a hydrological perspective. – Nord. Hydrol. 31: 207–228.

Julliard, R. et al. 2003. Common birds facing global changes: what makes a species at risk? – Global Change Biol. 10: 148–154.

Kerbiriou, C. et al. 2009. More species, fewer specialists: 100 years of changes in community composition in an island biogeographical study. – Divers. Distrib. 15: 641–648.

Kissling, W. D. et al. 2010. Woody plants and the prediction of climate-change impacts on bird diversity. – Phil. Trans. R. Soc. B 365: 2035–2045.

Lavergne, S. et al. 2010. Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. – Annu. Rev. Ecol. Evol. Syst. 41: 321–350.

Lindström, Å. et al. 2010. Monitoring population changes of birds in Sweden. – Annual report for 2009, Dept Biol., Lund Univ.

Loarie, S. R. et al. 2009. The velocity of climate change. – Nature 462: 24–31.

Menéndez, R. et al. 2006. Species richness changes lag behind climate change. – Proc. R. Soc. B 273: 1465–1470.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. – Annu. Rev. Ecol. Evol. Syst. 37: 637–669.

Raj, D. 1964. A note on the variance of the ratio estimate. – J. Am. Stat. Assoc. 59: 895–898.

Reif, J. et al. 2010. Contrasting effects of climatic and habitat changes on birds with northern range limits in central Europe as revealed by an analysis of breeding bird distribution in the Czech Republic. – Acta Ornithol. 45: 83–90.

Reside, A. E. et al. 2010. Weather, not climate, defines distributions of vagile bird species. – PLoS One 5: e13569.

Saether, B.-E. et al. 2004. Climate influences on avian population dynamics. – Adv. Ecol. Res. 35: 185–209.

Schielzeth, O. H. and Forstmeier, W. 2009. Conclusions beyond support: overconfident estimates in mixed models. – Behav. Ecol. 20: 416–420.

Sherry, R. A. et al. 2007. Divergence of reproductive phenology under climate warming. – Proc. Natl Acad. Sci. USA 104: 198–202.

Svenning, J.-C. et al. 2008. Postglacial dispersal limitation of widespread forest plant species in nemoral Europe. – Ecography 31: 316–326.

Svensson, S. et al. 2010. Species trends, turnover and composition of a woodland bird community in southern Sweden during a period of fifty-seven years. – Ornis Svecica 20: 31–44.

Van Turnhout, C. A. M. et al. 2007. Scale-dependent homogenization: changes in breeding bird diversity in the Netherlands over a 25-year period. – Biol. Conserv. 134: 505–516.

Virkkala, R. and Rajasärkkä, A. 2011. Climate change affects populations of northern birds in boreal protected areas. – Biol. Lett. 7: 395–398.

Visser, M. E. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. – Proc. R. Soc. B 275: 649–659.

Visser, M. E. et al. 2011. Genetic variation in cue sensitivity involved in avian timing of reproduction. – Funct. Ecol. 25: 868–877.

Wikelski, M. et al. 2003. Slow pace of life in tropical sedentary birds: a common-garden experiment on four stonechat populations from different latitudes. – Proc. R. Soc. B 270: 2383–2388.

Supplementary material (Appendix E7799 at < www. oikosoffice.lu.se/appendix >). Appendix 1.

Ecography

Supplementary material

Supplementary information: **correlation between STI values calculated with different sources of data (Lindström et al.)**

The CTI (Community Temperature Index) of a given assemblage is the average of species' STI (Species Temperature Index) occurring in this assemblage weighted by species abundance. An increase in CTI reflects the rate of replacement of individuals belonging to species with low STI by those with higher STI. When calculated using presence-absence data, CTI is simply the average of species' STI. In this case, the rate of change in CTI reflects the rate of replacement of species (not individuals) with low STI by those with higher STI. Thus, changes in CTI (either calculated with abundance or presence-absence) reflect how community composition is changing with respect to species' STI.

Therefore, to estimate the rate of change in CTI, one is more interested in the relative order of species along the STI gradient than in each species-specific STI value. In other words, the CTI calculated in a given place is less informative than its changes. In fact, STI can be calculated from different sources of data as soon as it allows the ordering of species from those dependent on low temperature to those dependent on hotter temperature. To illustrate this issue, we have tested the correlations between STI calculated with different sources of data.

Robustness of STI to changes in the area and datset considered

Monitoring_STI is calculated using the distribution of birds in Sweden estimated from the Swedish breeding bird survey

Swedish_STI is calculated using the distribution of birds in Sweden according to the European Atlas of Hagemeijer and Blair (1997)

European_STI is calculated using the entire species distribution according to the European Atlas of Hagemeijer and Blair (1997)

Scored_STI is calculated by sorting the species according to their European_STI and by attributing an increasing score to the species from 1 to 244.

Palearctic_STI is calculated using the Palearctic distribution of birds of Barbet-Massin et al. (2010).

Note that each of these STI (all calculated using April-August temperature) capture different ranges of temperature, land-mass, extent of the total species distribution etc. Some of these STIs are also estimated using very different sources of data (e.g. Monitoring data versus European atlas). The following graphs and table of correlations however show that they each provide similar distribution of species along the STI gradient. In other words, "hot-species" and "cold-species" are more or less the same, whatever the STI considered.
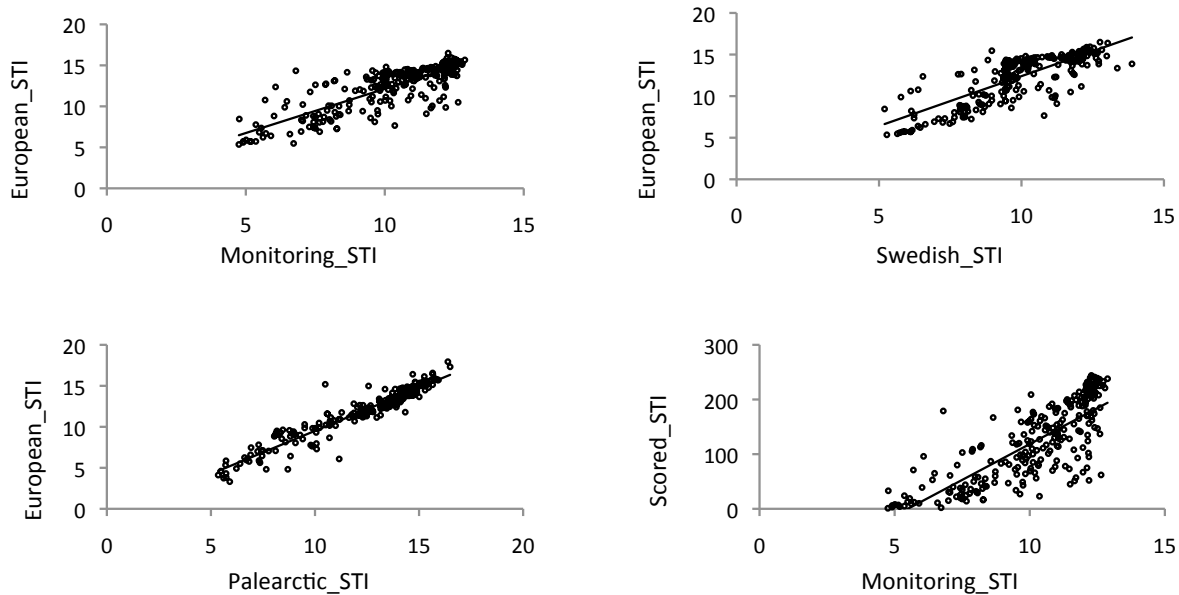
	Monitoring_STI	Swedish_STI	European_STI	Scored_STI	Palearctic_STI
Monitoring_STI	1				
Swedish_STI	0.93	1			
European_STI	0.82	0.78	1		
Scored_STI	0.78	0.78	0.95	1	
Palearctic_STI	0.81	0.78	0.96	0.91	1

Table S1. This table provides correlation coefficients between all pairs of STI gradient calculated for the 244 species using different sources of data. All correlations are highly significant ($p<0.0001$)


Robustness of STI to changes in the time-window considered

STI are calculated using temperature of the average breeding season of most species (April to August). However, species have different phenologies. Hence, while STI calculated using April to August temperature may be accurate for some species, other species might have more relevant STIs if calculated using a different time window, better adapted to their own phenology. However, here again, changing this species-specific information will not alter substantially how species are classified among each other along a STI gradient. For instance, March-September, and even January-December STI are all highly correlated as illustrated beow.
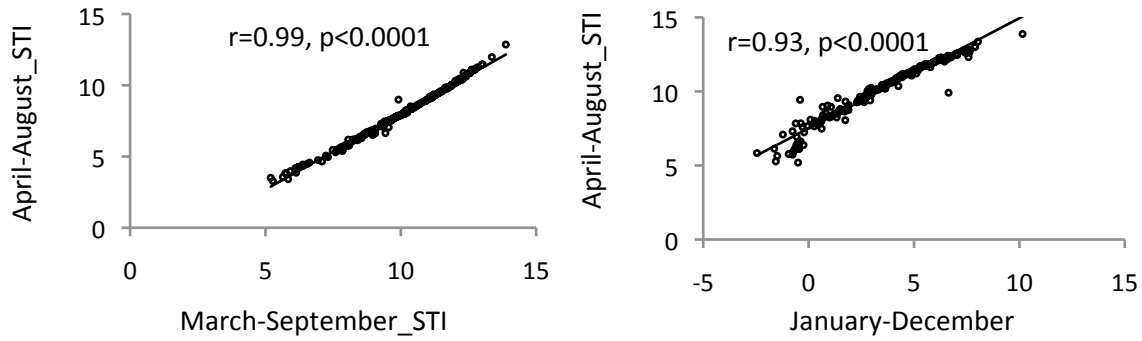
Robustness of STI to the subset of the species range considered

Finally, STI can also be estimated by focusing on a particular subset of the species' ranges. For instance, it is likely that northern parts of species ranges are delineated by populations more locally adapted to colder temperature. Therefore, rather than using STI calculated as the average of temperature over the species distribution, one can calculate STI for the northern part of the distribution only. This, however, will not alter the overall ranking of species according to their STI. For instance species' STI (April-August) calculated using the 5% of the coldest or the hottest European atlas cells are highly correlated to their STI calculated using the whole distribution:
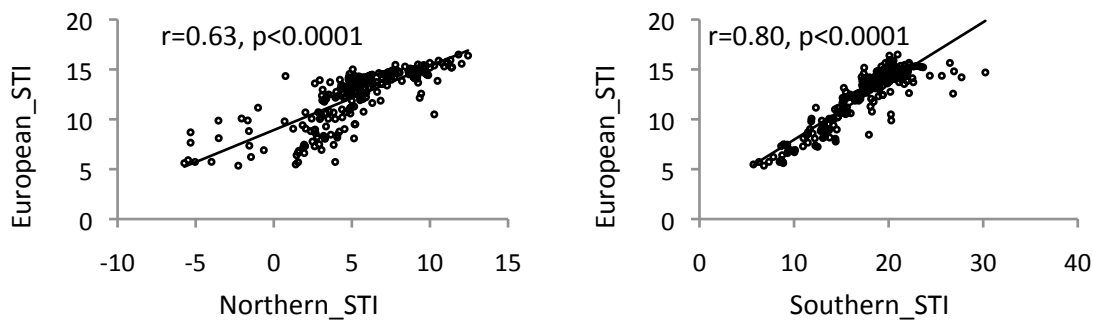
Barbet-Massin, M., Thuiller, W., Jiguet, F. How much do we overestimate future local extinction rates when restricting the range of occurrence data in climate suitability models? *Ecography* **33**, 878-886 (2010).

Hagemeijer, W. J. M. & Blair, M. J. The EBCC atlas of European breeding birds: their distribution and abundance. London, UK: T. & A. D. Poyser (1997).