Effects of high latitude protected areas on bird communities under rapid climate change

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Abstract

Anthropogenic climate change is rapidly becoming one of the main threats to biodiversity, along with other threats triggered by human-driven land-use change. Species are already responding to climate change by shifting their distributions polewards. This shift may create a spatial mismatch between dynamic species distributions and static protected areas (PAs). As protected areas represent one of the main pillars for preserving biodiversity today and in the future, it is important to assess their contribution in sheltering the biodiversity communities, they were designated to protect. A recent development to investigate climate-driven impacts on biological communities is represented by the community temperature index (CTI). CTI provides a measure of the relative temperature average of a community in a specific assemblage. CTI value will be higher for assemblages dominated by warm species compared with those dominated by cold-dwelling species. We here model changes in the CTI of Finnish bird assemblages, as well as changes in species densities, within and outside of PAs during the past four decades in a large boreal landscape under rapid change. We show that CTI has markedly increased over time across Finland, with this change being similar within and outside PAs and five to seven times slower than the temperature increase. Moreover, CTI has been constantly lower within than outside of PAs, and PAs still support communities, which show colder thermal index than those outside of PAs in the 1970s and 1980s. This result can be explained by the higher relative density of northern species within PAs than outside. Overall, our results provide some, albeit inconclusive, evidence that PAs may play a role in supporting the community of northern species. Results also suggest that communities are, however, shifting rapidly, both inside and outside of PAs, highlighting the need for adjusting conservation measures before it is too late.

Keywords: abundance shift, bird abundance, community temperature index, global climate change, protected area effectiveness

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Introduction

Humans are transforming the Earth's biological and abiotic systems in multiple ways and at an unprecedented pace. As a result, human-driven habitat loss, degradation and fragmentation, among other threats, are triggering the collapse of global biodiversity (Pimm *et al.*, 2006). During the current century however, anthropogenic climate change could become a major cause of species extinction via direct impacts on species or in synergy with other pressures (Thomas *et al.*, 2004, Mantyka-Pringle *et al.*, 2012; IPCC, 2013). In order to halt and revert the biodiversity collapse, a global network of protected areas has been established (Watson *et al.*, 2014). Protected areas currently cover just over 12% of the terrestrial realm and represent a powerful tool to mitigate threats to biodiversity and safeguard ecosystems and the services they provide (Watson *et al.*, 2014). Much focus has been recently placed onto identifying priority locations for expanding the network of global protected areas (Pouzols *et al.*, 2014; Venter *et al.*, 2014). However, it is equally important that the effectiveness of protected areas is evaluated, particularly under conditions of rapid environmental change (Andam *et al.*, 2008; Laurance *et al.*, 2012; Gillingham *et al.*, 2015b).

Under rapid climate change, species have been shown to shift poleward or upward, and the composition of biological communities has been shown to change accordingly (Devictor *et al.*, 2008; Chen *et al.*, 2011; Lehikoinen & Virkkala, 2016). Protected areas are, however, static entities in the landscape, and their value in protecting species under rapid change has been questioned (Heller & Zavaleta, 2009). Empirical evidence suggests that over the past decades protected area networks have continued to provide a good coverage for many species, whether they have shifted in distribution or sought a cooler microhabitat under warming conditions (see Thomas & Gillingham, 2015; and references therein). Protected areas have also been shown to act as stepping stones that may facilitate and

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accelerate species range shifts by providing suitable breeding and wintering habitat conditions (Thomas *et al.*, 2012; Hiley *et al.*, 2013; Pavón-Jordán *et al.*, 2015). Some evidence also suggests that, when effectively managed, protected areas may contribute to hinder climate-driven species declines (Thomas & Gillingham, 2015).

Ultimately, biological communities occurring within protected areas may be more resilient to climate-driven changes compared with communities occurring in unprotected land under multiple disturbance factors (Olds *et al.*, 2014; Gillingham *et al.*, 2015a). However, evidence regarding the potential role of protected areas in facilitating range shifts versus retaining initial communities is still scarce and typically based on studies of restricted spatial, taxonomic, or temporal coverage (but see Gaüzère *et al.*, 2016). Moreover, most previous studies investigating climate-driven species range shifts in relation to protected areas have used occurrence data (Araujo *et al.*, 2004, 2011). However, use of occurrence (presence–absence or presence-only) data may mask climate-driven population density shifts visible using abundance data (Virkkala & Lehikoinen, 2014).

A recent development to investigate climate-driven impacts on biological communities is given by the use of a community temperature index (hereafter CTI; Devictor *et al.*, 2008). By combining information on species-specific average temperature experienced across the species breeding range in the long term (the so called species temperature index, STI; (see more details below) with information on the relative species abundance in any given assemblage, it is possible to derive the community temperature index (CTI; Devictor *et al.*, 2008). Calculated as the average of each individual's STI in a given assemblage (which may represent a discrete unit in space or time), CTI provides a measure of the relative temperature average of a community in a specific assemblage. The CTI value will be higher for assemblages dominated by warm species compared with those dominated by cold-dwelling species (i.e. characterized by a low STI). CTI can thus be used to explore community changes over time or across space (Devictor *et al.*, 2008; Tayleur *et al.*, 2016), or in relation to protected areas (Gaüzère *et al.*, 2016).

Here, we make use of an over 40-year long nationwide dataset on bird abundance to explore, for the first time at high latitudes under rapid climate warming, the change in CTI within and outside of protected areas. The broad aim is to assess whether protected areas (hereafter PAs) are able to buffer against climate-driven community changes in species composition. Specifically, we first compare the change in CTI of species assemblages within and outside of protected areas in Finland, and across time (from 1970s–1980s to 2000s)

and space (along an over 1000 km latitudinal gradient). We also compare change in CTI with change in temperature over the same period in order to identify whether species responses are keeping pace with climate change (Devictor *et al.*, 2008). We then explore whether possible changes in CTI within and outside of PAs are mainly driven by changes in relative densities of species, considering densities of northern and southern species separately. We predict that PAs in Finland can buffer against climate-driven changes in species composition. We also predict that the buffering impact of PAs is most marked at northern latitudes where changes in CTI may be more dramatic (Tayleur *et al.*, 2016) and PAs are larger than in the south (Virkkala & Rajasarkka, 2007). Moreover, this buffering effect would occur through the retention of northern species within PAs.

Materials and methods

Line transect data

For this study, we use a rather unique dataset consisting on bird observations collected using the line transect method from across Finland starting from the early 1970s (Virkkala & Lehikoinen, 2014). The line transect method consists of a one-visit survey whereby all birds are counted along a transect band typically 3–6 km long on a predetermined location (see more details in Lehikoinen & Virkkala, 2016; Virkkala & Lehikoinen, 2014). Transects are carried out normally between 3:00 and 10:00 h in the morning mainly during June (typically 1–20 June in the south and 10–30 June in the north of Finland). The transect is divided into a 50-m wide (25 m on either side of the line) main belt, and a supplementary belt beyond the main belt and as far as birds can be detected. The main belt and supplementary belt form the survey belt. All bird observations recorded (e.g. from a singing individual to a flying flock) are later transformed into pairs. The census unit is thus a pair of birds, not an individual (Virkkala & Lehikoinen, 2014; Lehikoinen & Virkkala, 2016). The methodology is appropriate for counting birds over large areas and ultimately obtaining relative densities of species (Järvinen & Väisänen, 1975; Lehikoinen & Virkkala, 2016).

We classified each line transect according to its protection status, within protected areas (PAs) or outside (hereafter referred to as *unprotected*), and according to the period when it was carried out, considering two discrete time periods: 1970–1989 (hereafter 1970s–1980s) or 2000–2014 (hereafter 2000s). Transects running across the boundary of PAs were excluded. We then divided the country into 100-km squares (hereafter squares) and identified those squares having at least one line transect for each of protection and period combination (Fig. 1). The rationale for this was to obtain a balanced design in terms of the spatiotemporal coverage of the data that would allow for robust comparisons of observations between protection and period classes, and across space. Overall, 41 squares had
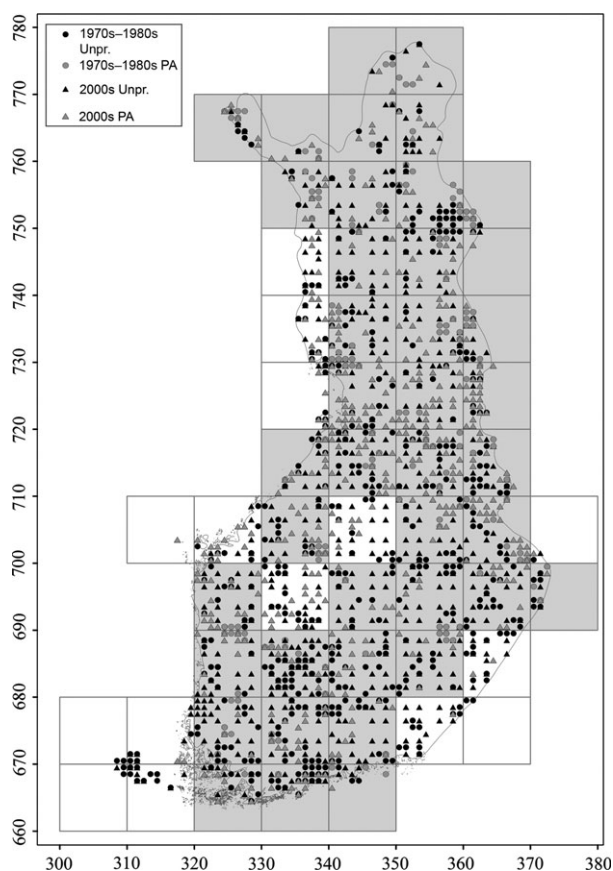
Fig. 1 Location of the line transect sites marked separately by period (1970s–1980s and 2000–2014) and by protection status [whether the transect was within a protected area (PA) or outside (Unpr.)]. The 100 km squares used as a set up for the study design are marked with grey lines. Squares that fitted the study design criteria, that is, had at least one transect for each period and protection combination, are marked with grey fill colour. The outer marks and values refer to the Finnish coordinate system.

sufficient line transect data to fit our design, covering most of the country across the two cardinal directions (Fig. 1). Therefore, our sample unit, which we hereafter call assemblage, is the observation of the community from one of the two periods and protection classes within a square (e.g. community from PAs during period 1970s–1980s and within square 15). The average year when the transect lines were carried out was 1983 for the first period, and 2008 for the second period, resulting in an average of 25 years interval between the two periods.

Community temperature index

We here use the same set of 128 bird species with sufficient data (i.e. at least 20 observations during the periods 70–80s and 2000s) as those used in the study by Lehikoinen & Virkkala (2016). We then derived the species-specific relative density (hereafter density) for each assemblage (i.e. from each

protection and period class combination within each square). Density was calculated by multiplying the survey belt observations over the transect length with species-specific detectability coefficient as given in the study by Lehikoinen & Virkkala (2016). This was necessary because previous evidence suggests that failure to account for species detectability may result in biased conclusions when exploring patterns at the community level (Johnston *et al.*, 2014). Without correction coefficients, species which can be detected from far away are overrepresented in the community estimates compared with species which can be only detected when from a short distance. To classify species into southern and northern species, we used the species-specific central gravity of densities given as a latitudinal value in the Finnish coordinate system (obtained from Lehikoinen & Virkkala, 2016) referring to the period 1970–1989, and scaled it from zero to one, with zero being southernmost species, and one being northernmost species. We call this the density distribution index.

Next, we divided species into two contrasting groups using the above-mentioned distribution index. Specifically, we classified species with density distribution index ≥0.66 as northern species, and with density distribution index ≤0.33 as southern species (*n* = 31 and 76 species, respectively; see Table S1 for a list of the 128 species and their grouping). Although the cutoff point for the above groupings is somewhat arbitrary, we believe the values used are appropriate to obtain contrasting enough classes to be meaningfully compared (see Results below).

We then obtained the species temperature index (STI) for each of the 128 species considered. The STI was calculated as the average temperature across the European breeding range of the species for the months from March to August and across the period 1950–2000 (for further details, see Devictor *et al.*, 2008). The species distribution data were based on EBCC atlas of European breeding birds (Hagemeijer & Blair, 1997) and the temperature data were obtained from WORLDCLIM database (www.worldclim.org). The obtained STI is a relative rather than absolute measure, as it may not cover the thermal conditions experienced across the full range of a species (e.g. North Africa). However, as stated also by Devictor *et al.* (2008), the relative STI is appropriate to further derive the community temperature index (CTI, see below). We thus calculated the CTI for each assemblage (i.e. within and outside PAs and for each period within a square) as the average across all STIs of the species in that assemblage weighted by the species relative density in that assemblage (Devictor *et al.*, 2008; Lindström *et al.*, 2013).

Statistical analyses

In addition to the CTI, we also derived the average latitude and longitude of all line transects comprising each bird assemblage. This was deemed as a more precise measure of the location of the transect lines within an assemblage compared to the simpler alternative of using the centre point of the square including the specific bird assemblage. Similarly, we also derived the overall length of all line transects comprising each bird assemblage.

We built three separate general linear mixed models (GLMMs). A first GLMM included as the response variable the CTI calculated considering all species altogether. A second and third GLMMs included the sum of relative density of selected species per square by period and by protection as a response, using in turn relative density of northern or southern species only. We also run separate models on relative density for central species (i.e. with density distribution index between 0.33 and 0.66), and on CTI based only on forest-associated species (as classified by Väisänen *et al.*, 1998). Results and details of the above latter models are provided in Supplementary Material. The response variable including sum of relative densities was log-transformed to fit normality. The sample unit was thus the CTI or sum of relative density calculated for the given species pool per square per protection status and per period (e.g. CTI of square 5 within PAs in period 2000s). All three models had the same structure including the identity of the square as random factor (to account for multiple observations within the same square), and transect length in square (log-transformed) included as a weight to account for the varying effort (e.g. giving more weight to observations based on larger amount of line transects). The set of predictor variables was also the same across all models and included period (1970s–1980s vs. 2000s), protection (unprotected vs. PA), latitude and longitude (both scaled using the following formula: $x = [(x_i - \min(x_i))/100\,000]$), (latitude)^2 and the full three-way interaction period*protection*(latitude)^2, including all relevant two-way interactions. Latitude and longitude, including the quadratic latitude, were included to explain linear and potential nonlinear patterns in CTI or relative density across space. In addition, the three-way interaction aimed to explore whether the interaction between period and protection varied nonlinearly across the latitudinal gradient.

We investigated whether bird communities are tracking climate change differently within and outside of PAs by building a model with similar structure the as those above on CTI, but using change in CTI (from 1970s–1980s to 2000s) as a response. In this model, we included as predictors protection status, change in temperature (one value of average temperature per 100 km square), latitude (including its quadratic term) and longitude. Finally, given the high variation in PA coverage across Finland, we built a specific model only using CTI values related to communities within PAs only aimed at verifying which variable, between latitude and PA coverage, has the strongest effect on CTI across Finland. The model included period, PA coverage (calculated as the coverage of PAs for each 100-km square relative to each period: 1970s–1980s and 2000s), latitude (including the quadratic term), longitude and two interactions: period*latitude^2 and period*PA coverage. For the latter, we ensured that the correlation between PA coverage and latitude was small enough ($r = 0.4$) for them to be included in the same model.

Model selection and validation

Across each model, we first fitted the full model (i.e. the one including the three-way interaction period*protection*(latitude)^2 as well as longitude) and checked the significance of the three-way interaction term. If the latter was significant, we considered that as the best model (Zuur *et al.*, 2009). If the three-way interaction was not significant, we applied multimodel selection by comparing the AICc (Akaike information criterion adjusted for small sample size) of all model combinations (but excluding the three-way interaction; see Appendix S2 for the relative ranking of best supported models, i.e. those with ΔAICc <4). If model uncertainty was apparent (i.e. ΔAICc between best and second best model was <2), we proceeded with multimodel inference and averaging (using the R package MuMin) from the best set of models with ΔAICc <4 (Bartoń, 2014). Ultimately, the best final model was thus considered as that where the three-way interaction was found significant (i.e. $P < 0.05$; Zuur *et al.*, 2009), or otherwise the model fitted using only the significant variables as indicated by multimodel averaging. We then validated these models by inspecting for possible unexplained patterns in the residuals as well as inspecting the spatial correlogram showing the extent of spatial autocorrelation by distance in the residuals (Zuur *et al.*, 2009). No spatial autocorrelation or patterns in the residuals were identified for any of the GLMMs, indicating that the structure of the models and the predictors used were adequate. All statistical analyses were conducted in R software version 3.0.3 (R Core Development Team, 2013).

Results

CTI of all species

When all 128 common land bird species are considered for calculating the community temperature index, the three-way interaction between period, protection and the latitude as a quadratic term was not significant (Likelihood Ratio = 0.001, $P = 0.975$). This interaction was then excluded, and multimodel selection and averaging were performed. High model uncertainty was apparent, with four models being similarly supported (i.e. with ΔAICc <4; see Table S2). Multimodel averaging indicated that period, protection, longitude and the quadratic term of latitude are all strongly significant ($P < 0.05$; see Table S3 for the statistics of the full model-averaged results) in explaining CTI. Specifically, CTI was higher in unprotected land than inside of PAs, and increased from the 1970s–1980s to the year 2000s (Fig. 2a). CTI also decreased nonlinearly towards the north (Fig. 2b) and also decreased linearly towards the east (Table S3). An analysis based on CTI restricted to forest-associated species ($n = 65$ species, see methods) shows qualitatively comparable results (see support Table S6 and Fig. S1) as the above findings based on all species in the community.

The analysis focused on change in CTI in relation to change in temperature revealed that within and outside of PAs in Finland, CTI has increased by 0.16 ± 0.03 and 0.19 ± 0.03 °C, respectively (least square means and SE of a model including also longitude, latitude and the
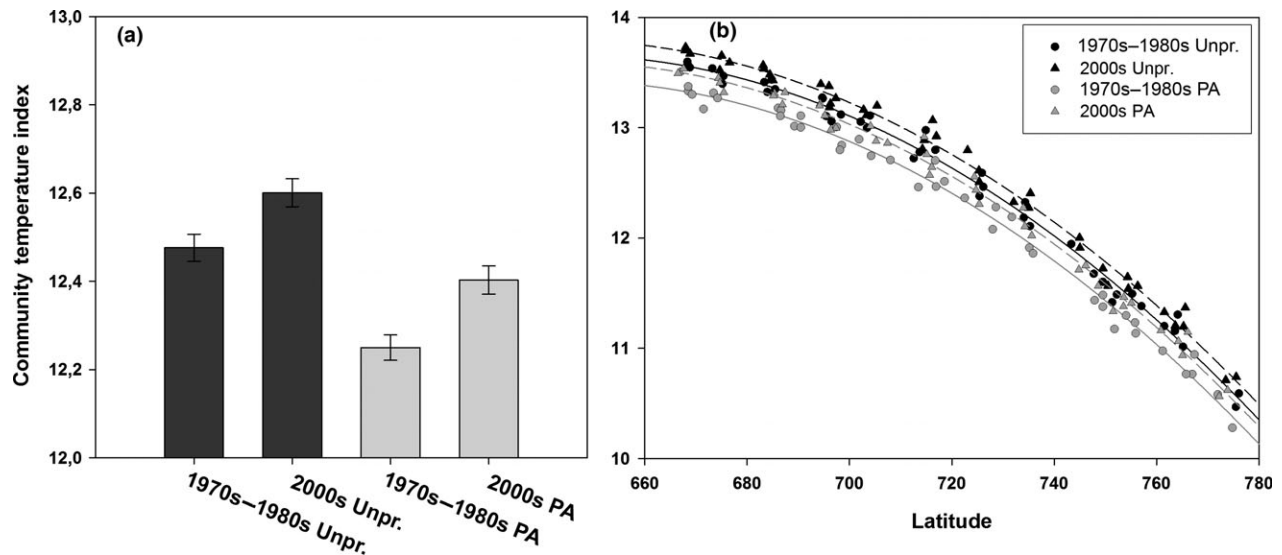
Fig. 2 Change in community temperature index (CTI) considering all 128 species across Finland. (a) Least square means (±SE) of CTI by period (1970s–1980s vs. 2000 onwards) and protection status (unprotected vs. protected area; Unpr. and PA, respectively). (b) Nonlinear decrease in CTI across the latitudinal gradient (south to north towards the right) separately by period and protection classes. Black fitted lines refer to unprotected land, grey lines to PAs, whereas continuous lines refer to the period 1970s–1980s and dashed lines to the 2000s.

quadratic term for latitude). The above increases in CTI are between five to seven times slower than the respective increase in temperature (1.06 ± 0.02 °C) over the same period, suggesting that Finnish bird communities are lagging behind climate change irrespective of protection (see Table S7 for full model-averaged results and Fig. S2).

Furthermore, from the model focused on CTI calculated from within PAs only, it appears that latitude has a much stronger (nonlinear) effect than the coverage of PAs in shaping change in CTI over the study period across Finland (see Table S8).

Density of northern and southern species

In the model on relative density of northern species only, the three-way interaction was significant ($LR = 4.001$, $P = 0.046$). Although this significance value may not appear convincing, inspection of residuals from the models with and without this interaction suggests that the three-way interaction largely contributed to explain patterns in the residual. On these bases, we considered the full model (i.e. the one with the three-way interaction) as the best in terms of fitting the data. Results from the full model indicated that, based on the three-way interaction, relative density of northern species was generally higher within than outside of PAs and in the 1970s and 1980s compared with the 2000s, but that these differences were most marked in the southern half of the country compared with the

northernmost areas (Fig. 3a). A nonlinear increase in relative density of northern species was evident towards higher latitudes, particularly within PAs in the 1970s and 1980s (Fig. 2a), whereas no effect of longitude was apparent ($t = -1.05$, $P = 0.30$).

In the model on relative density of southern species only, the three-way interaction was nonsignificant ($LR = 0.26$, $P = 0.608$). This interaction was then excluded, and multimodel selection and averaging were performed. High model uncertainty was apparent, with eight models being similarly supported (i.e. with $\Delta AICc < 4$; see Table S4). Multimodel averaging indicated that period and latitude were significant ($P < 0.05$; see Table S5) in explaining relative density of southern species, whereas protection was only marginally significant ($P = 0.061$). Specifically, relative density of southern species declined nonlinearly towards the north, increased over the study period and was marginally lower within than outside of PAs (Fig. 3b).

Finally, the density of central species was found to vary nonlinearly with latitude (quadratic term of latitude: $P < 0.001$), showing highest values towards central Finland, as expected for this group of species (see Fig. S3 and Table S9 for full model-averaged results).

Discussion

We show that the temperature index of the community (CTI) of Finnish land birds has markedly increased over the period of study (about four decades), with this
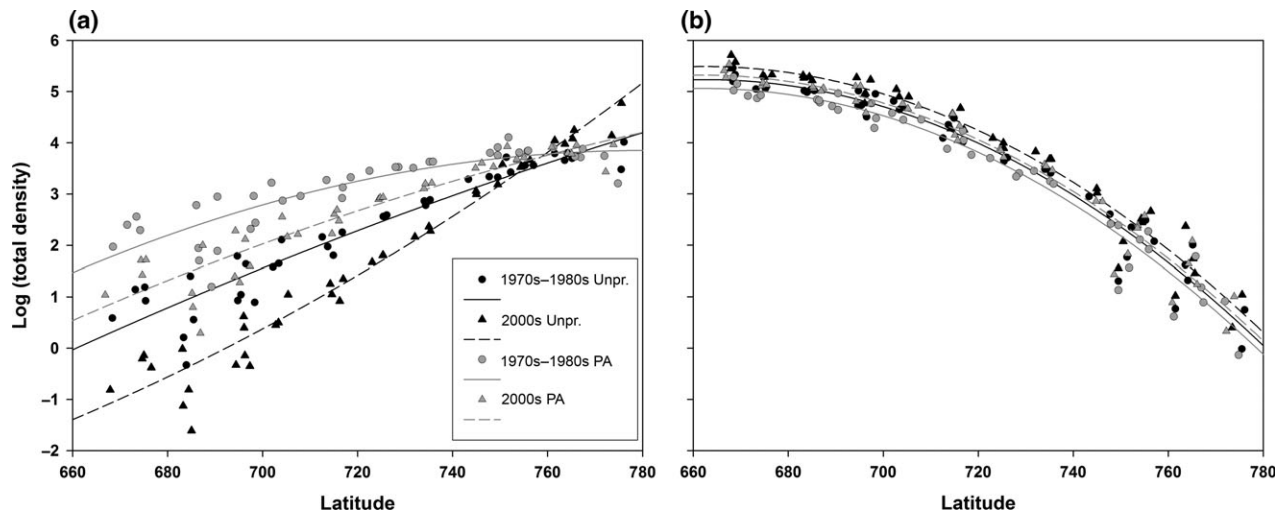
Fig. 3 Change in the sum of relative density (on the log scale) per square considering (a) northern species and (b) southern species along the latitudinal gradient (south to north towards the right) across Finland separately by period and protection classes. Black fitted lines refer to unprotected land, grey lines to PAs, whereas continuous lines refer to the period 1970s–1980s and dashed lines to the 2000s.

change being similar within and outside protected areas. However, we also show that the above increases in CTI are five to seven times slower than the temperature increase over the same period, suggesting that species are lagging behind climate change. Results also indicate that CTI has been constantly lower within than outside of PAs in both periods and that PAs nowadays still support communities which show colder thermal index than those in areas outside of PAs in the 1970s and 1980s. In addition, regions with a higher cover of the PA network are also associated with an overall lower CTI. Across Finland, CTI decreased linearly towards the east and nonlinearly towards the north, closely matching with the isotherms in the country (Lehikoinen & Virkkala, 2016). We also show that relative density of northern species was higher, but declining over time, within than outside PAs, which is in line with the lower CTI values observed inside compared with outside PAs. Conversely, relative density of southern species generally increased over the study period, was marginally lower within than outside of PAs and decreased nonlinearly towards the north.

Protected areas in Finland are mainly designated to cover boreal habitats of conservation concern, such as old-growth forests and mires mostly used by cold-dwelling species (Virkkala *et al.*, 2014). This may contribute to explain the lower CTI within PAs compared with outside, and also the negative relationship between PA coverage and CTI. However, the fact that the CTI increased over time similarly inside and outside of PAs may suggest that the Finnish PA network is still able to support the community of cold-dwelling species that was largely meant to protect. This community is nevertheless undergoing rapid change within PAs, which may reduce their value for covering cold-dwelling species in the future. Furthermore, the lag in community responses to increasing temperatures evident within and outside of PAs also highlights the importance of landscape level approaches for conservation beyond the boundaries of current PAs.

Previous evidence suggests that species range shifts, as well as changes in CTI, are most striking in areas undergoing fastest warming, such as those at high latitudes (Chen *et al.*, 2011; Tayleur *et al.*, 2016). We did not find evidence that this could be the case in Finland during the study period considered, as CTI appeared to increase over time similarly across the whole country (Fig. 2). A possible explanation for this result could be that in the north of the country, where temperatures are increasing most rapidly, the coverage and size of individual PAs are also largest compared with the situation at southern latitudes (Virkkala & Rajasarkka, 2007). Thus in the north, the large coverage provided by the PA network may counterbalance the impacts of more rapid climate change, ultimately masking otherwise visible patterns as observed in other countries (e.g. France; Gaüzère *et al.*, 2016). To this end, one might interpret our results as indicative of positive impacts of PAs at northern latitudes under rapid climate change. Larger PAs in the north may, for example, allow more possibilities for the cold-dwelling species to find suitable climatic conditions within the protected habitat. This may allow these species to persist in the area despite

changed climatic conditions (Cantú-Salazar & Gaston, 2010; Thomas & Gillingham, 2015).

In a recent study, Gaüzère *et al.* (2016) have shown that PAs in France can contribute to mitigate the impacts of climate change on birds, with strongest effects being apparent on northernmost species associated with colder thermal niche. Our results from the relative density shift in northern species are not apparently in line with those from France. Our findings in fact suggest that northern species have declined inside PAs, whereas southern species have increased inside, but also similarly outside of PAs, during the study period. These results are, however, in line with a previous study from Finnish PAs, suggesting that, over the past two decades, northern bird species declined and southern species increased in density (Virkkala & Rajasärkkä, 2011). These shifts are in line with the projected range shifts of those species groups under a warming climate (Virkkala *et al.*, 2008) and also provide partial support to recent findings from Sweden showing that overall changes in CTI are due to, among others, the extirpation of cold-dwelling species (Tayleur *et al.*, 2016). It is, however, important to notice that, although northern species have declined inside PAs, these areas are still able to support larger densities of northern species compared with unprotected areas, particularly at lower latitudes. Overall, we found some evidence, albeit inconclusive, that PAs may play a role in maintaining the community of cold-dwelling species. However, this effect appears stronger in the southern half of the country, which is in contradiction with our initial prediction of stronger buffering effects of PAs at northern latitudes. This may be explained by the fact that in Southern Finland the contrast in habitat quality (e.g. forest age and structure) within and outside of PAs is higher than in Northern Finland, and therefore, the effects of PAs may be more measurable in the south compared to the north. Because the PA network is sparsest in the south (Virkkala & Rajasarkka, 2007), increasing the amount of PAs in the southern part of the country could slow down the retraction of northern species. However, we also found that the effect of latitude is stronger than the effect of PA coverage in shaping CTI and also that CTI trends of the whole community are similar to those of forest-associated birds. This suggests that, while PAs and habitat-specific conservation approaches are important for preserving biodiversity in the short term, ambitious policies to mitigate climate change will be key to prevent future community and ecosystem disruptions.

Protected area networks have been found to play different key roles in biodiversity conservation under rapid climate change. Evidence on the role of PA networks in facilitating species range shifts by acting as stepping stones of favourable habitat during transition has been well documented (Thomas *et al.*, 2012; Gillingham *et al.*, 2015b; Thomas & Gillingham, 2015). Similarly, PA networks have been shown to have some levels of resilience against climate-driven changes (Gillingham *et al.*, 2015b; Thomas & Gillingham, 2015). Ultimately, whether PAs should facilitate the colonization by new species or retain the current species pool is an open question (Thomas & Gillingham, 2015). Achieving a sustainable balance between the above two key functions of PAs will likely depend on the biogeography of a given region, on key life-history traits (e.g. dispersal ability) of the species considered and on the conservation objectives. At the poleward edges of continental land masses (such as northern Europe and Fennoscandia) and for highly vagile species, such as birds, it is perhaps most important that PAs function more as retention for northern and cold-dwelling species rather than as a stepping stones facilitating range shifts of southern and warm-dwelling species (Thomas & Gillingham, 2015).

To this end, our results may sound encouraging for the conservation of northern bird species in the short term as they are still relatively well represented inside the Finnish PA network. However, the increase in the CTI of the community of all bird species coupled with the decline in density of northern species within PAs must be taken as an alarm call. Northern and cold-dwelling species have shown the steepest declines across Europe (Jiguet *et al.*, 2010), and in Finland, they are projected to lose much of their range due to rapid shifts in thermal conditions (Virkkala *et al.*, 2008; Lehikoinen & Virkkala, 2016). Moreover, northern species are typically migratory species that also face a range of important threats across their life cycle and are often poorly covered by PAs (Pavón-Jordán *et al.*, 2015; Runge *et al.*, 2015). At northern latitudes, cold-dwelling species may soon be driven outside of PAs, if the patterns we present here for the past 40 years will continue into the near future. However, at northern latitudes rapid and widespread changes in land use, triggered by forest logging and peatland conversion, are eroding habitats available for northern species to move in the near future. Ultimately, it will be of crucial importance that authorities will start already now planning for possible expansion of the PA network at high latitudes, as well as implementing sound management actions on unprotected land, before suitable future habitats are lost due to land-use change (Pouzols *et al.*, 2014).

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Supporting Information

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

Table S1. List of 128 species used to calculate the community temperature index, as well as the list of southern and northern species, and forest associated species used for further analyses (see main text).

Table S2. Best ranked models (ΔAICc < 4) used for the multi-model averaging and inference for the model on community temperature index (CTI) based on all 128 species.

Table S3. Results derived from averaging across the best ranked models (ΔAICc < 4; listed in Table S2) used for explaining community temperature index (CTI) based on all 128 species.

Table S4. Best ranked models (ΔAICc < 4) used for the multi-model averaging and inference for the model on relative density based on southern species only.

Table S5. Results derived from averaging across the best ranked models (ΔAICc < 4; listed in Table S6) used for explaining relative density based on southern species only.

Table S6. Results derived from averaging across the best ranked models (ΔAICc < 4) used for explaining CTI based on forest associated species only.

Table S7. Results derived from averaging across the best ranked models (ΔAICc < 4) used for explaining change in CTI from the 1970s–80s to the period 2000–2014 based on all bird species in the community.

Table S8. Results derived from averaging across the best ranked models (ΔAICc < 4) using as the response the CTI based on observations from within protected areas (PAs) only across Finland.

Table S9. Results derived from averaging across the best ranked models (ΔAICc < 4) used for explaining relative density based on central species (i.e. species with central distribution within Finland) only.

Figure S1. Change in community temperature index (CTI) considering the 65 forest associated species across Finland.

Figure S2. Predicted change in community temperature index (CTI) and in mean temperature across Finland from the 1970s–80s to the period 2000–2014.

Figure S3. Change in the sum of relative density (on the log scale) per square considering central species (i.e. species with central distribution within Finland) along the latitudinal gradient (south to north towards the right) across Finland separately by period and protection classes.