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Diversity and Distributions

BIODIVERSITY RESEARCH

Can protected areas mitigate the impacts of climate change on bird's species and communities?

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ABSTRACT

Aim Protected areas (PAs) are the mainstay of our conservation strategies. While they may succeed in locally preventing species and habitat degradation due to human activities, their ability to mitigate the impacts of climate change on biodiversity is still debated. We assessed whether community and species responses to climate change were related to PAs by testing three main predictions: (1) the thermal adjustment of community composition to temperature changes should be positively related to the proportion of PAs, (2) the species that benefit most from PAs should be less impacted by temperature change, and (3) the species *a priori* considered the most vulnerable to global change should be even more sensitive to the mitigating effect of PAs.

Location Mainland France.

Methods Data from a long-term, large-scale standardized monitoring programme, recording annual changes in the abundance of 116 breeding bird species in France between 2001 and 2012, were used. Local temporal trends in spring temperature, community reshuffling and bird populations over the country were estimated with a moving window approach (2094 spatial windows). Generalized additive mixed models were then performed to relate these responses to the local proportion of PAs.

Results Most PAs promote community adjustment to temperature changes. At the species scale, our results show that the more a species benefited from PAs, the less vulnerable it was to temperature changes. PAs were also more effective in mitigating the impact of climate change on the less common and northernmost birds.

Main conclusion Protected areas do seem to mitigate climate change impacts on species and communities. Our study argues for the use of integrative frameworks at different biological scales to assess the usefulness and relevance of PAs faced with climate change and suggests that PAs remain key effective conservation strategies in a changing climatic world.

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INTRODUCTION

Protected areas (PAs) are the mainstay of our conservation strategies and play a key role in the mitigation of human-induced threats (Rodrigues *et al.*, 2004). Threatened species or habitats are regarded as successfully managed when the processes negatively affecting their dynamics are removed or reduced. In this context, numerous studies have provided evidence that conservation areas are successful in mitigating many sources of disruption (Nelson & Chomitz, 2011). For instance, abundances of individual species and the diversity of species assemblages have been shown to be higher in PAs compared to their unprotected surroundings (Coetzee *et al.*, 2014). More specifically, a body of evidence suggests that PAs succeed in protecting biodiversity from habitat depletion (Andam & Ferraro, 2008), invasive alien species (Moseby *et al.*, 2009) and human exploitation (Gaston *et al.*, 2008).

However, human-induced global changes are not limited to these environmental disturbances. It is now acknowledged that the earth's climate has changed rapidly over the last fifty years, disrupting the geographical distribution of local climatic conditions (Ackerly *et al.*, 2010). Several studies have documented the numerous consequences of this climate change for biodiversity in almost all major functional and taxonomic groups, with some considering this pressure a major driving force of species decline and extinction (Parmesan, 2006). One of the most reported proofs is the stark distribution shifts of many taxa having already undergone rapid poleward and upward shifts (Thomas & Lennon, 1999; Parmesan & Yohe, 2003), while other continent-wide studies reported population declines (Gregory *et al.*, 2009).

While PAs may be effective in limiting human-induced disturbances of habitats, their ability to mitigate the impacts of climate change on biodiversity is still debated. PAs are by definition fixed and delimited in space. Therefore, climate-driven shifts in species distribution could invalidate conservation strategies relying on immutable areas devoted to conservation (Araújo *et al.*, 2011). However, this viewpoint is not necessarily straightforward. On the one hand, climate change is likely to chase many populations from fixed PAs, exposing them to additional threats (Hannah & Midgley, 2007; Coetzee, 2009; Hole *et al.*, 2009). On the other hand, populations living in PAs should be relatively less affected than unprotected ones. One can therefore expect protected ecosystems to be more resilient to climate change than ecosystems damaged by human disturbances (Srivastava & Vellend, 2005; Malhi *et al.*, 2008). Moreover, PAs could still be important tools for conservation by providing suitable areas that promotes colonization from and towards unprotected areas (Thomas *et al.*, 2012). While climate change may drive local species turnover in local PAs, the whole network of PAs could ensure biodiversity conservation at a larger scale. Conservation areas are likely to connect suitable areas (Mazaris *et al.*, 2013) and even promote the expansion of species ranges (Hole *et al.*, 2009; Thomas *et al.*, 2012). Which of these hypotheses should drive the future of our conservation strategies is currently unknown, and it is likely that they act together. Generally, the ability of PAs to mitigate the effects of climate change on biodiversity has rarely been tested (Mawdsley *et al.*, 2009). Yet, understanding where and how much PA could mitigate climate change impacts is central to conservation biogeography (Whittaker *et al.*, 2005).

Until recently, the investigation of these issues was limited by the absence of a robust analytical framework for relevant and fine-scale testing of hypotheses with a large taxonomic and spatial inference. For instance, most studies focusing on the effects of climate change on biodiversity have considered climate change a uniform warming and the associated linear trends in biodiversity dynamics at national (Devictor *et al.*, 2008; Davey *et al.*, 2012) or continental (Devictor *et al.*, 2012) scales. However, the impacts of climate change are the result of organism, population or community responses to local variations in climatic conditions, which are highly spatially heterogeneous at regional (Walther *et al.*, 2002) and local (Gaüzère *et al.*, 2015) scales. Therefore, how the spatial and temporal heterogeneity in temperature changes is linked to the spatial and temporal heterogeneity in population or community dynamics is still unclear (Walther *et al.*, 2002). A complex lattice composed of latitude, longitude, elevation, landscape and land use creates high variability in the rate and direction that isotherms shift through space and time (Loarie *et al.*, 2009). This variability is also true over time: temperature is mostly marked by yearly fluctuations rather than by a linear increase, particularly when considering the last decade (Coumou & Rahmstorf, 2012; Held, 2013).

Here, we propose a comprehensive framework tracking local changes in both community composition and species population related to local climate changes and the effect of PAs on these dynamics. Using the French Breeding Bird Survey (FBBS), a long-term and large-scale standardized monitoring programme, we investigated the ability of PAs to mitigate the impact of climate change by specifically testing three main predictions: (1) For a given change in temperature, a change in the community temperature index (CTI) reflects the community response to temperature change (increasing CTI indicates an increase in relative abundance of more thermophile species). Using this index, we expect that a thermal adjustment of community composition to temperature changes (i.e. how CTI change finely matches temperature change) in a given area should be positively related to the proportion of protected sites in this area. (2) Regarding the effect of PAs on population dynamics, we predicted that species which benefit most from PAs (i.e. the species for which PA has a positive effect on population trends) should be less impacted by temperature change (i.e. the negative effect of temperature change on their population trend should be mitigated). (3) Finally, we tested whether the ability of PAs to mitigate the impact of temperature change on species was distributed among three particular species traits expected to be related with the vulnerability of French breeding birds to global changes: the temperature preferences of species (Julliard *et al.*, 2003), their distribution breath (Godet *et al.*, 2015) and an integrative trait summarizing the life history of birds, the body mass (Owens & Bennett, 2000). We predicted that the PA mitigation should be more effective on the most vulnerable species (i.e. colder temperature preference, narrower distribution range and heavier species).

METHODS

Bird data

Data were obtained from the FBBS, a monitoring programme in which skilled volunteer ornithologists counted birds following a standardized protocol on the same plot, each year from 2001 to 2012 (Jiguet *et al.*, 2012). Species abundances were recorded inside 2 km × 2 km squares ($n = 2133$) whose centroids were located within a 10-km

radius of a locality specified by the volunteer (Fig. 1). To improve the representation of the diversity of habitats countrywide (Veech *et al.*, 2012), squares were randomly placed within the 10-km buffer. On each plot, volunteers carried out 10 point counts (5 min each, separated by at least 300 m) twice each spring within 5 weeks of the pivotal date of 8 May to ensure the detection of both early and late breeders. For a given plot point, counts were monitored in the same order on approximately the same date between years (± 7 days) and at dawn (within 1–4 h after sunrise) by a single observer. The maximum count per point for the two spring sessions was retained as an indication of point-level species abundance.

Climate data

Monthly means of 2-m air temperatures on an 8 km × 8 km grid were extracted from the SAFRAN meteorological model (Quintana-Seguí, 2008). These high-resolution monthly temperature data were matched to each of the 2133 2 km × 2 km squares monitored by the FBBS by relating each square centroid with the nearest centroid of climatic grid cells. From these data, the mean spring–summer temperature (April to August, in °C) for each of the monitored plots and years (Julliard *et al.*, 2004) was calculated to estimate the average temperature experienced by birds during their breeding season in each square each year.

Spatial distribution of climate change and protection level

A moving window approach was used in order to estimate several variables on a spatial continuum covering the whole study area. The principle lies in calculating particular metrics (see below) within a moving window delineated by a circle around a given monitored plot. The value of the estimated trend is then attributed to the central plot of the window. Then, the same process is repeated for all the plots in the studied area. Thereby, the temporal trends of each plot are estimated with values from the neighbouring plots. This approach is straightforward for summarizing locally spatial or temporal trends emerging from regional dynamics (Gaucherel, 2007; Gaucherel *et al.*, 2008) and has been used beneficially with this dataset (Devictor *et al.*, 2010; Godet *et al.*, 2015). More specifically, each plot was defined as the centre of an 80-km radius circle, encompassing at least 20 plots to ensure relevant estimations (Fig. 1). This approach provided 2094 spatial windows of similar spatial extent. Note that the chosen width resulted from a compromise between a sufficiently fine spatial resolution and the highest number of regions for the best cover of the study area. Within each of these windows and over the 12 years of the bird survey, two abiotic variables were first estimated: the change in mean spring temperature (T_s, see Table 1) over the period considered and the proportion of protected area (%PA, see Table 1).

Local temperature changes

In order to estimate the local temperature changes during the last 12 years in each window, we performed a linear regression of mean spring temperature over years as a continuous variable. Spatial autocorrelation was accounted for by implementing generalized least square models in which the spatial structure (exponential semi-variogram) was used to model the error term correlation structure. Note that the number of plots within windows varied (from 20 to 207, average ± SD = 89 ± 42). However, fixing the number of plots by a random sampling of 20 plots within each window did not qualitatively change our results.

Local proportion of protected area

Any area of the French national territory defined as National Parks (NP), Nature Reserves or Natura 2000 sites were considered as PAs. Nature Reserves are small and strictly PAs,
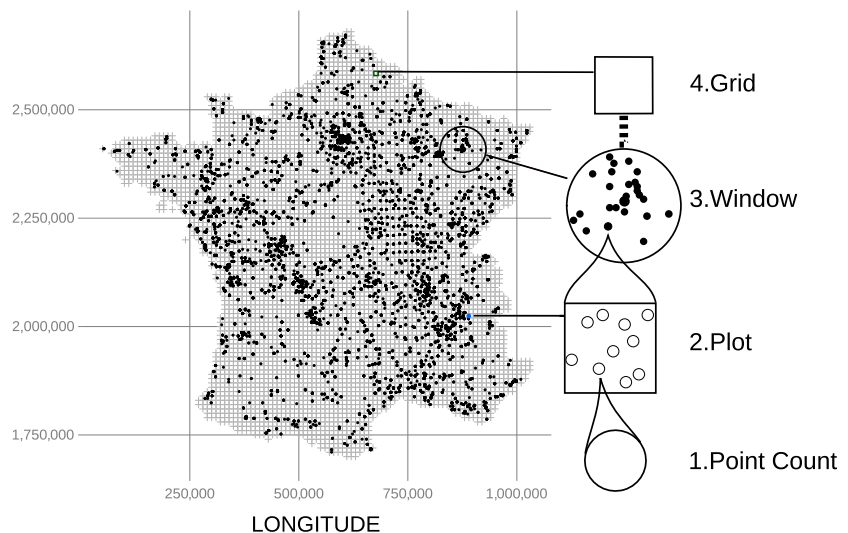

Figure 1 Spatial distribution of the plots monitored by the French Breeding Bird Survey and the spatial definitions considered. Ten point counts (1) were performed within each of the 2133 plots (2). Secondly, each plot was considered the centre of an 80-km radius window (3) containing at least 20 plots. Indices calculated for the 2094 regions retained were interpolated to 10 km × 10 km pixels (4) covering the whole country to obtain continuous maps for illustration.

Table 1 Summary of the variables used.

Variable	Abbreviation	Description	Biological meaning
Mean spring temperature	T_s	Averaged monthly mean temperature between April and August (in °C) within a site for a given year	Temperatures locally experienced by birds during their breeding
Percentage of protected area	%PA	Proportion of protected land area within a window	The probability, for a bird living in a given window, of being protected from human-induced threats
Community thermal index	CTI	Community abundance-weighted mean of the STI within a site for a given year	The relative abundance of cold versus hot dweller species within a community
Community thermal adjustment	CTA	Difference between change in CTI and change in mean spring temperature while considering the magnitude of these changes within a window	The accuracy of the community reshuffling induced by mid-term temperature change
Species thermal index	STI	The average temperature experienced by a species across its geographic range during the breeding season	The thermal preference of each bird species
Species thermal response	STR	The slope between the local species trends and the local temperature changes	The response (negative to positive) of the species population dynamics to temperature change
Species thermal sensitivity	STS	The amount of variance (*r*-squared) of the local species trends explained by the local temperature changes	The sensitivity of the species population dynamics to temperature change
Species protected area response	SPAR	The slope between the local species trends and the proportion of protected land area	The response (negative to positive) of the species population dynamics to protected areas
Species protected area sensitivity	SPAS	The amount of variance (*r*-squared) of the local species trends explained by the proportion of protected land area	The sensitivity of the species population dynamics to protected areas

usually managed for the protection of local threatened species or habitats. National Parks are large PAs, mostly located in mountains where traditional land use is preferred and human disturbance is strongly restricted. Natura 2000 is a Europe-wide ecological network of sites needing appropriate management (generally low-intensity agricultural practices) to be maintained in a 'Favorable Conservation Status'. Natura 2000 sites were designated by application of the Birds Directive of the European Union (79/409/EEC, amended 2009: 2009/147/EC) and the Habitats Directive of the European Union (92/43/EEC, consolidated 2007). We consider that, combined together, these PAs form a network of sites more likely to be favourable to biodiversity (as implicitly or explicitly assumed by their designation and management) and therefore to bird populations.

Relating community adjustment to climate change to protection level

To measure how community composition was affected by temperature, we first calculated a community-weighted mean reflecting the relative abundance of cold versus hot dweller species within a community for a given plot and year. Then, we estimated the temporal trend of this index over the last 12 years within each window. Species were first discriminated along a gradient of cold- to hot-dwelling species using

the species thermal index (STI, expressed in °C; see Table 1; Devictor *et al.*, 2008). Defined for each species, the STI is a species characteristic representing the thermal preference of each bird species. It corresponds to the average temperature experienced by a species across its geographic range during the breeding season. STI values were computed from 0.5° × 0.5° temperature grids (April–July averages for the period 1950–2000; Worldclim database, http://www.worldclim.org) coupled with Western Palaearctic species distributions at a 0.5° resolution from the EBCC atlas of European breeding birds (Hagemeijer & Blair, 1997). Note that the absolute values of STI could vary according to the spatial scale considered. For example, limiting its estimation to French, European or Western Palaearctic atlas temperature cells could affect the STI value of specific species. However, this variation should not affect our analysis because a temporal variation in CTI depends on the relative specie's STI rather than on the absolute value of each specific STI, and both French and European STIs are highly correlated (Devictor *et al.*, 2008).

Then, STI values were averaged in a community thermal index calculated for each plot each year. This index (CTI, expressed in °C; see Table 1; Devictor *et al.*, 2008) is a community abundance-weighted mean representing the average STI of species. For a given community, the CTI is expected to increase following temperature increase if species adjust

their abundances according to the corresponding change in temperature. For each plot monitored each year, the surveyed birds were considered as a community of N individuals and R species, with P_i the relative abundance of species i and STI_i the STI value of species i. The CTI value was computed as $CTI = \sum(P_i \times STI_i)$. Finally, the temporal trend in CTI was estimated within each window following the same model structure described for the estimation of T_s temporal changes, with CTI as the explained variable.

In order to assess whether bird communities adjusted their thermal composition (CTI) to the changes in T_s over the period considered (2001–2012), we computed, for each window, a metric called the community thermal adjustment (CTA, see Table 1) as $CTA = (\max((dC - dT)) - (dC - dT)) \cdot (dC + dT)$ where dC and dT are the scaled value of the CTI and spring temperature temporal trend, respectively. The CTA reflects the difference between the change in CTI and the change in T_s (the lower difference, the higher CTA value: $\max((dC - dT)) - (dC - dT))$ while considering the magnitude of these changes ($dC + dT$). CTA values were normalized to the range [0, 1] so they equalled c. 0 for a community that showed no CTI change related to temperature change, and/or for a community that did not experience temperature or CTI changes over the study period. CTA values tended towards 1 for communities showing the greatest changes in CTI in response to the greatest changes in spring temperature. For a more visual representation, see Fig. 2.

Finally, whether and how the thermal adjustment of community composition to temperature changes in a given area was related to the proportion of protected land in this area was tested. To do this, we implemented a generalized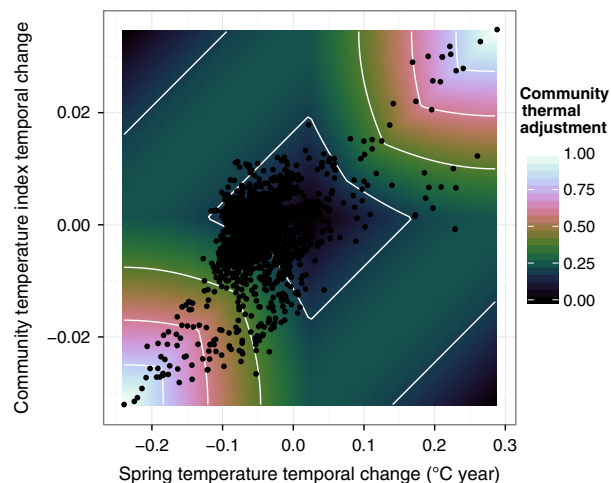 additive mixed model (GAMM) estimating the linear effect of the proportion of PA on community and population adjustment in windows, while taking into account structural spatial gradients over the country using smooth terms of geographical coordinates and the random effect of biogeographic domains. More specifically, the CTA (i.e. calculated for each window, $n = 2094$) was the response variable and the proportion of PA (log-transformed, also calculated for each window) was the explanatory variable. In order to avoid a skewed response variable and meet the assumption of its normality, the CTA was transformed by a hyperbolic arc-sine function (Fig. 3). Biogeographic domains (Mediterranean, Continental, Alpine, Atlantic) were declared as random effects to account for the variability in the climate and species regional pool between these areas. The non-independence in the data, yielded by inherent spatial autocorrelation, was included in the model by integrating the geographical coordinates in isotropic smooth terms with a free degree of freedom, according to the method of Wood (2006). Mountains areas are characterized by strong variations of temperature within a small distance which are known to promote the species tracking of climatic variations in space (Araújo et al., 2011; Regos et al., 2015; Thomas & Gillingham, 2015). In order to test whether and how elevational gradient was modulating the effect of %PA on CTA, we performed supplementary analysis assessing the effect of %PA while controlling for the effect of the elevational gradient.

Relating species responses to climate change with protection level

The response and sensitivity of a species to temperature change and to PA were assessed by estimating the extent to which their population growth rate was driven by these environmental variables. First, we estimated the local population trends of species by modelling the change in abundance for each species within each window using generalized linear mixed models. The species abundance was the explained variable, regressed over a continuous fixed effect of year (2001–2012) with a factorial random effect of the plot. The coefficient of the fixed effect of year thus provided the average growth rate of populations of each species within each window over the 12 years of the survey. To ensure reliable population trends, we limited our analysis to the species–window pairs that included at least one hundred occurrences of birds. However, each trend was not estimated with similar confidence because of the variability in the number of observations and monitored plots. We therefore accounted for the standard error associated with each trend in subsequent analyses.

Secondly, we calculated the species thermal response (STR, Table 1) and the species protected area response (SPAR, Table 1) for a given species as the slope coefficient of the population growth rate regressed over the absolute spring temperature change or the proportion of PA among our 2094 windows. The STR value was positive for species showing an increase in population related to spring

Figure 2 Community temperature index temporal change (CTI, y-axis) versus mean spring temperature temporal change (x-axis) calculated in each window of 80-km radius composed of 20 plots, $n = 2094$. Black dots represent the slope coefficient of the linear temporal trend calculated over the 2001–2012 period. The coloured background represents the surface value of CTA (the brighter the colour, the higher the value and conversely) along the CTI and mean spring temperature change values.
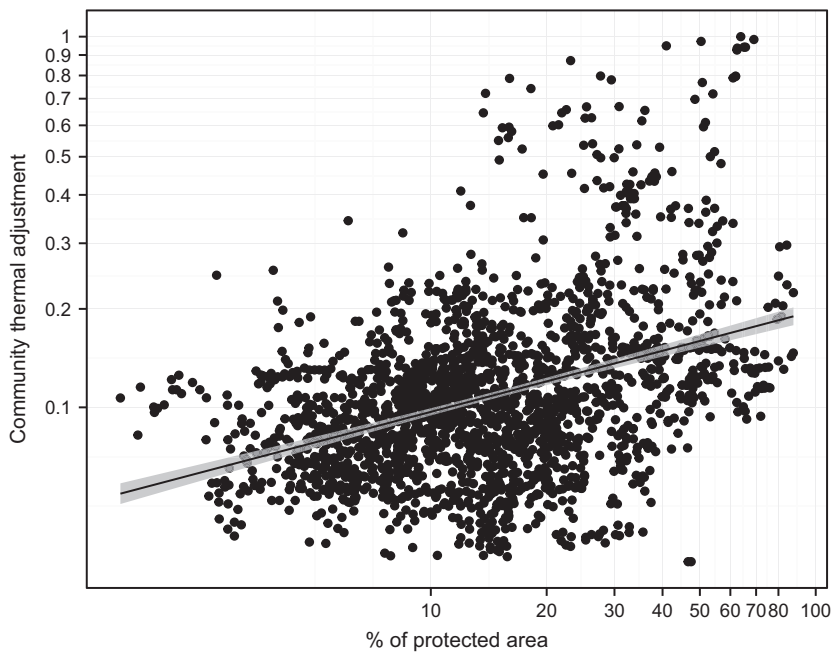
Figure 3 Community thermal adjustment (CTA, *y*-axis) versus percentage of PA (*x*-axis) calculated in each window of 80-km radius composed of 20 plots, *n* = 2094.

temperature changes, negative for species showing a decrease in population related to spring temperature changes and tended to 0 for species unaffected by temperature. The species thermal sensitivity (STS, Table 1) was defined as the *r*-squared associated with the regression coefficient. STS is an additional measure of how the population dynamics of a species are sensitive to temperature change, independently of the direction of this change. Its value was *c.* 0 for species whose population dynamics were not sensitive to temperature change, and tended to 1 for species whose population dynamics were totally explained by temperature change. Only the 82 species for which the population trends could be estimated within more than 400 windows were considered. This limitation ensured that all STR, STS, SPAR and SPAS values were estimated along the entire gradient of temperature change and PA. We predicted that species that benefit most from a PA should be less impacted by temperature change than others. In other words, we expected species with the highest SPAR values to have null to positive STR values. To test this assumption, we first performed a linear model using the STR as the explained variable and the SPAR as the explanatory variable taking into account a correlation structure imposed by the phylogenetic relatedness among species (extracted from Thuiller *et al.*, 2011). To take into account not only the response, but also the sensitivity of species to temperature changes, we integrated the STS of each species (i.e. the *r*-squared of the linear regression between population trends and temperature changes) as a weight in this model.

Thirdly, we investigated whether and how this species-specific relationship was different according to species' characteristics. We particularly focused on three species traits known to be related to species' vulnerability to global changes (Julliard *et al.*, 2003). Indeed, different species are

expected to respond differently to global change depending on particular traits. For instance, the southerly/warm-dwelling species are known to be less negatively affected by climate change than the northerly/cold-dwelling ones (Jiguet *et al.*, 2007), and the species with broader distribution ranges are increasing their relative abundance (Godet *et al.*, 2015) in response to global changes. We also considered the body mass as an integrative trait representing the life history strategy of birds and previously identified as a predictor of bird's extinction risk (Owens & Bennett, 2000). These traits were, respectively, given by (1) the STI (see above), (2) the species range index (SRI), and (3) the log-transformed species average body mass (BODYMASS). The SRI was calculated as the number of plots in which the species was detected over the period considered in the FBBS (Godet *et al.*, 2015). This index is highly correlated with different range sizes, estimated with a commonly used breeding bird atlas, and has been recently described as an integrative metric of the commonness of birds (Godet *et al.*, 2015). The log-transformed average body mass was calculated using data from the French ringing database, a proxy for most life history traits in birds describing their biodemographic strategy (Jiguet *et al.*, 2007). The effect of each trait was successively tested in a phylogenetic linear model relating the STR to the SPAR in interaction consecutively with the STI, SRI and BODYMASS of species.

RESULTS

Protected area effect on community thermal adjustment

Firstly, plotting the CTI temporal trend over the spring temperature temporal trend estimated within each window

showed a strong positive correlation between these two variables (Fig. 2). This result suggests that bird communities were finely tracking the temperature changes in space and time. A previous study has addressed this result more thoroughly (Gaüzère *et al.*, 2015); thus, here we focused more on how this relationship could be used to asses a CTA index. Seventy-two percent of windows experienced a null to moderate change in temperature (< 0.07 °C year^{-1}) over the period considered, and generally exhibited a null to slight positive or negative change in CTI, which corresponded to a low CTA value (i.e. < 0.25). The windows experiencing greater changes in temperature generally showed a fine response of CTI and thus depicted a gradient of CTA (from 0.25 to 1) depending on how the communities were finely adjusted (distance to the 1:1 slope) and the magnitude of CTI or temperature changes.

Secondly, our analysis showed that CTA increased with the increasing proportion of PA within a window (Fig. 3). The maps provided in Fig. 4 suggested that CTA was not consistently related to the proportion of PA at a local scale, with some large PAs being clearly related to high values of CTA, and others not (Fig. 4).

When looking at the national scale, the maps also suggested that a diffuse spatial gradient (from NW to SE) could have partly driven the overall relationship shown in Fig. 3. However, the GAMM performed to test the relationship between CTA and %PA and taking into account this spatial pattern still showed a significant and substantial effect of the proportion of PA on the CTA ($t = 5.06$, res.d.f. = 2064, $P < 0.001$, fixed effect marginal $R^2 = 0.08$). Removing the windows exhibiting the lowest temperature changes for which no CTI changes were expected (i.e. temperature changes < 0.07 °C year^{-1} following Gaüzère *et al.*, 2015) strengthened the positive relationship between CTA and %PA (Fig. S1 in Supporting Information). The supplementary analysis performed to control for the effect of topography

revealed that the effect of elevational gradient on the CTA was strong and significant (coef $\pm$ SE = 0.25 $\pm$ 0.03, $t = 8.22$, $P < 0.001$). The effect of %PA on the CTA was weaker when elevational gradient was considered as a covariable, but still highly significant (coef $\pm$ SE = 0.18 $\pm$ 0.01, $t = 10.08$, $P < 0.001$). Note also that the relationship between CTA and %PA was similar when considering windows with increase or decrease in spring temperature over the period considered (Fig. S2).

Protected area effect on species thermal response

The species responses to temperature changes (STR) and the proportion of PAs (SPAR) were positively related ($t = 2.8$, d.f. = 80, $P = 0.006$, adjusted $R^2 = 0.08$), especially when considering the sensitivity of species to temperature changes as a weight in our model ($t = 7.04$, d.f. = 80, $P < 0.001$, adjusted $R^2 = 0.38$, Fig. 5). This relationship was particularly driven by a limited number of species that experienced marked negative responses to both temperature changes and PAs, suggesting that species that benefit from PAs are generally less vulnerable to temperature changes than species negatively responding to PAs (Table S1).

Traits mediating the protected area effect on species thermal response

Our analysis showed that the effect of SPAR on the STR was significantly greater for low STI values (SPAR : STI interaction term = -76.7 ± 29.6, $t = -2.5$, $P = 0.012$*), low SRI values (SPAR : SRI interaction term = -117.1 ± 42.73, $t = -2.74$, $P = 0.0076$**). Although non-significant, higher BODYMASS were weakly increased the effect of SPAR on the STR (SPAR : BODYMASS interaction term = 71.04 ± 39.3, $t = 1.80$, $P = 0.074$). See Fig. 6 for a visual representation of these interaction terms.
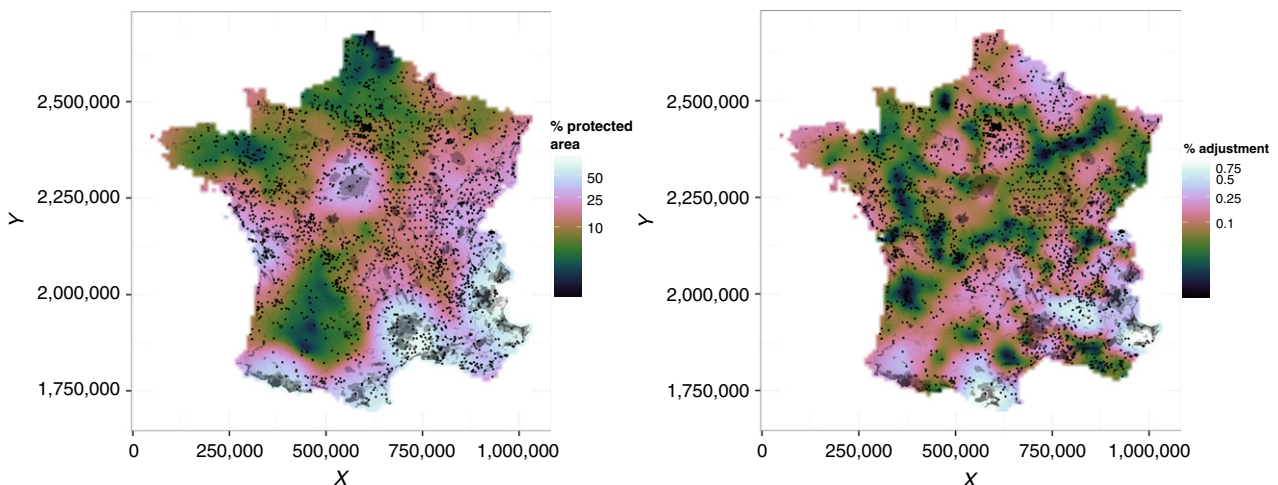

Figure 4 Spatial interpolations of percentage of PA (left panel) and CTA (right panel) calculated for each window of 80-km radius. The brighter the colour, the higher the value, and conversely. Black dots represent centres of windows used to perform spatial interpolations. Grey shaded areas delimit the PAs used to compute the percentage of PAs within each window.
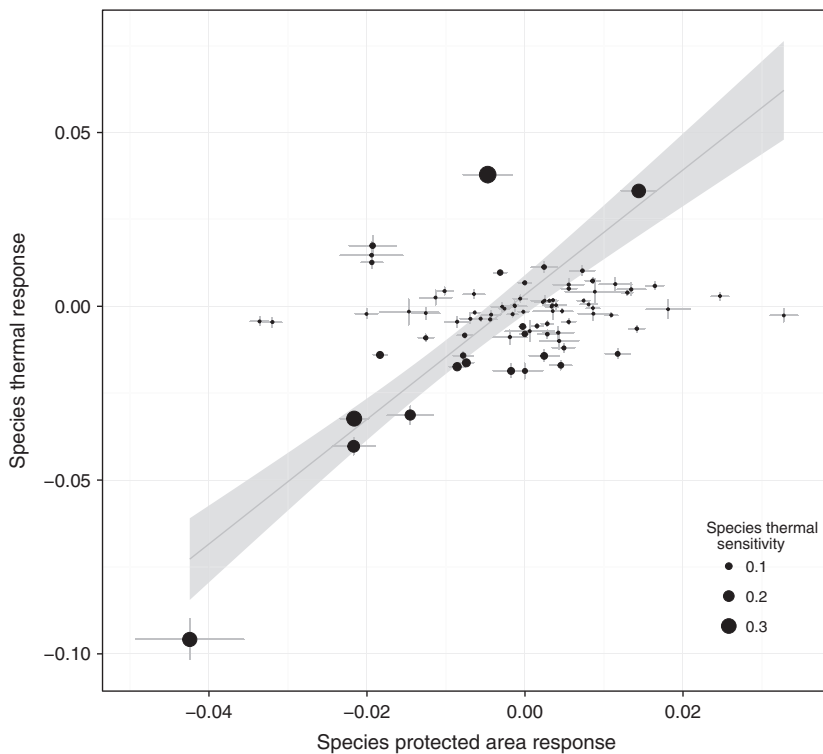
Figure 5 Species thermal response (STR, *y*-axis) versus species protected area response (SPAR, *x*-axis) calculated at a national scale. Dots represent estimates of slope coefficients from the linear model relating population trend and temperature change or PA for STR and SPAR, respectively. Horizontal and vertical lines represent standard errors associated with each slope coefficient. Dot sizes represent the species thermal sensitivity (STS) calculated as the *r*-squared associated with each slope coefficient.

DISCUSSION

Protected areas are successful in mitigating the impacts of climate change on birds

In this study, we investigated a crucial but still debated question for conservation biogeography: can PAs mitigate the impacts of climate change on biodiversity? To do so, we developed one of the first comprehensive frameworks tracking local changes in both community composition and species population related to local climate changes with a particular focus on the effect of PAs on these dynamics. We did not focus our analysis on the plot scale effect of protection, but rather on a landscape to regional effect of the amount of PAs within a given zone. Our results suggest that communities located in more PAs are more likely to adjust their composition in response to large temperature variations. At the species scale, we first showed that common breeding birds were generally less vulnerable to climate change when they benefited from PAs. We then highlighted that the ability of PAs to buffer species vulnerability to climate change was stronger for northernmost (colder thermal niche), less common and heavier species. Our analysis succeeded in relating a spatially explicit community response to species-specific dynamics at a national scale over a 12-year period. The community and species-scale results complementarity addressed two different issues, but revealed consistent results. Overall, this study suggests that PAs could constitute crucial spatial refuges and population sources for birds facing climate change.

Community adjustment to temperature changes: a fortunate outcome of conservation strategies

We first computed a metric describing the ability of communities to adjust their composition when experiencing temperature changes and showed that communities situated in the most protected areas were the most able to track temperature changes. Our metric, called the CTA, is based on several assumptions that need to be clarified. First, the variation in the CTI, a measure of the relative proportion of warm versus cold dwellers within a community, only indicates how the turnover of species is influenced by climate changes. In fact, we previously showed that only large temperature variations triggered CTI changes (Gaüzère *et al.*, 2015). This could suggest that any absence of community response is due to a lack of sensitivity of most species to slight changes in temperature (Rodríguez-Sánchez, 2012). In other words, if species did not reach their limit of phenotypic and phenological plasticity, they might not need to track spatially changes in temperature. Therefore, the lowest values of CTA could be the result of a true inability to track climate change spatially or an insensitivity to weak variations in climate conditions. However, the largest community-scale adjustments to temperature resulted from local colonization–extinction dynamics at the species population scale. Obviously, these dynamics are not only influenced by climate changes. Habitat and thermal niches are not totally independent (Barnagaud *et al.*, 2012) and CTI can therefore be influenced, at least to some extent, by changes in landscape structure and composition potentially blurring the net effect of climate change (Clavero *et al.*,
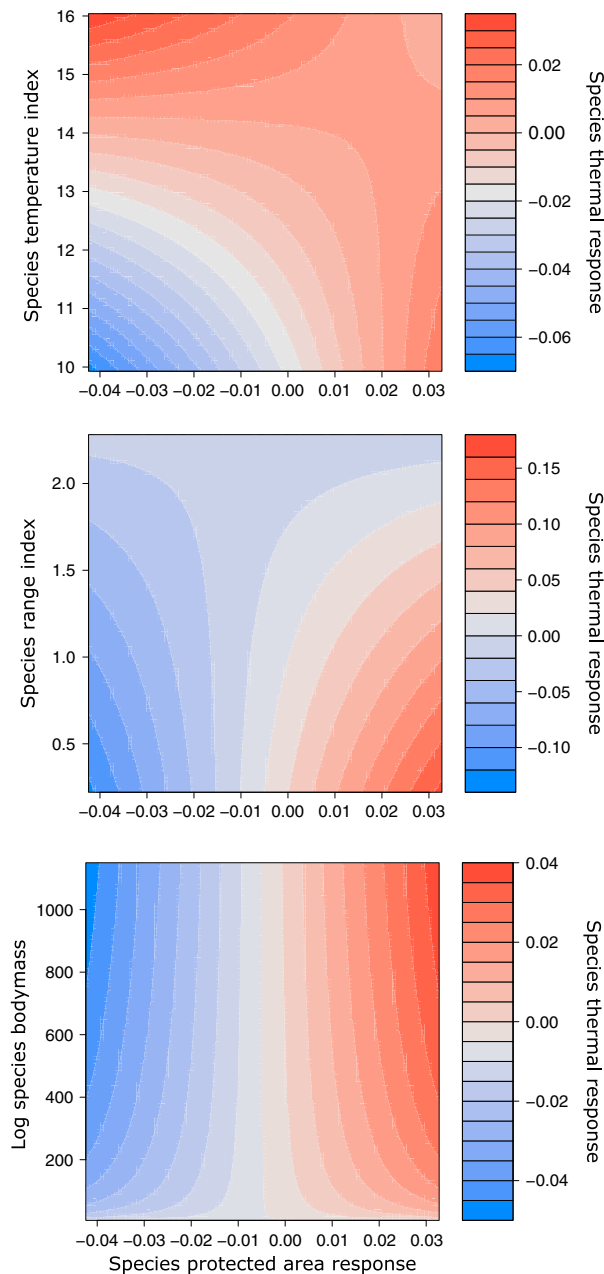
Figure 6 Filled contour plot showing the effect of the interaction between traits and species protected area response (SPAR) on the species thermal response (STR). *y*-axis: species temperature index (upper panel), species range index (middle panel) or body mass (lower panel). *x*-axis: species protected area response. Colour-filled surface: species thermal response, the warmer the colour, the higher the value, and conversely.

2011). Although recent analysis on the local-scale congruency between temperature and CTI changes showed that such bias are likely to be limited (Gaüzère *et al.*, 2015), a future development of our work lies in the investigation of the synergy of climate versus land use changes on the local change in CTI (Tayleur *et al.*, 2015).

Here, we observed that community adjustment to temperature change in a given zone benefited from the proportion

of PA in this zone. This result could be explained by fewer and relatively weaker human-induced disturbances in PAs. In accordance with this result, Coetzee *et al.* (2014) have recently analysed 30 years of studies comparing biodiversity characteristics inside PAs with those in surrounding areas. This meta-analysis identified overall higher species richness and population abundances in PAs, especially for European birds. This enhancement of coarse but indicative ecological properties seems related to the intrinsic characteristics of PAs. The best and more diverse pre-existing habitats are most likely to be protected, and this status subsequently protects them from anthropogenic disturbances. These particular habitat conditions are also likely to promote local colonization events within PAs (Thomas *et al.*, 2012) which could, in turn, explain the observed increase in CTA.

However, our results were partly based on a strong northwest to south-east gradient supporting the increase in both PAs and CTA. Thus, it is hard to consider the greater adjustment of most PAs as a direct process-based consequence of this protection. Instead, this congruence must be seen as a fortunate outcome of our conservation strategies. The Mediterranean Basin and surrounding mountains (Pyrenees and Alps) are known to be particular biogeographic regions. First, these regions generally shelter steep topography at landscape level, a well-known promoter of biodiversity response to climate variations in space. Indeed, marked elevational gradients create strong variations of temperature within small distances, lowering the velocity of climate change in this area (Loarie *et al.*, 2009) and finally facilitating the thermal reshuffling of communities (Bertrand *et al.*, 2011). However, PAs were still promoting the community adjustment to temperature variations when we controlled for the specific effect of the elevational gradient. In these highly protected regions, the palaeogeography and historical land use have created a complex mosaic of habitats (Médail & Quézel, 1999; Myers *et al.*, 2000) providing high levels of diversity (Devictor *et al.*, 2010). Conversely, northern areas of France are less diversified, which is probably related to the marked landscape homogeneity of this region dominated by farmland. Overall, conservation areas are generally designed to protect valuable biodiversity hotspots (Myers *et al.*, 2000), which are usually particularly diverse ecosystems, providing more micro-habitats and thus micro-climates for species and communities to adapt to global changes. These intrinsic characteristics, added to their conservation status, probably contribute to explain the promotion of the local colonization of species from and towards PAs leading to a higher CTA locally.

Species responses to PAs facing climate change

In the second part of our study, we estimated the species response and sensitivity to the proportion of PA and the magnitude of local temperature variation over the last decade. We found that species whose populations did not positively respond to PAs were the most vulnerable to climate change (i.e. species that have a negative response and a high

sensitivity to temperature change). Climate change is known to drive a large part of the dynamics of population trends (Johnston *et al.*, 2013) and distribution ranges (Chen *et al.*, 2011). While many studies have addressed the effects of such changes on conservation strategies (Araújo *et al.*, 2011; Hole & Huntley, 2011), the ability of PAs to mitigate these impacts has rarely been investigated (but see Pavon-Jordan *et al.*, 2015), particularly when looking at multispecies population trends. Here, we provide evidence for a buffering effect of PAs on the vulnerability of French breeding birds facing climate change. The positive effect of PAs on common birds has already been described (Devictor *et al.*, 2007), but whether or not this positive effect influences how species respond to temperature changes has, to our knowledge, never been investigated.

Moreover, this response was not randomly distributed among species: the northernmost and more specialist species were the most influenced by PAs. Again, the sustainable management of habitats and species in PAs probably explains our results. Specialization is an evolutionary response to habitat stability (Whittaker & Goodman, 1979; Futuyma & Moreno, 1988), and the management of disruptions within PAs has been shown to be effective in promoting greater habitat stability. Note, however, that this hypothesis should be confirmed by finer investigations of the relationships between habitat stability and PA, but relevant and high-resolution data on temporal land use changes are still lacking. Nevertheless, Canova (2006) and Meyer *et al.* (2015) showed that the process of habitat change (encompassing increasing urban areas, changes in farming and decreasing natural habitats) was substantially mitigated in PAs, and promoted higher species richness. Similarly, the greater stability of landscape dynamics is likely to explain the enhanced effect of PAs on specialist species. Secondly, these particular species characteristics of climatic niche and life history traits have been shown to indicate the vulnerability of birds facing global changes (Jiguet *et al.*, 2007). Therefore, it makes sense that those species mostly affected by global change are also most likely to benefit from the ability of PA to mitigate the adverse effects of climate change.

Implications for conservation biogeography

In a recent work, Inger *et al.* (2015) suggested that populations of the most common birds declined over the last 30 years, while those of less abundant species rose. This increase in rarer species is probably explained by the efficiency of direct conservation actions (Gregory *et al.*, 2005), while the dramatic drop in the most common birds is explained by land use change, particularly agricultural intensification (Donald *et al.*, 2006; Le Viol *et al.*, 2012). These results raise new challenges for our conservation strategies that lie in the conservation of common biodiversity. European conservation strategies relying on PAs generally target populations of locally rare species but have been reported as globally inefficient for protecting more common biodiversity

(Hoffmann *et al.*, 2010). In France, however, Devictor *et al.* (2007) and Pellissier *et al.* (2013) showed that common but declining bird species were benefiting from PAs. Our study considered a set of species limited to the most common breeding birds and distributed across the country. Although our results suggested that, within this set of species, the most specialized and less common species benefited most from PAs, these findings need to be extended to species with greater conservation issues for which PAs are established. Nevertheless, our results suggest that common French breeding birds actually benefit from PAs and that this protection is effective in mitigating the impact of climate change on these species. Overall, we argue that conservation strategies mainly based on the establishment and maintenance of fixed PAs could be more than ever relevant in the context of a declining common biodiversity faced with climate change.

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SUPPORTING INFORMATION

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

Figure S1. Community Thermal Adjustment (CTA, *Y*-axis) versus percentage of PA (*X*-axis) calculated in window where Spring Temperature temporal change was > 0.07 °C year^{-1}.

Figure S2. Community Thermal Adjustment (CTA, *Y*-axis) versus percentage of PA (*X*-axis) for increasing or decreasing temperatures.

Table S1. Values of each species specific responses (SPAR, STR, SPAS, STS) and their associated traits.

BIOSKETCHES

Pierre Gaüzère is undertaking a PhD in the BioDICée Team at the Institut des Sciences de l'Evolution de Montpellier. His research interests mainly focus on biodiversity responses to anthropogenic disturbances at macroecological scales, with a special attention on the impact of climate change on birds.

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Author contributions: P.G. and V.D defined the frame of the study, designed, conducted and interpreted the analysis. F.J. manages the database of the common breeding bird monitoring scheme in France. P.G. and V.D. led the writing in association with F.J.

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