



# A cross-taxon analysis of the impact of climate change on abundance trends in central Europe



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## ABSTRACT

Advances in phenology and pole- and up-ward shifts in geographic ranges are well-documented signs that species are responding to climate change. A deeper understanding of such responses across ecologically different species groups will help to assess future consequences for entire ecosystems. A less well-studied pattern linked with climate change is increases in abundances of warm-adapted species compared with cold-adapted species. To compare how recent climate change has affected the abundances of species across different taxonomic groups, we analyzed long-term local population trends and related them to the species temperature niche, as inferred from geographic distributions. We used population data sets collected in different regions of Central Europe, primarily Germany, for bats, birds, butterflies, ground beetles, springtails and dry grassland plants. We found that temperature niche was positively associated with long-term population trends in some of the taxonomic groups (birds, butterflies, ground beetles) but was less important in others (bats, springtails, and grassland plants). This variation in the importance of temperature niche suggested that some populations have been affected more than others by climate change, which may be explained by differences in species attributes, such as generation time and microhabitat preference. Our findings indicate that relating temperature niches of species to population trends is a useful method to quantify the impact of climate change on local population abundances. We show that this widely applicable approach is particularly suited for comparative cross-system analyses to identify which types of organisms, in which habitats, are responding the most to climate change.

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## 1. Introduction

Climate change is ranked alongside habitat loss as one of the major threats to biodiversity (Jetz et al., 2007; Sala et al., 2000).

Impacts of climate change have been reported in many taxonomic groups, with pole- and up-ward shifts in species geographic distributions and advances in phenology typically associated with climate change because it is the most likely cause (Callinger et al., 2013; Chen et al., 2011; Hickling et al., 2006; Parmesan and Yohe, 2003). As well as driving range shifts, climate change can affect local population abundances within species' ranges (Cahill

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et al., 2013; Parmesan, 2006; Saether et al., 2000) and, indeed, over most of the range, changes in abundance may be more apparent than changes in distribution. For instance, studying changes in the communities of breeding birds in France, Devictor et al., (2008) found evidence that changes in communities, consistent with climate change, were greater within species' ranges than at the edge. However, despite the implications of changes in abundance for local and global extinctions, there is still a poor understanding of the impact of climate change on population abundances of different species.

Multiple biotic and abiotic factors affect population dynamics, which complicates isolating the impact of climate change. Detailed single-species studies (Saether et al., 2000) and experiments (Biro et al., 2007) have proven to be useful approaches; however, they rarely allow extrapolation to the response of other species or whole communities. Species responses to environmental drivers can be predicted to depend on their traits, which determine how they interact with the environment (Luck et al., 2012; Webb et al., 2010). Trait-based analysis of population trends is a potentially powerful approach to develop a predictive framework of climate change vulnerability and, importantly, hypotheses can be developed about how traits modify species' response (Foden et al., 2013; Garcia et al., 2014). This approach can include both species traits, i.e., measurable at the individual level (Violle et al., 2007), as well as aspects of the realized niche, such as environment experienced over the geographic range (species traits and niche are hereafter referred to collectively as species attributes). In the context of climate change, a range of species attributes has been proposed as influencing species' response; however, many of these may also affect species' response to other drivers of biodiversity change, such as land use change (Foden et al., 2013; Garcia et al., 2014). Temperature niche is a key attribute that is expected to mediate the response of species to climate change (Deutsch et al., 2008; Kampichler et al., 2012) and has the advantage that it can be directly linked to climate change. A simple prediction can be made: if climate change affects local population abundances, temperature niche should be positively related to population trends.

Differences in the population trends of warm (or lower latitude) versus cold (or higher latitude) adapted species in a community have already been recognized as a "fingerprint" of climate change alongside changes in distribution and the timing of phenological events (Parmesan and Yohe, 2003) but have received less attention. Temperature niche has been shown to explain variation in the recent population trends of bird species within Europe (Jiguet et al., 2010b; Reif et al., 2011; Thaxter et al., 2010). Similarly, the proportion of warm-adapted species in communities of butterflies and birds throughout Europe (Devictor et al., 2008, 2012) and plants and lichens in parts of Europe (Bertrand et al., 2011; Tamis et al., 2005; van Herk et al., 2002) has increased in recent decades. It has also been speculated to be important for changes in abundance of other taxa, for example, freshwater fish and bumblebees (Daufresne et al., 2004; Rabitsch et al., 2010; Williams et al., 2007). More commonly, studies have focused on the relationship between population trends and species latitudinal distributions, which may to some extent act as a proxy for temperature niche, e.g. for fish (Holbrook et al., 1997), butterflies (Breed et al., 2013) and various marine invertebrate groups (Beaugrand et al., 2002; Sagarin et al., 1999; Southward et al., 1995), and their findings support the general assumption that higher latitude species show more negative population growth, while lower latitude species show more positive growth.

Exploiting these signs of the impacts of climate change and comparing the strengths of these signals across different species will enrich our understanding of how and why species are being affected. Such an analysis is essential for understanding the

widespread importance of climate change; identifying conservation priorities and understanding how communities as well as biotic interactions might change under climate change (Schweiger et al., 2010). Meta-analyses of advances in phenology have shown that taxa from terrestrial, marine and freshwater systems are all responding, but they have also suggested that plants (Thackeray et al., 2010) and amphibians (Parmesan, 2007) are responding the fastest. Range shifts have been reported to vary as much within as between major taxonomic groups (Chen et al., 2011) but were positively related with diet breadth in passerine birds (Angert et al., 2011) and mobility in butterflies (Pöyry et al., 2009), and negatively related with size and age at maturation in marine fish (Perry et al., 2005).

There has not yet been a joint attempt at a standardized assessment and comparison of the impacts of climate change on local population trends within species' ranges across major taxonomic groups. An important aim of this project was to extend the taxonomic groups beyond the well-studied ones, such as birds and butterflies. We include data for bats, ground beetles, springtails and dry grassland plants as well as birds and butterflies, collected in different regions of Central Europe, mostly in Germany. Using the relationship between temperature niche and population trends, we test whether there are generalities in the response of local population trends to climate change across different major taxonomic groups. Within each community (data set), we assume that species have been similarly exposed to climate change and therefore that any variation in species response is best explained by variation in species characteristics. Assuming that climate change acts as a long-term driver, we focus our analysis on long-term population trends. First, we test the prediction that increases in ambient temperature have favored the population growth of warm-adapted species over their cold-adapted community members. We control for variation explainable by habitat preference, which may covary with species temperature niche and thus confound patterns (Barnagaud et al., 2012; Clavero et al., 2011). Second, we compare the relative importance of maximum, mean and minimum temperature niche to identify the best predictor of population trends. Third, we discuss the factors that might be responsible for causing differences in the importance of temperature niche among the different data sets. For instance, generation time can be expected to affect how quickly population abundance changes as a result of individual responses to temperature.

## 2. Materials and methods

### 2.1. Population trend analysis

Each data set comprised species abundance data for multiple species in a community collected in on average 16 years (range: 6–32) over a 21 year time period (8–32) (further details on each data set provided below, additional descriptors in Table 1 with lists of species in Table S1 and a map showing the data set locations in Fig. S1). Most of the data were collected in Germany; however, the bird survey extended into Switzerland and Austria. The first step of our analysis was to estimate species long-term population trends. We aimed to make the analyses as similar as possible across data sets (taxa) but also to make some limited adjustments to address specific issues of some of the data sets. Because we always compared population trends within data sets, i.e., using species data that had been similarly collected, we assume that any difference in census collection methods does not affect the comparison of population trends of species within data sets (see discussion for consideration of how this might affect the comparison among data sets). We calculated the population trend of each species as the average annual population growth. In the standard analysis, these

**Table 1**

Basic descriptors of each data set showing the time span, number of census years, region, number of sites, and number of species from this data set included in our main analysis. All regions are within Germany, except Lake Constance, which also extends into Austria and Switzerland.

Taxa/dataset	Time span	#Census years	Region	#Sites (size)	#Species
Bats	1990–2011	22 <sup>a</sup>	Bavaria	310 roosts	11
Birds	1980–2002	3 <sup>b</sup>	Lake Constance	303 (4 km <sup>2</sup> )	130
Butterflies	1980–2011	32 <sup>a</sup>	Saxony	17 (c.132 km <sup>2</sup> )	28
Ground beetles	1998–2005	6	Middle Elbe	48 (100 m <sup>2</sup> )	69
Springtails	1986–2003	4/5 <sup>c</sup>	Baden-Württemberg	60 (25 m <sup>2</sup> )	46
Dry grassland plants	1980–2005	23	Near Halle	3 (1 m <sup>2</sup> )	11

<sup>a</sup> We included sites visited in at least 70% of census years.

<sup>b</sup> Censuses were conducted over three periods: 1980–1981; 1990–1992; 2000–2002.

<sup>c</sup> Censuses were conducted over 8 years in total but each site was visited in 4 or 5 of these years.

trends were estimated using a generalized linear model with Poisson errors including year (a continuous variable) and site (a factor) as predictor variables, as well as an autoregressive term to account for residual autocorrelation of counts as a function of time between censuses, which was fitted by Bayesian inference (Rue et al., 2009) using R-INLA (<http://www.r-inla.org/>). Because we were interested in the species long-term population trend, we only considered the linear trend over time and used the slope as an estimation of population trend. Our approach deviated slightly for the different data sets to be able to account for the possible additional but data set-specific issues affecting each one. Modifications to this standard analysis are given below.

Some of the data sets contained species only observed on a few occasions. Because the trends estimated for such species are less reliable, we applied two approaches to deal with this issue. First, in most cases, we restricted analyses to all species with a median regional abundance of five individuals or more across years (with the exception of the small data sets on bats and plants for which we used those with a median abundance greater than zero); however, we also repeated the analyses using consistent and lower thresholds, Fig. S2) and the results were similar unless indicated otherwise. Second, we used the inverse variance of the trend estimate as a measure of the uncertainty of the trend and as weights in the second step of our analysis in which we related trends to species attributes.

## 2.2. Data sets

Annual population data for bats were provided by a monitoring project coordinated by the Bayerisches Landesamt für Umwelt (Meschede and Rudolph, 2010) in Bavaria, Germany (see Table 1 for main descriptors). We used winter roost (cellars, mines and caves) census data collected by bat biologists and trained volunteers. Bats were counted individually by vision with strong lamps; all walls, ceilings and as many crevices as possible of the sites were systematically scanned. One census was made per roost per winter at a fixed week; in a small number of cases when an unusual weather episode affected either census ability or was suspected to affect bat hibernation behavior (e.g. warm weather delayed its onset), a second census was made later in the winter season and the maximum count of the winter censuses was used in the analysis. Because of the large variation in the number of years each site was visited, we restricted analysis to those visited in at least 70% of census years.

The Lake Constance bird atlas was collected by the international working group “Ornithologische Arbeitsgemeinschaft Bodensee” (Lemoine et al., 2007). We used the same data on regional abundance as Lemoine et al., (2007), in which regional abundance was calculated by summing the geometric mean of the abundance classes recorded in all census grids. We removed data for two non-native species (ring-necked pheasant, *Phasianus colchicus* and

Canada goose, *Branta canadensis*). Because of the fewer time points, we deviated from the standard analysis and calculated the population trend as the mean of log-transformed growth rate between the consecutive decadal censuses and then divided this by 10 in order to generate a comparable estimate of annual growth.

Butterfly data were provided by the Sächsisches Landesamt für Umwelt, Landwirtschaft und Geologie, based on observations throughout the year in Saxony, Germany collected mostly by amateur entomologists. Data sheets supplied included date, observer, German ordnance survey map grid, species and number of individuals observed. The data were filtered to identify the subset of the study area that had been most consistently surveyed. We excluded records submitted by those observers reporting just one species on a given date (because these data probably do not reflect observers undertaking a serious survey); without an observer ID and from sites that were visited in less than 70% of the census years. We focused on data collected between May and September because there was at least one record between these months in all years. Counts greater than 500 of the same species on the same day by the same observer were set to 500 because of uncertainty of the precision of such large counts (<0.001% of records). For species with a median regional average abundance of five or more across years, there were on average 15.8 complete observation records per year (range: 4.8–35.1). Because of the strong phenological patterns of abundance and variation in survey effort within and among years, as modifications to the standard analysis, we accounted for seasonal trends by adding month as a fixed effect and year as a random effect, with monthly total counts as the response. In addition, as this was not a standardized survey, we attempt to account for variation in effort over time by adding number of person-days (log-transformed) as an offset term.

Ground beetle population data came from the RIVA project, which conducted a standardized floodplain grassland survey in the Middle Elbe, Germany (Henle et al., 2006). Sites in humid grassland, dry, elevated grassland and intermediate grassland were sampled in September and October, with five pitfall traps per site separated by 5 m, retrieved biweekly (Gerisch et al., 2012).

Springtail communities were surveyed across forest sites in Baden-Württemberg, Germany. Sampling took place in spring, summer and winter in each census year, with three soil cores (diameter 6.2 cm, depth 4–8 cm) taken in each site at each sampling event (9 cores total per site and year). Microarthropods were extracted from the soil samples using a Macfadyen-type extractor for 10–14 d and collembola were sorted and determined to species level under a phase-contrast microscope.

Dry grassland plant species were surveyed near Halle, central Germany (Matesanz et al., 2009). The plant communities occurred on porphyritic outcrops within an agricultural landscape but were mostly unmanaged. Counts of the number of individuals of each species were made during spring or early summer in each site.

### 2.3. Species attributes

To provide a comparable temperature niche metric for all taxonomic groups, we approximated the temperature niche by using the usual species distribution modeling approach (Thuiller et al., 2008) of estimating the realized temperature niche based on broad-scale species distribution data. This has some support from studies incorporating data from physiological measurements of thermal tolerances (Calosi et al., 2010; Sunday et al., 2011). We aimed to use the best distribution data available while taking the same approach for a particular taxonomic group. Range map data for the birds and bats were taken from BirdLife international (BirdLifeInternational and NatureServe, 2012) and the IUCN (IUCN, 2012), respectively. Plant distribution range maps were compiled from published distribution maps (Meusel et al., 1992, 1978, 1965), occurrence data from the Global Biodiversity Information Facility (GBIF, <http://www.gbif.org>), national and regional floristic databases, and further maps from the floristic literature. Contiguous large areas of occurrence, where the species are reported to be very common, were generalized as range polygons; spatially isolated occurrences were digitized as single point locations. For butterflies, temperature niches were directly extracted from the publicly available data base CLIMBER, which is based on average climatic data between 1971 and 2000 (Schweiger et al., 2014). Ground beetle distribution maps were scanned from Turin (2000) and georeferenced and digitized using ArcGIS Desktop v 10. For the springtails, we downloaded point occurrence records from GBIF, combining data for recognized synonyms; we excluded older records (before 1950) and those without at least one decimal place of accuracy in geographic coordinates. Because of the potential bias of GBIF data, we also compared our results using temperature niche based on national checklist data from de Jong (2013). Poor distribution data quality was potentially a problem for some less-studied species; however, our methodology only needed to capture the variation in species temperature preferences – to separate out the warmer versus cooler-temperature preferring species.

To calculate each species temperature niche using the distribution data, we used the E-Obs gridded climatic data layer (Haylock et al., 2008) of average annual temperature between 1961 and 1990, projected onto a 25 km equal area grid and delineated to Europe, and extracted the grid temperatures from locations intersecting with each species' distribution. We restricted calculation to a European temperature map because, for most species, the best distribution data available were restricted primarily to Europe (for the bats and plants we could calculate a global temperature niche using CliMond global data (Kriticos et al., 2012) and similar results were obtained). Because there were very few GBIF records for some springtail species, we only calculated temperature niche if there were occurrence records within more than 10 climatic grid cells. For the bird data set, which included long-distance migratory species, we calculated temperature niche as the European breeding temperature niche using average temperature data between April and June and the range maps restricted to breeding or resident areas. Using the average temperature data layer, temperature niche was summarized for all species in terms of the mean temperature across the range (mean of all occupied cells, weighted by grid cell coverage for range maps and removing duplicate records within the same cell for GBIF point occurrence data) as well as the maximum and minimum (mean of the five occupied grid cells with the warmest/coolest average temperature). We also calculated the temperature range as the difference between the maximum and minimum. Because our calculation of temperature niche was not necessarily inferred from the full distribution of the species, and does not reflect the species fundamental temperature niche, we do not regard our estimates as approximating

species absolute temperature niche but rather reflecting the ranking of species from those preferring warmer to those preferring cooler temperatures.

Because it may be necessary to control for additional sources of variation in population trends in order to detect an effect of temperature niche, we also included further species attributes in our analysis. We collected data, with a few exceptions, in the following categories: (1) habitat preference, which might covary with climatic niche (Barnagaud et al., 2012) and/or explain important variation due to land use change or related drivers, (2) body size (for animals) as a variable that might explain variation related to a number of life-history traits. Bat attributes included body size (mass in g) and habitat preference (forest-dependent or independent) from the literature (Boye et al., 1999; Dietz et al., 2009). For birds, we included main breeding habitat (wetland, farmland, forest or urban), migratory strategy (resident, short-distance migrant or long distance migrant) because previous analysis indicated its importance (Lemoine et al., 2007), as well as size (mass in g) (Bezzel 1985, 1993). Butterfly attributes on body size (average male forewing length in mm) and habitat preference (habitat moisture: wet, dry or mesophilic; habitat structure: open land, scrubs or forest) had been compiled previously from Higgins and Riley (1978) and Reinhardt et al., (2007). Ground beetle attributes on habitat preference (habitat moisture: wet, mesophilic or dry; habitat structure: open, partially shaded or shaded), size (body length in mm) and wing morph (brachypterous, dimorphic, macropterous) had been previously compiled (Gerisch, 2011). For springtails, data on size (body length in mm) were obtained from Ulrich and Fiera (2010) and main habitat preference [most common in forest (coniferous or deciduous) or open habitat (grassland or arable land)] and habitat breadth [coefficient of variation of abundance across habitat classes, an approach used by others e.g., (Barnagaud et al., 2012)] was assessed using data contained within Edaphobase (<http://portal.edaphobase.org>). For the dry grassland plants, number of inhabited floristic zones, and leaf persistence were taken from the BiolFlor database (Kühn et al., 2004) and life history (annual or perennial) from Matesanz et al. (2009).

### 2.4. Relationships between species attributes and population trends

Our main interest was in testing the effect of temperature niche on population trends; we thus wished to control for any important variation in population trends that could be explained by alternative species attributes. Relationships between population trends and attributes were analyzed with linear models that included the inverse variance of the slope estimates as weights. In the case of the birds, we used log median abundances as weights. We used a Levene's test to test whether there were differences in the extent of interspecific variation of temperature niche among the data sets. We tested the effect of each temperature niche metric (mean, maximum and minimum) on population trends separately in a multiple regression model. To improve the spread of the data, we transformed variables when appropriate (log-transformation for size and minimum temperature niche for birds and square-root transformation for mean and maximum temperature niche for bats and mean temperature niche for springtails). Continuous variables were centered and standardized to units of standard deviation. Along with temperature niche, we initially included the additional species attributes but removed any of these additional attributes that were not retained in any model with  $\Delta AICc < 2$  from the best model. For the plant and bat data set, we only considered simple regression models because of the smaller number of data points. Before including terms in the model, we checked that they were sufficiently uncorrelated (i.e., that  $r < 0.7$ ). We also tested the inclusion of temperature range (temperature maximum minus temperature minimum) in models including temperature mean along

with the interaction between temperature mean and temperature range. In a small number of cases, data were not available for all attributes and these species were dropped from the analysis. The “lmg” metric was used as a measure of the explanatory power of each variable (Lindeman et al., 1980).

Because species do not necessarily provide independent data points because of shared ancestry, we tested whether phylogeny or taxonomy explained any variation in our models. Phylogenies with branch lengths were obtained from Jetz et al. (2012) for the birds, using TreeAnnotator of Beast (Drummond et al., 2012) to produce a maximum credibility clade tree; from Fritz et al. (2009) for bats; from Durka and Michalski (2012) for plants and from an undated phylogeny for the butterflies from a molecular phylogenetic maximum likelihood analysis of the genes cytochrome c oxidase I and elongation factor 1 alpha (Wiemers and Schweiger, unpubl). For the ground beetles (all within the family Carabidae), we grouped species into genera and for the springtails, the taxonomic classification was taken from the Synopses on Palaearctic Collembola (Dunger and Burkhardt, 2012) and the Edaphobase (<http://portal.edaphobase.org/>); the taxonomy was then used to create a tree, setting branch lengths to 1. To check whether there was a phylogenetic signal in the residuals of the multiple regression models of population trends, we used Abouheif's *Cmean* test (Münkemüller et al., 2012) as implemented by the R package *ade4* (Jombart et al., 2010). In most cases, there was no evidence that phylogeny or taxonomy explained any residual variation in the multiple regression models. However, in cases when it did, we specified a *corPagel* correlation structure using the R package *ape* (Paradis et al., 2004) in a generalized least squares model. All analyses were conducted with R vers. 3.0.2 (R Core Team, 2013).

### 2.5. Exposure to climate change

To assure that observed differences in the importance of temperature niche were not caused by differences in the extent of climate change among the regions where the data sets were collected (Menzel et al., 2006), we also compared local temperature trends. We used geographic coordinates of census sites in each data set (except the plants, see below) to extract temperature data from temperature maps. Maps of average annual, summer (June – August) and winter (December–February) temperature were derived from daily means of air temperature at stations of the Deutscher Wetterdienst (DWD) station network integrated over seasons and years from 1 km grid fields and/or jpg-pictures that were provided by National Climate Monitoring of the DWD. For the plant data set, weather data had been collected from a nearby weather station. We tested the interaction between year and region to assess the evidence for differences in the trends of average annual, average summer and average winter temperatures over the study periods and among the regions of which the data sets originated.

## 3. Results

In all data sets, there was evidence of some species with positive or negative population trends over the study period. Positive trends (95% CI greater than zero) were seen in 9/11 of the bats, 27/69 beetles, 20/28 butterflies, 12/46 springtails and 1/11 plants while negative trends (95% CI less than zero) were seen in 26/69 beetles, 3/46 springtails and 3/11 plants. Within the birds, 39 (of 130) species showed consecutive positive population growths between censuses; 45 showed consecutive negative growth. No differences in the temperature trends were found among the regions where the data sets were collected (time:region interaction – winter average:  $P = 0.41$ ; summer average:  $P = 0.65$ ; annual

average:  $P = 0.68$ ; Fig. S3). In general, average annual temperatures increased significantly by  $0.041\text{ }^{\circ}\text{C y}^{-1}$  ( $\pm 0.009$ ;  $P < 0.01$ ).

Interspecific variation in temperature niche differed among the taxonomic groups (Levene's test,  $P < 0.01$ ). The highest/lowest variation for temperature mean was found in the bats/butterflies (see Fig. S4); for temperature minimum in the springtails/ground beetles and for temperature maximum in the dry grassland plants/springtails. There was some covariation between temperature niche and habitat preference within the birds, butterflies, ground beetles and springtails but it was generally weak ( $0.17 < |r| < 0.43$ ) (see Table S2).

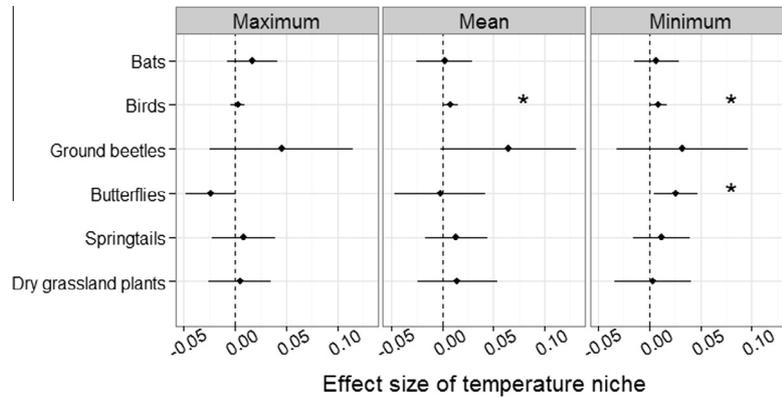
In the multiple regression models, mean temperature niche was positively related to long-term local population trends of the birds and minimum temperature niche was positively related to trends of birds and butterflies (Figs. 1 and 2, Table 2). For the ground beetles, the effect of mean temperature was dependent on temperature range, being larger for species with smaller temperature ranges, and was marginally insignificant at average temperature range (Table 2). For the bats, springtails and dry grassland plants, none of the temperature niche variables showed a significant relationship with population trends. There was a significant effect of temperature range on population trends only for the butterflies (Fig. 3), but the effect was negative such that species with a broader temperature niche had more negative population trends; however, temperature range was strongly negatively correlated with minimum temperature niche ( $r = -0.92$ ,  $P < 0.01$ ).

The patterns were generally robust to whether species points were weighted by the inverse variance of the trend coefficient or whether rarer species were included in the analysis (Fig. S2). For the butterflies, the trend-temperature niche relationship weakened when rarer species were included in the analysis – but this may be a consequence of the non-standardized survey method, which may lead to less reliable data for rarer species. In contrast, including rare species increased the statistical significance of temperature niche for the ground beetles. After removal of four influential points with Cook's distance  $> 0.5$ , an effect of mean temperature niche was found for the springtails when including rarer species, based on analysis with alternative coarser (country-level) distribution data ( $0.035 \pm 0.011$ ,  $P < 0.01$ ; see Fig. S6). A phylogenetic signal was found in the residuals of the bat analysis, and ground beetles and springtails when including the rarer species, but this had little effect on the results.

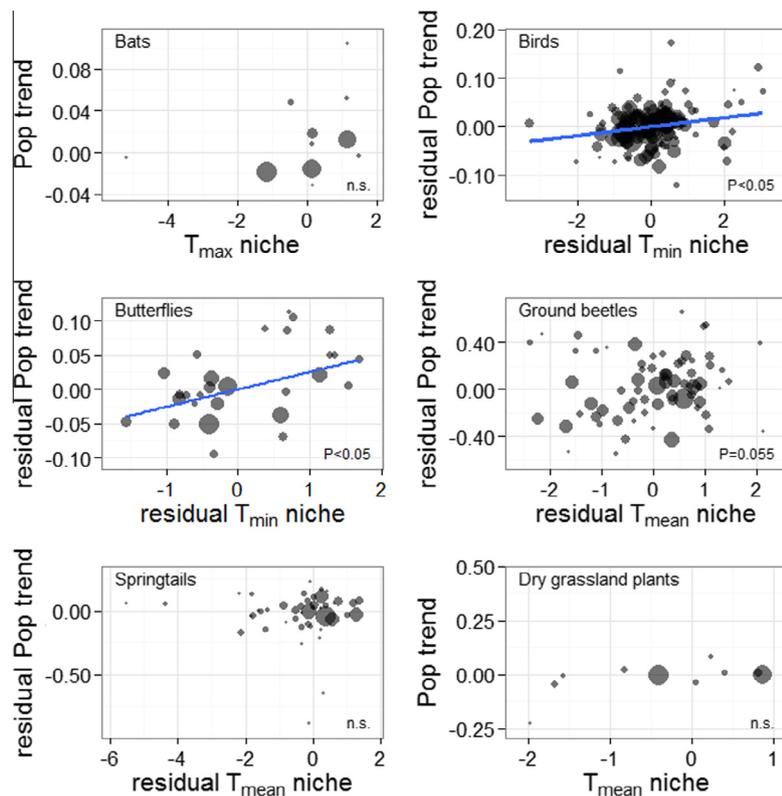
## 4. Discussion

If climate change has been an important driver of changes in population growth, we expected a positive relationship between temperature niche and population trend (Parmesan and Yohe, 2003; Devictor et al., 2008). Temperature niche explained a significant amount of variation in the population trends of birds, butterflies and ground beetles. Despite the influence of other environmental drivers on these population trends, we showed that a simple analysis of the relationship between temperature niche and population trends reveals fingerprints associated with climate change. For the birds and butterflies, this is consistent with other studies (Devictor et al., 2012; Jiguet et al., 2010b), but it had not been previously assessed for the other taxonomic groups.

Many studies have suggested ways in which species attributes should modify species vulnerability to climate change (Foden et al., 2013; Garcia et al., 2014). Exothermic thermoregulation and a short generation time may explain the responses observed for the ground beetles and butterflies (Robinet and Roques, 2010). These taxa have also displayed range shifts that are believed to be in response to climate change (Hickling et al., 2006; Warren et al., 2001). Previous studies have shown effects of temperature niche



**Fig. 1.** Point estimates and 95% confidence intervals for the effect of maximum, mean and minimum temperature niche (i.e. their regression coefficients from the multiple regression models) on long-term local population trends (average annual growth) of different taxonomic groups. \* indicates confidence intervals that do not overlap zero.



**Fig. 2.** Partial regressions between long-term local population trends (average annual growth) and the best temperature niche metric (out of temperature maximum, temperature mean, temperature minimum, assessed by the model with the lowest AICc). Each point represents a species and its size indicates the species weight (certainty regarding long-term population trend) in the model. See Table 1 for additional variables included in the models. and Fig. S5 for graphs showing all three temperature niche metrics for each species. Relationships are significant for the birds and butterflies. For the ground beetles, for which the interaction between temperature mean and temperature range was significant, we present the partial relationship at average range size, which is marginally insignificant.

on bird population trends in Europe (Jiguet et al., 2007, 2010b) and also have indicated that they may be responding slower than butterflies (Devictor et al., 2012). Our findings are consistent with this suggestion as the effect size of temperature niche on birds was smaller than that for the butterflies. Migratory strategy and habitat preference, probably indicating effects of land use change, were also important for explaining variation in the bird population trends (Lemoine et al., 2007), which may have affected the relative importance of climate change. Particular “winner” species at these study sites that had both relatively warm-temperature niches and high population trends, not explainable by other attributes, were the black-necked grebe, *Podiceps nigricollis*, and the meadow brown,

*Maniola jurtina*, while “loser” species with relatively cool temperature niches and negative population trends were the sand martin, *Riparia riparia*, and the black-tailed godwit *Limosa limosa*. Minimum temperature niche showed the most consistently positive relationship with trends for these groups (although not significantly so in the case of the ground beetles), which may indicate that minimum temperature tolerances are most important for response to climate change. We found no evidence that temperature range was consistently related to population trends. In the butterflies, the negative effect of temperature range was most likely explainable by the strong negative correlation between temperature minimum and temperature range – arising from the greater

**Table 2**

Results of the multiple regression models between temperature niche and population trends (annual average growth). In each case, we examined the effect of temperature niche after controlling for variation due to any additional species attributes that were retained in models  $\Delta AICc < 2$ . For presentation purposes, we show the results for whichever temperature niche metric (maximum, mean or minimum) resulted in the lowest AICc. For supplementary statistics, we also present the  $P$ -values of  $F$ -tests of the species attributes and  $R^2$  contributions that were calculated using the lmg metric, which calculates the increase in  $R^2$  due to term inclusion, averaged over all possible term orders. Continuous variables were centered and standardized. See Table S3 for the simple regressions of all variables that were tested.

Taxa	Temperature niche	$R^2$ (%)	Estimate (SE)	$F$ -test $P$ -value	Other attributes	$R^2$ (%)	Estimate (SE)	$F$ -test $P$ -value
Bats (11 sp)	Temp max	21.1	0.0168 (0.0109)	0.155	None			
Birds (130 sp)	Temp min	4.3	0.0093 (0.0039)	0.019	Habitat <sup>a</sup>	9.3	(F) 0.0235 (0.0084) (U) 0.0273 (0.0108) (W) 0.0245 (0.0107)	0.021
					Migration <sup>b</sup>	9.1	(S) -0.0043 (0.0077) (L) -0.0272 (0.0085)	0.006
					Mass	2.2	0.0034 (0.0037)	0.354
Butterflies (28 sp)	Temp min	11.9	0.0256 (0.0103)	0.020	Wing size	25.0	-0.0275 (0.0090)	0.005
					Habitat moisture <sup>c</sup>	13.6	(M) 0.0645 (0.0277) (W) 0.0179 (0.0317)	0.038
Ground Beetles (69 sp)	Temp mean	3.9	0.0645 (0.0330)	0.055	Wing morph <sup>d</sup>	20.4	(D) 0.1417 (0.1499) (M) 0.4326 (0.1446)	<0.001
	Temp range	0.5	-0.0042 (0.0340)	0.902	Habitat <sup>e</sup> openness	6.3	(PS) 0.1512 (0.0874) (S) 0.2350 (0.0795)	0.015
	Temp mean: Temp range	6.8	-0.0982 (0.0401)	0.017	Length	3.0	0.0498 (0.0326)	0.132
Springtails (45 sp) <sup>g</sup>	Temp mean	1.3	0.0137 (0.0153)	0.376	Habitat <sup>f</sup>	1.9	(C) -0.0339 (0.0365)	0.359
Dry grassland plants (11 sp)	Temp mean	7.7	0.0149 (0.0172)	0.408	Length	8.5	-0.0334 (0.0158)	0.041
					None			

<sup>a</sup> Farmland was the reference group. F = forest; U = urban; W = wetland.

<sup>b</sup> Resident was the reference group. S = short-distance migrants; L = long-distance migrants.

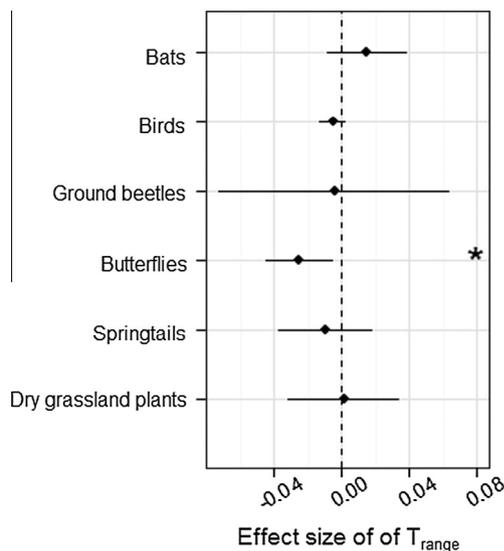
<sup>c</sup> Dry habitat was the reference group. M = mesophile; W = wet habitat.

<sup>d</sup> Brachypterous was the reference group. D = dimorph; M = macropterous.

<sup>e</sup> Open was the reference group. P = partially shaded; S = shaded.

<sup>f</sup> Open was the reference group. C = closed.

<sup>g</sup> One outlier species was removed but this did not affect the significance of temperature mean.



**Fig. 3.** Point estimates and 95% confidence intervals for the effect of temperature range on long-term population trends (average annual growth). \* indicates confidence intervals that do not overlap zero.

variation in temperature minimum (and upper latitudinal range extent) than temperature maximum (and lower latitudinal range extent).

For the other taxa, springtails, dry grassland plants and bats, our analysis indicates other factors affecting population trends were more important than species' temperature niche. Most of the bat species showed positive population growth, which may reflect some recovery after widespread declines throughout Europe during the 20th century due to habitat loss and agricultural

intensification (Haysom et al., 2013). Currently, effects of climate change may be outweighed by the success of conservation measures and availability of habitat (Mehrer et al., 2011). Further, behavioral thermoregulation and roost use may reduce their exposure to climate change. Previous analysis of the dry grassland plant data set found that weather variables, including temperature, were associated with inter-annual changes in plant cover, indicating that climate change could be significant (Matesanz et al., 2009). In this arid system, any climate change impacts may be mediated more by attributes that affect tolerance to water stress than by temperature niche, which would explain why temperature niche was not positively related to trends. In addition, these species are already living in one of the warmest climatic sites of Germany and may be preadapted to such conditions. However, other studies indicate that plant communities are generally showing slow distribution and composition changes in response to climate change (Bertrand et al., 2011; Honnay et al., 2002). For instance, Roth et al. (2014) compared the extent of community shifts toward warm-adapted species in plants, butterfly and birds over an 8-year period in Switzerland and found the lowest rates in plants.

Exposure to climate change not only depends on regional climate change but also the particular habitat of the species. Even in the same region, different species might experience climate change differently due to small-scale heterogeneity in climatic conditions (Graae et al., 2012; Suggitt et al., 2011). De Frenne et al. (2013) found that a dense forest canopy cover could moderate the on average greater success of warm-adapted species in different plant communities. For springtails, we suggest that their soil microclimate might similarly reduce the effects of increasing average ambient temperatures, which could explain why temperature niche was less important. However, the indication of an effect when we included rarer species in the analysis may suggest that at least some species are being affected.

Because each taxonomic group came from a different data set, we have to consider how variation in attributes of the data sets themselves may have affected our results. In terms of number of species and/or sampling area, the bat and plant data sets were the smallest. Patterns related to climate change may be harder to detect in smaller data sets due to overriding local environmental factors or simply decreased statistical power; thus, we cannot rule out that the smaller scales explains the weaker evidence of effect in these data sets. Thus, ideally, our results should be retested on larger data sets for these taxonomic groups. The limited availability of distribution data for springtails means that inaccuracy in their temperature niche estimates was probably higher than that of the other taxonomic groups, which would lead to a weaker relationship with population trends than whatever true relationship exists. The butterfly data set was not based on a standardized survey and therefore we cannot exclude changes in the behavior and effort of observers from affecting our results; however, our finding of an increase in warm-adapted species is consistent with observations of butterfly communities throughout Europe (Devictor et al., 2012). Differences in interspecific variation in temperature niche could have also affected our approach because trait-based approaches rest on species having interspecific variation in traits. Although there were some differences in the variances of temperature niches among the taxonomic groups, the strongest evidence for a positive relationship between temperature niches and trends were not found in the taxonomic groups with the largest variation in temperature niche. Thus, differences in the variances of temperature niche among the data sets do not explain our results. Finally, our analysis only focused on effects of climate change directly mediated through temperature and is unlikely to capture other climate change impacts, for instance, through biotic interactions.

A potential problem with the interpretation of the effect of temperature niche is its covariation with other species attributes. We focused particularly on habitat preference as this trait has been shown previously to covary with temperature niche (Barnagaud et al., 2012), but we cannot rule out that temperature niche is related to other covarying traits. In our data set, bird species using urban and wetland habitat as their main breeding habitat had a warmer temperature niche. Effects of habitat preference on population trends may also be related to climate change impacts (Cahill et al., 2013), however it is also possible they capture responses related to other drivers of global change such as land-use change. For instance, the increase in the abundance of avian wetland species has been previously linked with release from hunting pressure and the restoration and protection of wetland habitat (Lemoine et al., 2007). For this reason, we focused on temperature niche, which can be more straightforwardly linked with climate change, and accounted for any variation explainable by habitat. In general, it would be sensible to consider covariation between temperature niche and habitat preference when analyzing associations between temperature niche and species response to climate change (Clavero et al., 2011).

We explored the effects of species attributes on their responses as a way to investigate the effects of an environmental driver on a community. A more direct approach to understand the importance of climate, or at least weather, would be to analyze the relationship between changes in annual population abundances and ambient temperatures (Eglington and Pearce-Higgins, 2012; Saether et al., 2000). Not all the data sets were collected annually, which would be optimal for such an analysis. In addition, as climate change is assumed to be a persistent driver, we assumed its effects would be visible on species long-term population trends. However, a deeper understanding of the mechanism through which changes in temperature affect abundances would be aided by analysis of the direct effects of temperatures, especially during different time periods of the year, on population abundance and/or demographic variables. Whether and how ambient temperatures affect a

particular species would also be predicted to depend on the difference between temperatures being experienced and its thermal preferences. Individuals in a population that is close to their thermal limits may be more affected by a given change in temperature than those living nearer their optimum (Deutsch et al., 2008). Our temperature niche estimates are unlikely to represent the absolute preferences of species and thus we do not make this comparison. In addition, research by Jiguet et al., (2010a) suggest that bird populations are not just being affected in the warmest and coolest parts of their range, but linearly across their range within France, The Netherlands and Sweden. However, at least at some resolution, it seems likely that there is some non-linear relationship within which, over some range, changes in average temperatures are unimportant (Khaliq et al., 2014).

Although we found temperature niche could partly predict long-term population trends for some taxonomic groups, there was considerable scatter around this relationship and, even in cases when it was statistically significant, it only explained between 4% and 12% of the variation in population trends. Temperature niche also explained less variation than the other species attributes, which suggests that other factors are more important for determining their population trends at these study sites. In the bird data set, the common linnet, *Carduelis cannabina*, was found to have a relatively warm mean temperature niche, yet it also had a lower than average population trend, even after accounting for its habitat preference, migratory strategy and size, inconsistent with the predicted impact of climate change via its temperature niche. Clearly, climate change is not the only driver of population trends and interspecific variation in trends could also be caused by variation in susceptibility to other drivers. In addition, species response to climate change will depend on other species attributes and not only temperature niche (Foden et al., 2013; Garcia et al., 2014).

We showed that local population trends of different species in central Europe, primarily Germany, reveal fingerprints of climate change. Our findings also suggested that the impacts of climate change may differ among organisms according to their traits, habitat preferences and the relative importance of other drivers affecting population growth. Our results suggest the focus of previous studies on mobile groups such as birds and butterflies do not necessarily provide generalizable results to other taxonomic groups. We believe that this approach, which can be applied to any species, is particularly suited for comparative cross-system analysis to identify which types of organisms, in which habitats, are responding the most to climate change.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2015.03.034>.

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