



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 also 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

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