

Extraordinary range expansion in a common bat: the potential roles of climate change and urbanisation

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Abstract Urbanisation and climate change are two global change processes that affect animal distributions, posing critical threats to biodiversity. Due to its versatile ecology and synurbic habits, Kuhl's pipistrelle (*Pipistrellus kuhlii*) offers a unique opportunity to explore the relative effects of climate change and urbanisation on species distributions. In a climate change scenario, this typically Mediterranean species is expected to expand its range in response to increasing temperatures. We collected 25,132 high-resolution occurrence records from *P. kuhlii* European range between 1980 and 2013 and modelled the species' distribution with a multi-temporal approach, using three bioclimatic variables and one proxy of urbanisation. Temperature in the coldest quarter of the year was the most important factor predicting the presence of

P. kuhlii and showed an increasing trend in the study period; mean annual precipitation and precipitation seasonality were also relevant, but to a lower extent. Although urbanisation increased in recently colonised areas, it had little effect on the species' presence predictability. *P. kuhlii* expanded its geographical range by about 394 % in the last four decades, a process that can be interpreted as a response to climate change.

Keywords Chiroptera · Distribution · Global change · Pipistrelle · Model

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Introduction

Species distribution may change in response to a variety of factors that act at different spatial scales. Climate change and land cover modifications are two major global change processes affecting animal distributions worldwide, with critical implications for conservation (Jetz et al. 2007; Van Dyck 2012; Visconti et al. 2015).

Climate change is expected to impact heavily on European fauna in the near future, with significant loss of diversity—particularly in southern Europe—that will not be offset by species shifts, thus producing a continental biological homogenisation. The same general trend is predicted for the Mediterranean basin, with mammalian communities potentially being deeply modified by extinctions and range shifts (Maiorano et al. 2011). Climate-change-related range shifts or reductions have been frequently documented both in latitude (Shoo et al. 2006; Chen et al. 2011) and altitude (Moritz et al. 2008; Rowe et al. 2010), particularly in specialised taxa. By contrast, range expansions involving generalists or highly adaptable species appear rare.

Urbanisation is another global change process potentially influencing the distribution of organisms whose effects may not be easily distinguished from those of climate change (e.g. Tomassini et al. 2014). Urbanisation is a non-directional process characterised by the replacement of natural habitats with built-up areas (Antrop 2004). Europe has a long-standing history of human-induced landscape modification starting in the Holocene, 10,000 years ago (Antrop 2004), and landscape transformation has by no means ended: recent trends show that urbanisation is still taking place in vast areas of the continent, particularly in central and eastern regions (Palang et al. 2006). This dramatic process is certainly among the most powerful drivers of changes in wildlife distribution in the Anthropocene (Steffen et al. 2011). Besides replacing and fragmenting natural habitats, expanding urban areas are also typically associated with chemical, light and noise pollution (Antrop 2004; Chace and Walsh 2006; Bradley and Altizer 2007; Stone et al. 2009; Perugini et al. 2011; Bennie et al. 2014). Although most animal species avoid urban areas, some, called “synurbic” species, may either tolerate urbanisation or even successfully exploit human settlements (Patterson et al. 2003; Chace and Walsh 2006; Baker and Harris 2007).

Bats are well-suited models to explore wildlife responses to human-induced habitat modifications. These mammals are in most cases multiple-habitat specialists, which depend on specific roosting and foraging habitats, whose loss or alteration have therefore seriously affected the population status of many species (Van der Meij et al. 2015). Many bat species find few or no foraging and roosting opportunities in urban areas (for a review, see Russo and Ancillotto 2015). In contrast, other species tolerate or even thrive in urbanised landscapes, for instance because they roost in buildings or forage at streetlamps (Kunz 1982; Rydell 1992). Activity patterns of bats are closely linked to climatic conditions, particularly temperatures, which strongly influence both their daily torpor as well as hibernation (Stawski et al. 2014), and thus may affect individual survival and reproductive success.

Both modelling and empirical studies suggest that climate change influences bat distribution (Rebelo et al. 2010; Sherwin et al. 2013; Razgour et al. 2013). Yet, to our best knowledge, no study has attempted to disentangle the genuine effects of climate change from those of land-use modifications to identify the key factors actually driving changes in bat distribution. Urbanisation and climate change may both play a role in inducing range shifts or expansions. In particular, they may act synergically on species adapted to warmer climates (e.g. Mediterranean species) as large urban settlements can act as “thermal islands” favouring distributional changes (Arnfield 2003).

Kuhl’s pipistrelle (*Pipistrellus kuhlii*) offers a unique opportunity to investigate the relative effects of climate change and urbanisation on species distributions for a number of reasons. First, in a climate change scenario, this typically Mediterranean species is expected to expand its range in response to increasing

temperatures (Rebelo et al. 2010), as regions at higher latitudes would become suitable for the species. Second, *P. kuhlii* has synurbic habits (Dietz et al. 2009; Russo and Ancillotto 2015), roosting frequently in buildings and commonly foraging at streetlamps (Barak and Yom-Tov 1989; Russo and Jones 1998; Serangeli et al. 2012). Finally, despite its sedentary behaviour (Dietz et al. 2009), *P. kuhlii* has expanded its range northeast in recent years, colonising regions of central and Eastern Europe during the last three decades (Sachanowicz et al. 2006). In most cases, the first records of single individuals (initially regarded as vagrants) have been followed by observations of reproductive bats or maternity colonies, indicating successful colonisation of the new region.

In this study, we assess the roles of climate change and urbanisation as drivers of *P. kuhlii* range expansion. We apply species distribution modelling to predict how the species probability of presence changed in Europe since 1970, and compare the relative contributions of climate and urbanisation. Particularly, we tested two hypotheses, namely whether *P. kuhlii* range expansion is influenced (1) by climate change only or (2) by a synergic concurrence of climate change and urbanisation. In the former scenario, we predict that *P. kuhlii* has been able to colonise areas where the climate has become warmer, whereas in the latter scenario, we predict that climate change has combined with an increase in urbanisation to provide more roosting and foraging opportunities.

Materials and methods

Data collection

We set up a database of all reliable records of *P. kuhlii* (based on authors’ direct observation or acoustic identification or provided by bat specialists) for which both point precision and collection date were known, totalling 25,132 occurrence points. To assess the extent of *P. kuhlii* range expansion after 1980, we calculated and compared the area of historical extent of occurrence (after Stebbings and Griffiths 1986) with that of the current extent of occurrence, based on our dataset, and obtained a 100 % minimum convex polygon following IUCN (2012). To model species distribution, we employed three bioclimatic variables and one variable of urbanisation potentially influencing *P. kuhlii* range. To select variables, we considered the thermophilous nature of this bat, the fact that it hibernates in winter (Dietz et al. 2009) and its significant exposure to water loss linked to the dry Mediterranean summer (Russo et al. 2012). Therefore, we selected the environmental predictors that were most likely to limit *P. kuhlii* distribution, i.e. the average minimum temperature of the four coldest months, mean precipitation and precipitation seasonality (=standard deviation of mean precipitation). Layers of monthly minimum temperatures and mean precipitations were downloaded from

the Climatic Research Unit website (CRU TS Version 3.22; http://www.cru.uea.ac.uk/cru/data/hrg/cru_ts_3.22/). Because the species' range expansion is thought to have begun in the 1980s (Sachanowicz et al. 2006), we averaged these monthly layers to derive three covariates representative of four time steps (1971–1980, 1981–1990, 1991–2000, 2001–2013). We employed artificial illumination as a proxy for urbanisation because the two factors are strongly associated with each other and the former is important in favouring *P. kuhlii* foraging success (Tomassini et al. 2014). We downloaded 1992–2012 annual layers of nocturnal stable artificial lights from the National Oceanic and Atmospheric Administration (NOAA) archives (<http://ngdc.noaa.gov/eog/dmsp/downloadV4composites.html#AXP>). These layers were averaged to correspond to two time steps respectively representing 1992–2000 and 2001–2012. Older records of nocturnal stable light corresponding to years 1971–1990, as well as other variables representing urbanisation, were not available.

Time steps selected for environmental variables had unequal lengths due to constraints in data availability: rather than considering a final 3-year step, which might have been too short to be representative and thus could be influenced by random fluctuations, we included such years into the preceding time step. This was assumed to have negligible effects on the comparison of values between time steps.

A source of bias in species distribution modelling is spatial autocorrelation of data points. These must be independent otherwise they might bias the predictions towards areas with higher pseudo-replication. In addition, species distribution models based on presence-only data assume an even sampling effort in the study area (Elith et al. 2010), i.e. that no geographic bias occurs in the presence dataset. Opportunistic data collection is generally biased toward well-sampled areas, and when geographic bias in sampling effort correlates with environmental gradients, Species Distribution Model (SDM)'s predictions may reflect the joint distribution of probabilities of presence and sampling effort (Guillera-Aroita et al. 2015). In order to avoid spatial autocorrelation in point data, and environmental biases, we followed a two-step approach. First, we retained only one point per 5-km cell, corresponding approximately to the size of individual home ranges of the species (Serangeli et al. 2012), resulting in 8882 points. Second, we developed a 1°-resolution grid covering the whole study area: points falling in each grid cell were given a weight which was inversely proportional to the number of points occurring in the cell, so that each grid cell had the same total weight. This step allowed us to attribute a greater weight to the points in under-sampled areas than to those in areas characterised by a higher sampling effort, thus reducing the spatial bias towards Mediterranean countries where the species is abundant and frequently observed.

Species distribution models

Illumination satellite data were only available since 1992, so we developed two distribution models following a multi-temporal approach (Maiorano et al. 2013) in which we included points from all years to each of which we assigned the covariate values of the respective time step. The rationale for using a multi-temporal approach is that the observed distribution of species might not reflect the species distribution potential; hence, a species distribution model fitted on current data may underestimate the potential distribution when projected in time and/or space. A multi-temporal approach makes it possible to use data points corresponding to a broad temporal window, and thus better approximate the species fundamental niche (Maiorano et al. 2013).

A first model was trained on all occurrences using only climatic variables, and was projected for the four time steps between 1970 and 2013. A second model was trained only on occurrences recorded after 1990 in order to use both climatic and light variables, and was projected for the last two time steps.

We sampled 10,000 pseudo-absences (Barbet-Massin et al. 2012) distributed in each time step proportionally to the temporal distribution of presence points across the time steps, and assigned them a weight intermediate to the weights calculated for presence points in order to have an equal overall weight of presences and absences. It is widely acknowledged that the relative performances of alternative distribution model algorithms depend on several conditions. An ensemble forecasting approach makes it possible not to rely on a single modelling algorithm but to combine different models (Araújo & New 2007). We adopted an ensemble modelling approach using the R Biomod2 package (Thuiller et al. 2009) by averaging five different models: generalised linear models (GLMs), generalised additive models (GAMs), artificial neural networks (ANNs), generalised boosted models (GBMs) and multivariate adaptive regression splines (MARS). Each modelling algorithm was replicated 50 times using 80 % of the data as the training dataset and the remaining 20 % as the testing dataset. We built the ensemble model by applying a weighted average on the True Skill Statistics (TSS) (Allouche et al. 2006). We then projected the ensemble model predictions for each time step.

Results

Overall, the extent of occurrence of *P. kuhlii* (Fig. 1) estimated with a minimum convex polygon expanded from 1,510,116 to 5,946,351 km², corresponding to an almost fourfold (393.7 %) increase.

In both models, the mean temperature of the coldest quarter was the most important variable constraining *P. kuhlii* distribution. The second and third variables in order of decreasing importance were mean precipitation and its variability across the

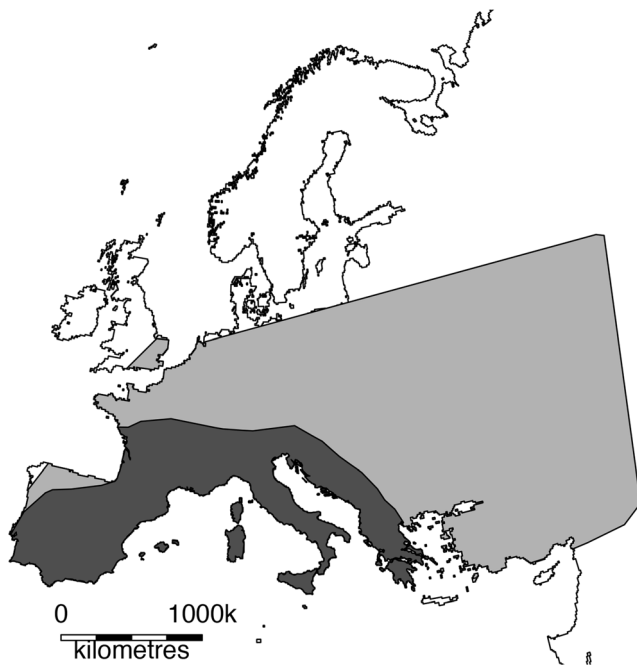


Fig. 1 Eurasian range of *Pipistrellus kuhlii* (shades of grey). Dark grey historical range (after Stebbings and Griffiths 1986), light grey current range comprising 1980–2013 occurrence data

year. In the second model also including illumination, this variable yielded a positive relationship with the probability of presence of the species, although it was less important than the other three predictors (Table 1). Both ensemble models had very high Receiver Operating Characteristic (ROC) values. Adding artificial light did not improve model predictions (Table 2).

In the model built with climatic variables only, the probability of presence estimated within the expansion range showed an increase since 1970, with an inverse trend in the last decade in Ukraine, Belarus and western Russia, and decreased also in the Balkans (Fig. 2). In the model including light (Fig. 3), the inverse trend of the last decade in Eastern Europe was partly compensated by an increase in artificial illumination (Fig. 4).

In the last two decades, the points of new occurrence were characterised by a considerable increase in minimum temperature and to a lesser extent by an increase in artificial illumination (Online Resources 1 and 2).

Table 1 Mean importance (\pm SD) of model predictors averaged across five models (GLM, GAM, ANN, GBM, MARS) for the distribution of *Pipistrellus kuhlii* using three climatic variables (climate model) and the same variables plus a proxy of urbanisation (climate + light model)

Predictor	Climate	Climate + light
Mean temperature of the coldest quarter	0.63 \pm 0.08	0.53 \pm 0.04
Precipitation seasonality	0.13 \pm 0.11	0.18 \pm 0.14
Mean precipitation	0.22 \pm 0.21	0.10 \pm 0.12
Light		0.08 \pm 0.03

Table 2 Model evaluations for the distribution of *Pipistrellus kuhlii* using three climatic variables (climate model) and the same variables plus a proxy of urbanisation (climate + light model)

	Testing data	Sensitivity	Specificity
Climate only			
ROC	0.971	96.347	90.464
Climate + light			
ROC	0.97	96.96	90.44

Discussion

Our results strongly support the hypothesis that in the last four decades climate change has acted as the major driver of *P. kuhlii* range expansion across northeastern Europe. Particularly, increasing mean winter temperatures seem to be the most important factor explaining the species' expansion. The other climate factors we considered, i.e. precipitation seasonality and mean precipitation, were also relevant predictors, as expected for factors affecting water and insect availability (Frick et al. 2010) and thus influencing bat survival and reproductive success (Tuttle 1976; Berková et al. 2014). Yet, in the study period, both precipitation factors fluctuated rather than change in a specific direction. The increase in artificial light that occurred in the last decades, which we assumed to be a proxy of urbanisation, was a less powerful predictor of *P. kuhlii* range expansion despite the strong dependence of this bat on urban areas (Goiti et al. 2003).

Pipistrelles are adaptable bats, exhibiting pronounced behavioural and ecological plasticity (Ancillotto et al. 2015; Russo and Ancillotto 2015). For example, the migratory *Pipistrellus nathusii* has been suggested to react to climate change by modifying its wintering and breeding ranges (Martinoli et al. 2000; Lundy et al. 2010; Ancillotto and Russo 2015). For this species, however, only a relatively small-scale expansion in range was recorded. *P. kuhlii* is actually the first bat species for which a continent-scale range increase was recorded (Sachanowicz et al. 2006). The species was originally restricted to the Mediterranean basin, east to the Balkans, west to the Iberian Peninsula, south to the Maghreb coastline and north to the Alps and western France (Stebbins and Griffiths 1986). In the 1980s, *P. kuhlii* was reported from northern France (Leger 1992) and Bulgaria (Ivanova and Popov 1994), then in a number of other countries, including northern (UK: Bat Conservation 2010; Russia: Sachanowicz et al. 2006) and eastern regions (Czech Republic: Reiter et al. 2007; Slovakia: Cel'uch and Ševčík 2006, Danko 2007; Ukraine: Kedrov and Seshurak 1999; Hungary: Fehér 1995; Romania: Ifrim and Valenciu 2006, Dragu et al. 2007; Bulgaria: Ivanova and Popov 1994, Benda et al. 2003; Serbia: Paunović and Marinković 1998; Poland: Sachanowicz et al. 2006, Popczyk et al. 2008).

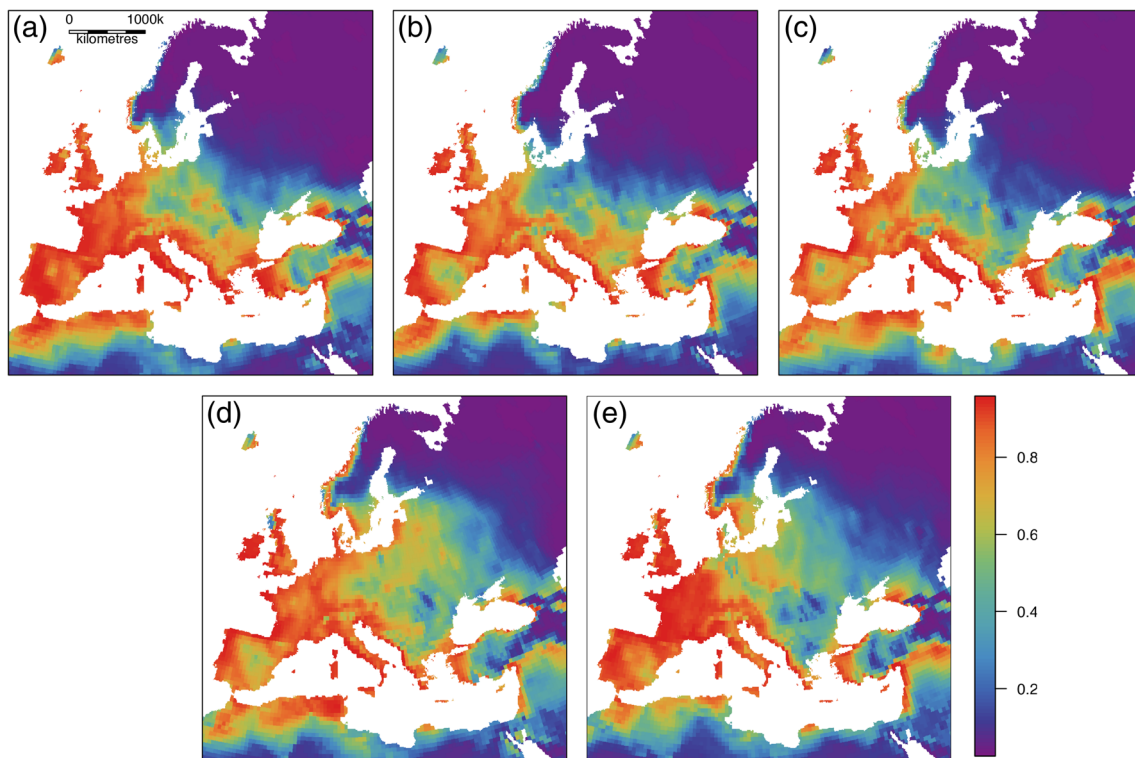
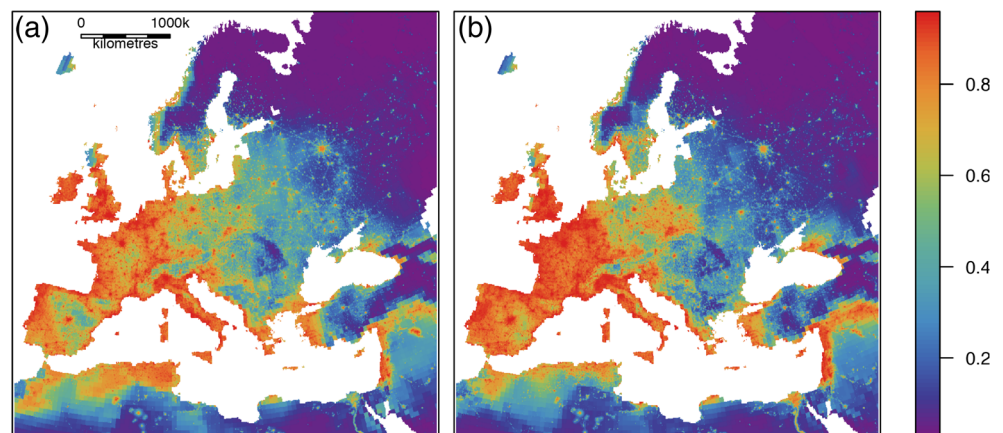


Fig. 2 Predicted distribution of *Pipistrellus kuhlii* at five 10-year time steps (a 1961–1970, b 1971–1980, c 1981–1990, d 1991–2000, e 2001–2012) according to three climatic variables: mean annual precipitation, precipitation seasonality and mean temperature of the coldest quarter

In agreement with our first hypothesis, climate change alone could explain *P. kuhlii* range expansion. The relative importance of climate and urbanisation is however likely to be scale-dependent: the pattern we found is best explained according to climate change, but urbanisation could have played a role in some areas such as Eastern Europe, still undergoing fast industrial and urban development (Palang et al. 2006). The probability of presence of *P. kuhlii* in the climate-only model decreased in Eastern Europe in the last 40 years; yet, this effect disappeared in the model including urbanisation, in which the probability of presence remained stable.

Although this result might actually relate to an effect of urban expansion, the model accounting for the presence of artificial illumination did not perform better than the climate-only model, indicating a negligible contribution of urbanisation. Climate might influence the species' large-scale distribution whereas illumination—per se or as an urbanisation proxy—might be important at a local scale and thus go unnoticed in large-scale models such as ours. While colonisation of new areas is likely to have been prompted by climate, the availability of buildings may have locally helped new bat colonies to establish themselves in the newly reached regions. In

Fig. 3 Predicted distribution of *Pipistrellus kuhlii* at two 10-year time steps (a 1991–2000, b 2001–2012) according to three climatic variables (mean annual precipitation, precipitation seasonality and mean temperature of the coldest quarter) and one urbanisation variable (stable nocturnal artificial lights)



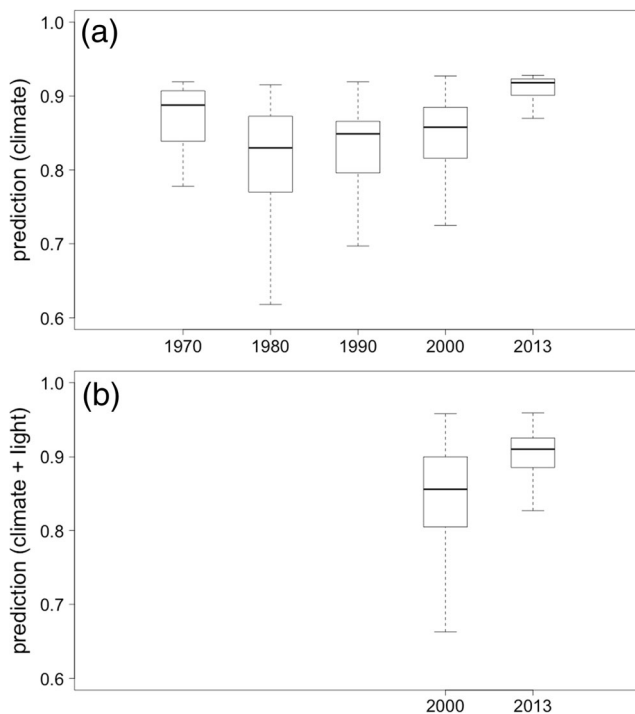


Fig. 4 Change in the predicted probability of presence of *Pipistrellus kuhlii* by species distribution models including **a** three climatic variables and **b** such climatic variables plus an urbanisation variable (stable nocturnal artificial lights) in different time steps

accordance with this interpretation, most “first occurrence” records of *P. kuhlii* were reported for small towns, villages and large cities (e.g. Ifrim and Valenciu 2006; Sachanowicz et al. 2006; Dragu et al. 2007; Popczyk et al. 2008), while an increase in artificial light levels in the areas where *P. kuhlii* expanded in the last four decades was evident from our analyses. The advantage obtained in the urban habitat may have concerned especially roost availability, whereas given its versatile foraging behaviour (Russo and Jones 2003; Di Salvo et al. 2009; Serangeli et al. 2012), the species could have found profitable feeding grounds in a variety of habitats in newly colonised areas besides human settlements. It could be argued that the 1980s reference range we used (Stebbing and Griffiths 1986) may have underestimated the real extent of the species distribution as bat surveys were less common in those times. Although of course we cannot rule this out, the presence of synurbic bats is easily recorded, so there is little risk that the observed expansion would in fact be an artefact of different research efforts over time.

Detecting and quantifying a species’ range shift or expansion is a fundamental step to predict, and thus prevent, potential impacts on other species and ecosystems. Such impacts may have serious consequences: for example, when the red fox (*Vulpes vulpes*) invaded northern Alaska in response to climate change (Hersteinsson and Macdonald 1992), it outcompeted the arctic fox (*Vulpes lagopus*). Population

expansion of *Pipistrellus pipistrellus* in Switzerland, presumably sustained by an expansion of artificial illumination, may have caused the decline of the more sensitive *Rhinolophus hipposideros* by competition for food (Arlettaz et al. 2000). Range shifts and expansions of adaptable species may also lead to community-level alterations, as in the case of altitudinal shifts due to climate change documented in small mammal communities (Moritz et al. 2008; Rowe et al. 2010), where high-altitude specialists tend to disappear, replaced by mesic-adapted species. Biotic homogenisation may result from range shifts, including those driven by climate change (McKinney and Lockwood 1999), because while few species spread, many sensitive species experience a contraction of their ranges and eventually go extinct (Thomas et al. 2004).

In conclusion, although a correlative approach such as that of our modelling exercise cannot detect any cause and effect relationship, it nonetheless strongly supports the climate change hypothesis; so climate is the factor best explaining *P. kuhlii*’s range expansion recorded over the last 40 years. According to our work *P. kuhlii* is a “winner” in the context of climate change: given its high ecological flexibility, it might be a strong competitor of other bats in the newly occupied regions and have serious consequences on bat assemblages, a scenario that certainly deserves careful investigation.

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Compliance with ethical standards

Conflict of interests The authors declare that they have no competing interests.

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