ABSTRACT

**Aim** We used ecological niche modelling to test different models explaining the lineage age–area relationship. We hypothesized that lineage age should influence the proportion of potential range unfilled by phyllostomid bat species. We made explicit predictions about possible relationships between the proportion of unfilled potential range and lineage age. Our goal was to analyse empirical data and fit the model that best describes our data.

**Location** South America.

**Methods** We modelled the ecological niche of 49 phyllostomid bat species using MAXENT and Support Vector Machine (SVM). We calculated the proportion of unfilled potential range as the amount of area outside the current distribution divided by the current distribution (realized range size). Using a dated phylogeny, we regressed the proportion of unfilled potential range on lineage age. To compare our predictions we also regressed realized range size on lineage age.

**Results** Unfilled potential range was weakly associated with lineage age. This relationship was an inverse function of lineage age, explaining between 0 and 17% of the proportion of unfilled potential range. Furthermore, the relationship between realized range size and lineage age exhibited a logarithmic function, with lineage age explaining between 13 and 20% of the variation in realized range size.

**Main conclusions** Different regression models indicated that old phyllostomid species have smaller unfilled ranges than young species. That is, old species have filled most of the areas that are suitable for them. Furthermore, old species have larger realized ranges than young species. We thus refuted both the lineage age–area and taxon cycle models and lent support to the stasis post-expansion model. This suggests that bat species can reach most of their potential range rapidly after cladogenesis and such occupation remains more or less constant through time.

**Keywords** Age–area model, ecological niche modelling, environmental suitability, potential range, stasis post-expansion model, taxon cycle model, unfilled range.

INTRODUCTION

Maps of species geographic distributions are very useful, for instance to inform where a species might occur and to derive species richness patterns over large geographic areas. Nonetheless, such maps provide little information about range dynamics across an evolutionary scale and falsely imply distributional stasis. However, species ranges are not constant over time. In fact, evolutionary processes such as speciation and extinction are among some of the most important underlying factors that drive the dynamics of species ranges. For example, a species can increase its range but by chance some population may be
isolated and the process of speciation begins, decreasing range size of the mother species. Alternatively, isolated populations can go extinct reducing a species’ range (Gaston, 2003). Range dynamics over time can also be affected by climate change. Climate variation can move and reallocate a species’ distribution (Parmesan, 1996). Climate change can increase the area suitable for a species or decrease drastically the suitable areas for a species driving it to extinction, which can be faster when associated with anthropogenic impacts (Nogués-Bravo et al., 2008).

Phylogenetic information (based on time from a most recent common ancestor, MRCA) has also been proved to be useful for predicting variation in range size and its dynamics in many groups such as plankton (Liow & Stenseth, 2007), plants (Willis, 1922; Paul et al., 2009), molluscs (Jablonski, 1987), beetles (Abellán & Ribera, 2011), birds (Ricklefs & Cox, 1972; Webb & Gaston, 2000; Böhning-Gaese et al., 2006) and mammals (Jones et al., 2005). Willis (1922) proposed that geographic range size does not stabilize but increases with time, and as a consequence, old clades should be more widely distributed than younger clades because they have had more time to increase their ranges through dispersal and colonization of new environmentally suitable areas (Willis, 1922). This proposal is known as the age–area model and according to it other variables can also influence range size, but clade age should be the most important.

The age–area model has received mixed support, with some authors proposing nonlinear or even negative relationships between lineage age and range size (Ricklefs & Cox, 1972; Jablonski, 1987; Webb & Gaston, 2000). One of these alternative models, the stasis post-expansion model (Jablonski, 1987), suggests that species rapidly increase their ranges after speciation and that range size remains more or less constant through time. Some variation in size can occur after reaching stasis, but this variation is not sufficient to change the overall pattern. This model was proposed on the basis of the fossil record of molluscs, which arose approximately 2 million years before the end-Cretaceous mass extinction. The range size of these mollusc species did not differ from those that arose in the previous 14 million years (Jablonski, 1987).

Another model of variation in range size over time is the taxon cycle (Ricklefs & Cox, 1972). Based originally on temporal patterns of colonization, extinction and speciation dynamics on islands, this model suggests that after speciation species rapidly reach new areas. A widespread distribution is maintained for some time and then the process of speciation begins through morphological and ecological differentiation and reproductive isolation within islands, creating endemic species on different islands, each with a more restricted geographic range (Ricklefs & Cox, 1972).

The taxon cycle model is based primarily on colonization, extinction and speciation events, and does not account for environmental conditions. However, for a species to colonize a new area, the area must meet the environmental conditions, or fundamental niche, necessary for that species’ survival (Soberón & Peterson, 2005). Thus, the colonisation of new areas can be determined by dispersal and by biotic and abiotic conditions as well (Soberón & Peterson, 2005; Peterson et al., 2011). In the case of islands, environmental variables should be similar across different islands within an archipelago because abiotic conditions that determine species distribution tend to be spatially correlated (Brown, 1995). This could be one reason why environmental conditions are not considered in the taxon cycle model. Although not well recognized, the taxon cycle could operate on continental land masses as well (Webb & Gaston, 2000; Jones et al., 2005), and considering that abiotic conditions tend to vary widely over larger areas we think that environmental conditions must be considered in mainland analyses.

Despite these relationships between age and area, range size can vary randomly through time without a predictable direction; the idiosyncratic model (Gaston, 2003). Pigot et al. (2012) showed that even the observed patterns of range dynamics can be a result of a ‘random walk’ without any particular process through time affecting species range. In such a case, the differences among species increases as a function of time since their divergence from a common ancestor. However, processes affecting species range size may be so ecologically complex and subject to historical factors that patterns of clad age on range size evolution may appear random (Anderson, 1985).

The age–area, stasis post-expansion and taxon cycle models have received some support (e.g. Willis, 1922; Ricklefs & Cox, 1972; Jablonski, 1987; Webb & Gaston, 2000; Jones et al., 2005; Böhning-Gaese et al., 2006; Abellán & Ribera, 2011), but which model has more empirical support remains an open question. Empirical tests published so far on range dynamics regress the size of current distribution of species on time of divergence (e.g. Webb & Gaston, 2000) or regress geographic extent on species lifetime (Foote et al., 2007; Liow & Stenseth, 2007). The mechanism is inferred from the conceptual model that best fits the data. However, there are other variables besides lineage age that influence species distribution, such as dispersal ability, biotic interactions (e.g. the presence of competitors, predators and mutualists) and abiotic conditions (e.g. climate) (Soberón & Peterson, 2005; Böhning-Gaese et al., 2006; Abellán & Ribera, 2011).

Abiotic conditions influence species distribution and are also the main framework for modelling ecological niches over geographic space (Franklin, 2009; Peterson et al., 2011). The ecological niche of a species is the set of environmental conditions and resources that define the requirements of a species where it is able to survive and reproduce (Hutchinson, 1957). By gathering local species records and environmental layers and applying ecological niche modelling (ENM), researchers can generate maps of species potential distribution within a geographic space. ENM can be used to estimate areas of high environmental suitability to evaluate if such areas are inside or outside the current distribution for a given species (Paul et al., 2009). Potential range is the area outside the current distribution over which a species would be found if all limitations to its dispersal were to be overcome and realized range is the smaller area within which the species does occur (Gaston, 2003). The potential range of a species has multiple interpretations and is sometimes equated to overprediction in ENM (Franklin, 2009). It can result from modelling error caused by data characteristics and/or the
Figure 1 (A) Prediction curves for the relationship between lineage age (in Ma) and realized range size and (B) prediction curves for the relationship between proportion of unfilled potential range (unfilled range) and lineage age (in Ma) for each of the four models: 1, age–area; 2, taxon cycle; 3, stasis post-expansion; 4. idiosyncratic.

Under this model there should be greater variation in unfilled range, assuming younger species having large unfilled ranges. If there is no relationship between realized range size and lineage age, then species range may have evolved idiosyncratically (Fig. 1(4A)). Consequently, we predict no relationship between unfilled range and lineage age (Fig. 1(4B)).

We modelled the ecological niche of 49 phyllostomid bat species in South America and estimated unfilled range, which was regressed on lineage age. Phyllostomid bats represent an ideal clade for this kind of analysis because their geographic distribution is well known (Gardner, 2007) and their phylogeny well resolved (Bininda-Emonds et al., 2007). According to predictions described before, we can expect four outcomes from this analysis regarding the relationship between unfilled range and lineage age: (1) a negative relationship, thus supporting the age–area model; (2) better described by a positive quadratic function, thus supporting the taxon cycle model; (3) better described by an inverse function of lineage age, supporting the stasis post-expansion model; and lastly (4) no relation, thus range filling is not influenced by lineage age. To our knowledge, this is the first study to present and test these predictions using ENM.

**MATERIAL AND METHODS**

**Ecological niche modelling**

We gathered species occurrence records for all species of Phyllostomidae that occur in South America from literature review and from the online datasets Species Link (http://splek.cria.org.br/) and GBIF (http://www.gbif.org/). Because we used species that also occur in Central and North America, we chose only those species with wide ranges in South America (e.g., >75% of species ranges). ENM for each species was generated using **MAXENT** version 3.3.k (Phillips et al., 2006) and **SUPPORT VECTOR MACHINE** (SVM) (Drake et al., 2006; Muñoz et al., 2011). Details of ENM are given in Appendix S1 in Supporting Information.

Both MAXENT and SVM outputs provide an ecological niche model of environmental suitability, which ranges from 0 (unsuitable) to 1 (highly suitable). We performed statistical
analyses based on two suitability thresholds, ≥ 0.7 and ≥ 0.5. The threshold of 0.7 was chosen because it indicates areas of high suitability that are thought to be more prone to colonization than areas of lower suitability (Peterson, 2003). The threshold of 0.5 is a more flexible threshold used by convention and indicates the probability of the species presence being positive (Manel et al., 1999). A species list with number of presences and area under the curve (AUC) values for each model is presented in Appendix S2.

Age and area

We used the dated mammal supertree (Bininda-Emonds et al., 2007) to obtain branch lengths which were used as a measure of distance to the MRCA for each phyllostomid species, i.e. the lineage age of each taxon (Stevens, 2011). We estimated lineage ages for polytomic genera (see Appendix S1 for details).

We did not take into account extinct species in the phyllostomid phylogeny. Species missing from the phylogeny (extant or extinct) may overestimate lineage ages (Webb & Gaston, 2000) and carry the perceptual bias of increasing diversity through time (Ricklefs, 2007). Therefore we considered the distance to the MRCA, the most recent node that is shared by any two taxa in a phylogenetic tree, as a measure of lineage age (Stevens, 2011). Distance to the MRCA measures the length of the evolutionary pathways that connect a given set of species (Faith, 1992). Species with short branch lengths can be considered relatively younger taxa than species with longer branch lengths. Species with a long root distance represent taxa that are more diverged from the common ancestor of Phyllostomidae than species that have small root distances (Kerr & Currie, 1999; Stevens, 2006, 2011).

We used two sources to obtain the realized range size of 49 phyllostomid species: range extension maps from the International Union for Conservation of Nature (IUCN; a knowledge-driven approach) and minimum convex polygons (MCP; a data-driven approach) (see details in Appendix S1). After conducting ENM for each species in Maxent and in SVM, we overlapped the realized range map (MCP and IUCN polygons) with the map obtained by ENM with suitability values ≥ 0.7 and ≥ 0.5, and selected the unfilled potential range. We, then, calculated the realized and unfilled potential range areas (in hectares) for each species. After that, we calculated the proportion of unfilled potential range in relation to the realized range (MCP and IUCN polygons) as the variable for analysis (unfilled range). Hereafter, the proportion of unfilled potential range derived from the IUCN polygons is called IUCN unfilled range and the proportion of unfilled potential range derived from the MCPs is called MCP unfilled range. Area calculation of both realized and unfilled ranges were performed using Hawth’s analysis tools (Beyer, 2004).

Statistical analyses and phylogenetic autocorrelation

We used a generalized linear model (GLM) with a gamma family error distribution to evaluate the unfilled range as a function of lineage age. We performed GLM analyses considering two suitability thresholds (≥ 0.7 and ≥ 0.5). We also modelled the realized range as a function of lineage age using a GLM with a gamma family error distribution to compare it with the predictions shown in Fig. 1. We compared both models (IUCN and MCP unfilled range versus age of lineage and IUCN and MCP realized range versus age of lineage) to assess whether one was an inverse function of the other.

Related species tend to have traits that are more similar than expected by chance, violating the assumption of independence in statistical analyses and increasing Type I error (Harvey & Pagel, 1991; Pavoine & Ricotta, 2012). We evaluated the strength of phylogenetic autocorrelation using Moran’s I index calculated from residuals of regression models when coefficients of determination were significant (Gittleman & Kot, 1990). Otherwise, we did not test phylogenetic autocorrelation in the residuals. All analyses were performed in R (R Development Core Team, 2011) using the package adephylo (Jombart & Dray, 2013).

RESULTS

We did not find any significant phylogenetic autocorrelation in residuals of GLMs between MCP unfilled range and age of lineage (SVM model with suitability ≥ 0.5, I = −0.03, P = 0.61; SVM model with suitability ≥ 0.7, I = 0.01, P = 0.43). We also did not find phylogenetic autocorrelation in the residuals of the regression models between IUCN unfilled range and age of lineage (SVM model with suitability ≥ 0.5, I = 0.04, P = 0.3; SVM model with suitability ≥ 0.7, I = 0.01, P = 0.45; Maxent model with suitability ≥ 0.7, I = −0.038, P = 0.65).

The relationship between MCP unfilled range and lineage age was different between modelling algorithms. MCP unfilled range with suitability ≥ 0.5 derived from Maxent did not relate to lineage age (R² = 0.013, P = 0.43). The relationship between MCP unfilled range and lineage age and suitability ≥ 0.7 was also non-significant (R² = 0.0008, P = 0.845) (Fig. 2A,B). On the other hand, MCP unfilled range and suitability ≥ 0.5 derived from SVM show a trend of decreasing inversely with lineage age (R² = 0.15, P = 0.006). The same pattern was found with suitability ≥ 0.7 (R² = 0.16, P = 0.009) (Fig. 2C,D).

In contrast, the relationship between IUCN unfilled range and lineage age did not differ between modelling algorithms. IUCN unfilled range with suitability ≥ 0.7 derived from Maxent showed a trend of decreasing inversely with lineage age (R² = 0.01, P = 0.03) (Fig. 3B). Similarly, IUCN unfilled range with suitability ≥ 0.5 and ≥ 0.7 derived from SVM also showed a trend of decreasing inversely with lineage age (R² = 0.17, P = 0.002; R² = 0.15, P = 0.006; respectively) (Fig. 3C,D). The relationship was only not significant with suitability ≥ 0.5 derived from Maxent (R² = 0.06, P = 0.06) (Fig. 3A).

We did not find significant phylogenetic autocorrelation in the residuals of either model: MCP and IUCN realized range versus age of lineage (I = 0.03, P = 0.36; I = 0.12, P = 0.1, respectively). The relationship between MCP realized range size and lineage age was significant, with lineage age explaining 20% of
the variation in realized range size ($R^2 = 0.2$, $P = 0.004$). The relationship between IUCN realized range size and lineage age was also significant, with lineage age explaining 13% of variation in realized range size ($R^2 = 0.13$, $P = 0.03$). Regardless of the source of the realized range (MCP or IUCN polygons), both models showed the same trend of stabilization of realized range size through evolutionary time (Fig. 4).

**DISCUSSION**

Our results indicate that unfilled range is larger for very young species but becomes rapidly smaller over time. This suggests that species can reach most environmentally suitable areas rapidly after speciation (c. 5 Ma), as predicted by the stasis post-expansion model (Jablonski, 1987). We did not find a linear trend and a gradual increase in range size as a function of lineage age, as suggested by the age–area model. We did find a stasis or equilibrium in range size after 5 Ma, supporting the stasis post-expansion model. This pattern also resembles the two phases recognized by Croizat (1958) in the biogeographic history of a group of organisms: mobilism and immobilism. In the mobilism phase the organisms (of a young species) tend to spread in a given geographic area until they meet restrictive barriers or constraints, when the area of distribution would...
become stable. In the immobilism phase, after the stabilization of the distribution, organisms would be dependent on dynamics of the region (e.g., tectonics, climate change). So if changes in distribution occur, they would be more idiosyncratic and due to these processes of change.

Competition, dispersal limitation and/or time since origin could explain the absence of a clade from regions where environmental conditions are suitable for its presence (Wiens & Donoghue, 2004). Competition is unlikely to explain why old species have filled their potential ranges whereas young species have not, because there is no empirical evidence to support that, in general, old species are better competitors than young species or vice versa. Dispersal limitation might play a leading role in organisms with lower dispersal ability (e.g., crawlers or passive dispersers) than bats. For instance, trees are absent from suitable areas reflecting dispersal limitation into those areas (Svenning & Skov, 2004). For highly vagile organisms such as bats, the increase in range right after speciation may be limited by reproduction because a population must first grow and then send individuals to emigrate and colonize new areas. Once a species is established, it may quickly increase its range to a maximum extent because the initial problems associated with establishment have potentially been solved in the earlier part of the species’ life (Liow & Stenseth, 2007).

However, a species may not colonize all the potential range when unoccupied suitable areas are far from the source population (Paul et al., 2009), even though rare long-distance dispersal events could establish populations far from the source, especially older species that have had more time to disperse into those areas. Indeed, there is a positive relationship between time for immigration since glacial retreat and the occupancy of European plant species (Svenning et al., 2008). New studies including potential range extent (Paul et al., 2009) can provide more clues about age–area relationships.

Our results on lineage age–area relationships showed that MCP and IUCN unfilled range were related differently to lineage age. For instance, there was no relationship between MCP unfilled range and lineage age when potential ranges were derived from Maxent. On the other hand, IUCN unfilled range derived from Maxent was related to lineage age. Such a difference may result from creating a MCP that includes many areas where a species does not occur, because MCP is a data-driven approach that only creates the minimum boundary envelope encompassing all the marginal occurrence points. The IUCN polygons, on the other hand, are drawn by specialists on each group of species based on expert opinion. This knowledge-driven approach creates more complex boundary envelopes that can exclude inhospitable environmental areas or areas where the species does not occur for historical reasons. So, when using a MCP we may have included more unoccupied areas as part of the realized range of a species than when using IUCN polygons. This may have decreased the area of the unfilled range and may probably have hidden the relationship between unfilled range and lineage age.

The IUCN unfilled ranges did not reveal differences in the relationship between unfilled range and lineage age according to distinct modelling algorithms. On the contrary, the relationship between MCP unfilled range and lineage age was different between modelling algorithms, with a significant relationship presented only by SVM. Such a difference may be due how the algorithms fit the data. SVM is a non-probabilistic statistical pattern recognition algorithm that seeks to define a hyperplane in predictor space that separates the target classes. SVM tends to predict a larger area of potential distribution compared with other algorithms, therefore minimizing the omission error (Guo et al., 2005; Franklin, 2009). Maxent is a machine learning algorithm that estimates the most uniform distribution (maximum entropy) across the study area given the constraint that the expected value of each environmental predictor variable under this estimated distribution matches its empirical average (Phillips et al., 2006). Maxent tends to fit data tightly and to predict a smaller area of potential distribution than other algorithms, minimizing commission error (Phillips et al., 2006; Franklin, 2009). These differences can explain the variation found in the results using Maxent and SVM. Therefore, the area predicted by Maxent seems to be a better descriptor of the realized range (Tòrres et al., 2012) while the predicted area by SVM may be closer to the potential range (Guo et al., 2005; Drake et al., 2006). That may explain why SVM provided unfilled ranges that are better associated with lineage age than Maxent. However, it is interesting that when the relationship was significant, they all showed the same pattern regardless of the modelling algorithm and extension range maps used to derive unfilled range (Figs 2 & 3).

Many factors determine the geographic distribution of a given clade, among them the ancestral ecological niche, dispersal limitation (generally imposed by abiotic conditions or a large barrier like the Andes and/or the presence of other competing species) and clade age, which determines how much time it has...
taken for niche evolution and dispersal to occur (Wiens & Donoghue, 2004). Clade age in particular was considered by Willis (1922) to be the main factor driving realized species range size. A positive and linear relationship between age and realized range size is based on the assumption that young species have not reached their climatic boundaries because they have not had enough time to do so (Willis, 1922). However, there is no linear trend between age of lineage and realized range (Fig. 4). Although, the age–area model seems intuitive at first glance, other factors such as climatic tolerance, competitors, predators and physical barriers can prevent range expansion (Gaston, 2003).

Although we modelled unfilled range as a function of lineage age, the scatter plots of this relationship are similar to a constraints envelope (Figs 2 & 3). In this envelope young species exhibit both large and small unfilled ranges whereas old species have only small unfilled ranges. This envelope is a consequence of absence of older species having larger unfilled ranges. This indicates that colonization of potential areas through evolutionary time is based on time after speciation. Older species are more diverged from the common ancestor and have larger range filling than younger species.

Natural disturbance such as climate change and anthropogenic impacts have shifted species ranges in the past (Nogués-Bravo et al., 2008) as well as in the present (Parmesan, 1996). Some models such as age–area and stasis post-expansion did not explicitly include extinction in their predictions. However, extinction is a natural evolutionary process, and this is an underlying mechanism for all models on age and area (Foote et al., 2007; Liow & Stenseth, 2007). Anthropogenic impacts such as deforestation and climate change caused by greenhouse gases can accelerate the extinction process and distort the relationship between potential/realized range and lineage age, mostly affecting those studies that analyse species occupancy throughout species ranges. There are three ways that species extinction accelerated by anthropogenic impact can hide age–area relationship: (1) the youngest species having both small range size and small population size can be driven to extinction even before they are discovered by scientists; (2) after species establishment, they cannot increase their range because there is no suitable habitat to colonize; and (3) species that are increasing their ranges are forced to stop increasing their range and/or decrease their range.

Most fossils of young bat species, such as *Pygoderma bilabiatum*, *Mimon bennettii* and *Chiroderma doriae* that arose c. 5 Ma (early Pliocene), have been found within their current distribution (Czaplewski & Cartelle, 1998; Hadler et al., 2010). Therefore, the fossil record suggests that young species are living in areas occupied since at least the Pleistocene (2 Ma). We cannot claim that the range of a species has increased over time by relying on the fossil record alone because we do not know with certainty when and where a species has arisen. However, the occurrence of fossils where species are found currently does indicate that those areas occupied in the past are still suitable at present. Nevertheless, climate and vegetation have not been stable over geological time. In South America, mammalian clades of the Amazon are closely related to the mammals of the Atlantic Forest (Costa et al., 2000). The Amazon and Atlantic Forest were connected in the past, suggesting that species ranges may have been larger. Changes in climate, and consequently in vegetation, across the Pleistocene probably shifted mammal species ranges in South America (Costa, 2003). Most phyllostomids in South America seem to have arisen in the late Miocene (mean age 8.2 Ma) and they probably suffered range expansion/contraction because of changes in vegetation cover caused by climate change in the Pleistocene. Unfortunately, the fossil record for bats is scarce and mostly from the same geological epoch (Eiting & Gunnell, 2009), making inferences on species range shifts weaker.

We found support for the stasis post-expansion model. However, Pigot et al. (2012) showed that a stochastic model can generate all empirical age–area relationships. They suggested that trends in range dynamics cannot be simply interpreted as evidence of a directional range size evolution. Moreover, different effects of lineage age on realized range size tend to be clade specific (Webb & Gaston, 2000; Paul et al., 2009), considering the evolutionary differences that distinct clades are subjected to and that all species interactions affect population dynamics, which should be greater for more related species. Furthermore, Pigot et al. (2012) also suggested that the fossil record might provide a more reliable signal of range evolution than phylogenies such as the one used here.

However, our conclusions do not rely exclusively on the relationship between lineage age and realized range size but also on the relationship between unfilled range and lineage age. Both approaches (unfilled range and realized range versus lineage age) used here indicated that phyllostomid species can increase their distributions and fill their potential ranges rapidly after speciation and once a species has reached stasis in range size (c. 5 Ma), this equilibrium is maintained for a longer time-scale before species go extinct. Similar results were found in large African mammals, which have initially small ranges after speciation and increase their ranges through time, reaching a long-term equilibrium abundance by c. 1 Myr later (Vrba & DeGusta, 2004). Jones et al. (2005) also found support for models of rapid range expansion for primates and carnivores, but they suggest that the taxon cycle is a better approximation for the pattern found. Our results suggest that the stasis time can be longer through the entire existence of a species. Once a species reaches stasis in range size (c. 5 Ma) this condition is maintained for a long period of time, at least 20 Ma, before going extinct (Fig. 3).

In summary, we have shown by using different regression models that old phyllostomid species have smaller unfilled ranges than young species. That is, old species have filled most of their suitable areas and this condition (stasis) is maintained over time, thus supporting the stasis post-expansion model. Furthermore, old species have larger realized ranges than young species. However, no species will exist forever since extinction is a natural evolutionary process. When this natural process is associated with anthropogenic impacts extinction rates can be quick. Moreover, understanding how species occupy current suitable climates is critical for understanding and forecasting the poten-
tial responses of species to climate changes (Munguia et al., 2012). Abundance levels at range boundaries can be used to estimate range expansion/contraction. Thus, new studies addressing abundance levels of phyllostomid species at the boundary of their distribution could support the idea that ranges of very old species are declining if abundance is low. On the other hand, if distributions of young species are expanding, we would expect such species to be relatively more abundant at their boundaries.

ACKNOWLEDGEMENTS

We are grateful to Jayme A. Prevedello, Lorelei E. Patrick and Maria Mercedes Gavilanez for reviewing the first draft of this manuscript. We would also like to thank three anonymous referees and the handling editor José Alexandre Diniz-Filho for criticisms and suggestions that improved the earlier version of this manuscript. M.M.W. is grateful to CAPES for his scholarship, and C.E.V.G. to CNPq for a research productivity fellowship and grants, and to FAPERJ for the JCE Project.

REFERENCES

Abellán, P. & Ribera, I. (2011) Geographic location and phylogeny and grants, and to FAPERJ for the JCE Project.


**SUPPORTING INFORMATION**

Additional supporting information may be found in the online version of this article at the publisher’s web-site.

**Appendix S1** Supplementary methods.

**Appendix S2** List of bat species considered in this study.

**BIOSKETCH**

**Marcelo M. Weber** has a PhD in ecology from the Federal University of Rio de Janeiro (UFRJ). His interests are macroecology, biogeography and the use of ecological niche modelling to understand macroecological and biogeographic patterns.

Editor: José Alexandre Diniz-Filho