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Climate change and amphibian diversity patterns in Mexico

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ABSTRACT

The aim of this article is to characterize at fine scale alpha and beta diversity patterns for Mexican amphibians and analyze how these patterns might change under a moderate climate-change scenario, highlighting the overall consequences for amphibian diversity at the country level. We used a geo-referenced database gathered from museums worldwide as a basis for climatic envelope models, based on the working assumptions that we can accurately model the ecological niche, niche conservatism, and that the future climate scenario is realistic. We generated six sets of models with different parameters (threshold of presence and dispersal capability) in the modelling processes. We simulated the base line (2000) and future scenarios for Mexican amphibian diversity (2020, 2050, 2080), using climate data layers constructed for Mexico. Using moving-window analyses of different sizes (9, 25, 100, 225 and 400 km^2) we calculated beta diversity with R.H. Whittaker's formula $\beta = \gamma/\alpha_{\mathrm{mean}}$. We analyzed the changes of alpha- and beta-diversity spatial patterns during these periods, and performed an analysis of sensitivity for the beta-diversity patterns. We found that setting low dispersal capability generates high levels of species extinctions, but the overall geographic pattern of beta diversity remained *stable*. Zones of high beta diversity resulted that were associated with topographic formations, while the values of beta diversity initially increased, and then declined over time. Extinctions (complete loss of range within country boundaries) were particularly intense during the period 2020–2050. The results implied that heterogeneous zones associated with mountain ranges will remain particularly important for amphibian diversity and thus constitute areas for continued conservation prioritization in the face of climate change.

1. Introduction

We live in an era of accelerating global environmental changes. One of the most important global change processes is habitat fragmentation, which has been recognized as the principal cause of terrestrial diversity loss (Cushman, 2006). However, many scientists argue that climate change may become a greater threat in the next few decades (Malcolm et al., 2006).

It has long been recognized that climate is a major controlling factor for species distribution (e.g. Currie, 1991; Hawkins et al., 2003; Pearson and Dawson, 2003). Recent evidence shows a direct effect of climate change on shifts in species distributions, including the expansion, reduction, and disappearance of individual species ranges (Hughes, 2000; Walther et al., 2002; Perry et al., 2005). Climate change effects on complete assemblages have been less studied and those studies have been focused on coarse-scale datasets (e.g. Araújo et al., 2006; Jetz et al., 2007; but see Peterson et al., 2002). Based on modelled species range shifts, studies have shown general changes in projected patterns of diversity. A common emergent finding is that the location of hotspots and areas with high numbers of endemic or endangered species will change and some may disappear (e.g. Malcolm et al., 2006).

Amphibians have been identified as one of the most threatened groups in the world (Young et al., 2001; Rohr et al., 2008) and there is concern that global climate change may greatly increase threats to many amphibian populations (Blaustein et al., 2001; Corn, 2005). Mexico is home to more than 372 species and possesses one of the highest levels of endemism worldwide (>65%). Mexican amphibians may be anticipated to be severely threatened by climate change (García, 2006) because around 80% of the endemics are actually micro-endemics (Ochoa-Ochoa et al., 2011), with the highest concentration in the south of the country. Mexican amphibians exhibit both a latitudinal gradient in species richness (Ochoa-Ochoa and Flores-Villela, 2006), and high beta diversity at fine (e.g. Pineda and Halfter, 2004) and coarse scales, with higher values towards southern latitudes (Flores-Villela et al., 2005). Surprisingly, despite the high species richness and endemism, there have been no fine-scale analyses of the effects of climate

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change on the biodiversity patterns of this group of vertebrates for Mexico (e.g. Hof et al., 2011).

Alpha (species richness within a community), gamma (species richness in a landscape) and beta diversity (variation in species composition across communities within a landscape) are important concepts to understand the patterns and the processes of communities. Geographical gradients of species richness (alpha and/or gamma) have long been studied (e.g. Pianka, 1966; Hawkins et al., 2003) and while a single global model of spatial variation in species richness remains elusive, a high proportion of variance in regional and global biodiversity models is attributable to climate, especially to the dynamics of water and energy regimes (e.g. Whittaker et al., 2001; Hawkins et al., 2003; O'Brien, 2006).

Beta diversity metrics provides insight into the spatial pattern dynamics of species (Drakare et al., 2006; Soininen et al., 2007) and are relevant in conservation planning (Gaston et al., 2001). For example, the high beta diversity of Mexican mammals reflects the existence of a large number of range restricted species within the country (Arita and León-Paniagua, 1993). Similar characteristics in spatial variations of beta diversity for amphibians can be observed across Mexico as there are many micro-endemic species, a high proportion of which are associated with specific mountain ranges, featuring strong environmental gradients. From a conservation biogeography perspective (Whittaker et al., 2005) diversity patterns of amphibians for the country would thus be better characterized by the variations in beta than alpha diversity.

Until now no consensus about the form of the relationship between beta diversity and latitude have emerged (Rodríguez and Arita, 2004; McKnight et al., 2007), as it depends on the method and scale of analysis selected (Koleff et al., 2003). Notwithstanding that environment seems to play a crucial role in the structure and patterns of beta diversity (Legendre et al., 2005), we may expect a latitudinal gradient due to the location of micro-endemics, but we currently lack a clear basis for predicting the form of the pattern and how it may change as a function of changing climate in the study region.

In principle, under a climate change scenario, spatial patterns in local 'alpha' and regional 'gamma' diversity could, to some extent, be decoupled during a period of species distributional resorting (cf. Whittaker et al., 2001). As beta diversity registers the re-arrangements of species distribution ranges across space, following the patterns of beta diversity may thus provide early indication of how ongoing local changes in distribution impact the biodiversity patterns. Following this, there are three possible outcomes in terms of beta diversity pattern at the scale of Mexico as a whole: no change, homogenization, or increased differentiation. The first scenario, of unchanging beta diversity pattern, can be defined as the *stable beta hypothesis*. For this scenario, the mean of distribution range sizes has to remain more or less the same, and any increase or decrease in alpha and gamma diversity has to be proportional across the study system, e.g. if gamma decreases alpha decreases at the same rate. A second scenario, in which decreasing values of beta diversity occur, can be termed the *homogenization hypothesis*. In this case the mean size of the distribution ranges would increase, either through the extinction of micro-endemics, or due to the expansion of species ranges. The third case, whereby beta diversity increases, could be termed the *heterogenization hypothesis* and would correspond with a decrease in the mean of the distribution range sizes, either through the incursion of micro-endemic species into the study area, or through the net contraction of species ranges. These projections of course take no account of any gains from migration into Mexico of non-native species. These three scenarios outline a set of hypothetical responses to climate change in biodiversity measures that are based on differing abilities of species to accommodate environmental change locally (i.e. broad–narrow fundamental niches), resulting in changing local patterns of species richness, and in turn altering patterns of beta diversity. We suggest that these hypotheses can theoretically be applied to any group and place.

In this paper we used Mexican amphibians as an assemblage and climate change scenarios as the only driver to explore the changes of diversity patterns from a baseline to three future points in the 21st century, with an emphasis on the patterns in beta diversity, focussing on the three possible scenarios described above. In addition, to explore sensitivity of our analyses to input values, we evaluated the effects of altering parameters for presence–absence threshold, dispersal capability and window size.

2. Materials and methods

2.1. Distribution ranges in the baseline

We used a database containing around 418,500 data points of amphibians and reptiles, with 27,419 unique collecting localities, corresponding to 363 of the 372 species of amphibians that inhabit Mexico (Museums and projects that contributed data are listed in Appendix A). The database consists of geo-referenced species presence records, gathered from various museums worldwide, and was geographically and taxonomically verified by experts (for further details, see Ochoa-Ochoa and Flores-Villela, 2006). These records were used to model the range distribution of each species through a climatic envelope modelling approach (CEM). This modelling approach assumes that climate is a major contributing factor for species distributions (Pearson and Dawson, 2003). Thirty micro-endemic species from 145 inhabiting the country (Ochoa-Ochoa et al., 2011) were found too have too few data points to generate an accurate model for the baseline. The remaining analyses reported below are thus based on models for the remaining 115 micro-endemic species, as well as all the non-micro-endemic (218 species). In total 333 species were analyzed.

There are several papers that discuss CEM caveats, ranging from the concepts (e.g. Hirzel and Lay, 2008; Soberón and Nakamura, 2009) to the methods (e.g. Pearson et al., 2006, 2007). In general, limitations of databases, sampling bias, decisions made on choice of modelling method, the climate change scenarios adopted, and parameters such as threshold of presence and dispersal rate allowed in the modelling are each important in determining model outputs (Whittaker et al., 2005; Lozier et al., 2009; Phillips et al., 2009; Pineda and Lobo, 2009). The spatial representation of the resulting ecological niche model in CEM analyses is therefore best regarded as a *proxy* of the range distribution of the species (potential distribution) in the context of a particular set of assumptions about future climate and species response capabilities.

For the CEM process we used climate layers (monthly precipitation, maximum and minimum temperature) developed for Mexico, with a spatial resolution of $0.008'$ or $\sim 1\ \text{km}^2$ (Téllez, 2004) to generate 19 climate variables using Hijmans' script (2006). Several of these data layers capture the interactions between temperature and precipitation, reflecting key aspects of climatic seasonality (Table A1 in Appendix A). We used a Maximum Entropy modelling approach (MaxEnt; Phillips et al., 2004, 2006) to model the species distribution ranges based on climate data for Mexico. We selected 2000 as the baseline. We used climate data averaged across the 30 year period up to 2000 to provide robust estimates of climate means. We also evaluated other sources of variability such as threshold of presence, dispersion and window size. To assess the importance of the chosen threshold, four levels were tested, following precedents established in previous work: these were 50% probability of presence, 70% probability of presence, the 10th percentile training presence of the logistic threshold of the distribution model, and the lowest presence threshold (see Liu et al.,