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Linking diversity and distribution to understand biodiversity gradients and inform conservation assessments

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Abstract. Broad-scale patterns of species richness result from differential coexistence among species in distinct regions of the globe, determined by the species' ranges and their properties such as size, shape and location. Thus, species richness and ranges are inherently linked. These two biodiversity features also yield primary information for conservation assessments. However, species richness and range size have been usually studied separately and no formal analytical link has been established. In my PhD thesis, I applied and extended a recently developed conceptual and methodological framework to study geographical association among species and similarity among sites. This range–diversity framework, along with stochastic simulation modelling, allowed me to jointly evaluate the relationship between diversity and distribution, to infer potential processes underlying composite patterns of phyllostomid bats, and to use this approach to inform conservation assessments for the Mexican avifauna. I highlight the need to explore composite patterns for understanding biodiversity patterns and show how combining diversity and distributional data can help describe complex biogeographical patterns, providing a transparent and explicit application for initial conservation assessments.

Keywords. species richness, range size, diversity field, range–diversity plots, conservation biogeography, stochastic models

One of the most conspicuous biodiversity patterns is the geographical variation in species richness. Its proper description and assessment form the basis of informed conservation actions (Willig et al. 2003, Knight et al. 2006). However, explaining the causes of geographical species richness patterns remains elusive (Mittelbach et al. 2007). These patterns result from the differential coexistence of species in different regions of the globe, in turn determined by the properties of species' geographical ranges such as size, shape, location and overlap (Gotelli et al. 2009). Traditionally, correlative approaches have identified climate variables describing geographical variation in species richness, assuming that climatic gradients underlie biodiversity gradients (Field et al. 2009). More recently, alternative approaches favour the inclusion of processes determining species' geographical ranges within a mechanistic modelling framework to assess the potential causes of macroecological patterns. Following this approach, biodiversity gradients can be studied by simulating

the dynamics of ranges under different combinations of underlying variables (Colwell et al. 2009).

In most of these approaches, species richness has been the sole response variable, with the predictive power of different models being assessed using various goodness-of-fit statistics comparing observed versus expected richness values (Gotelli et al. 2009). However, evaluating single predictions (i.e. one response variable) based on correlates of empirical patterns represents only weak testing of mechanisms (McGill 2003). Alternatively, comparing different patterns between observed and modelled data, such as range-size frequency distributions (Rangel et al. 2007), mean range size of species assemblages (Hawkins and Diniz-Filho 2006), nestedness (Ulrich et al. 2009) or the variation in beta diversity (Tuomisto 2010) can be used to compare results among different models, providing more comprehensive tests of potential underlying mechanisms (Stevens et al. 2013).

Response variables from any biological sur-

vey can be summarized in species x sites matrices, with entries representing attributes of species over sites (Bell 2003). For instance, such a matrix can record the occurrence of a given species in a given site, either as binary (occurrence) or quantitative (abundance) data. At broad spatial scales, abundance data are seldom available; thus macroecological studies typically rely solely on species occurrences at a collection of sites or grid cells, obtaining presence–absence matrices (PAMs). The two most basic variables for macroecology and conservation biogeography, species richness of sites and range sizes of species, can be easily calculated from such a PAM. However, even when both variables come from the same basic information (presence–absence data), they are usually treated separately and a satisfactory link between species richness and range size has not yet been reached (Borregaard and Rahbek 2010). Arita et al. (2008) developed a framework to forge this link by defining composite variables simultaneously considering species richness and range size. They also introduced Range–Diversity (RD) plots to depict and evaluate the inherent relationship between these variables, enabling researchers to link patterns of diversity and distribution when testing biogeographical hypotheses and conducting conservation assessments (Borregaard and Rahbek 2010, Arita et al. 2012).

In my PhD dissertation I applied and extended this recently developed theoretical framework to analyze geographical patterns of biodiversity, simultaneously linking diversity (species richness) and distribution (geographical range). More specifically, I applied it to explore geographical associations among species (co-distribution) and similarity among sites (co-diversity) to infer their potential causes, and extended it to inform conservation assessments based on species richness and range size. The thesis was divided into three main chapters with the following objectives: 1) describe the species-richness frequency distribution (SRFD) and internal structure of species' ranges, using the New World leaf-nosed bats (Phyllostomidae) as a case study (Villalobos and Arita 2010); 2) evaluate co-distribution and co-diversity patterns in this bat family under a null

modelling approach (Villalobos et al. 2014); and 3) apply the conceptual and analytical tools developed during my PhD for conducting conservation assessments, using the diversity–distribution relationship of the Mexican avifauna as an example (Villalobos et al. 2013a).

For chapters 1 and 2, I built a database of geographical information based on the continental (non-insular) distribution of phyllostomid bat species. Distributional maps (extents of occurrence) were built using ArcGIS with data from the primary literature up to 2007 and from the Nature Serve database (Patterson et al. 2007). I generated the presence–absence matrix by overlying an equal-area grid (0.5° cell resolution) onto the distributional maps. In chapter 1, I explored each species' 'diversity field' (the set of species-richness values of sites within the range of a given species) and applied two null models that stochastically simulated scattered and cohesive ranges, respectively. In chapter 2, I investigated both co-distribution among phyllostomid species and co-diversity among phyllostomid assemblages (sites). For this chapter, I explicitly evaluated the relative contributions of climate and niche conservatism in shaping co-distribution and co-diversity patterns. I did this by generating different scenarios derived from stochastic null models simulating contrasting forms of range construction, namely range growth controlled by climate and the inheritance of geographical location and climatic preferences (i.e. niche conservatism) among closely related species. By-species and by-sites RD plots (Arita et al. 2008) were built to depict co-distribution and co-distribution patterns, respectively. Variance-ratio tests (Schluter 1984, Arita et al. 2012) were used as descriptive parameters summarizing such patterns, and for statistical inference based on contrasting observed parameters against those generated by the null models.

In chapter 3, I wanted to extend the range–diversity framework to inform and compare among different conservation assessments. Therefore, I needed more detailed data, not only on distribution but also on previously conducted conservation assessments on a regional scale. Thus, I decided to use the relatively well known Mexican

avifauna to apply the novel range–diversity framework. I obtained maps of terrestrial and resident bird species from the Mexican Commission for Biodiversity (CONABIO) and created the presence–absence matrix by overlying an equal-area hexagonal grid (256 km² per cell) onto these maps. I repeated the analyses including only those species endemic to Mexico. I then examined spatial congruence between species richness and rarity of Mexican birds using a by-sites RD plot, describing the assemblages (in terms of per-site range size) to determine whether sites harbouring high numbers of species were inhabited by restricted-range or more widespread species. I used a quantile approach to define subsets of sites with different combinations of richness and range-size values. A ‘richness–rarity’ quartile represented those sites lying above the third quartile of species richness (i.e. cells with highest proportional richness) and below the first quartile of range size values (i.e. cells with lowest mean range size).

Chapter 1 (Villalobos and Arita 2010) introduced the concept of ‘diversity field’ to analyze the internal structure of species’ geographical ranges and represented the first analysis of SRFDs and their statistical properties in a major taxon (bat family Phyllostomidae) and individual species. Phyllostomid bats showed a strong pattern of positive geographical association among species that differed from null-model expectations. Most of these bats coexist with a higher number of other phyllostomids than the average richness within the continent. A detailed description of co-distribution and co-diversity patterns for this family of bats was done in Chapter 2 (Villalobos et al. 2014), under a null modelling approach and using variance ratios to evaluate the patterns’ statistical significances. The effect of range cohesion through climatic conditions and niche conservatism among species was identified, as well as the influence of other factors such as domain boundaries and continent size and shape in creating analogue statistical signals between observed and modelled patterns (richness variation, positive co-distribution and co-diversity). Significant deviations from expected patterns suggested the influence of additional historic and adaptive mecha-

nisms (speciation, extinction, dispersal) contributing to a stronger geographical association among species and a resulting similarity among sites occupied by phyllostomid bats.

Range–diversity plots and the ‘diversity field’ and ‘dispersion field’ concepts (Borregaard and Rahbek 2010) can be readily applied to identify geographical patterns of biodiversity relevant to biological conservation planning (Villalobos et al. 2013a). Studying the diversity–distribution relationship in the Mexican avifauna, under the ‘by-sites’ approach, I discovered a negative relationship between species richness and mean per-site range size. That is, species-rich sites tend to be occupied by birds with relatively restricted ranges (rare species). A similar pattern was found for endemic birds, although I also identified species-poor sites occupied by geographically restricted birds. Also, I identified a set of sites with both attributes (high richness and restricted ranges: richness and rarity), whose representation within priority sites turned out to be low. Additionally, I detected a set of restricted species coexisting with few other birds. These species, and the aforementioned sites for endemic birds, could easily be omitted from conservation plans formulated only from species richness patterns (so-called hot-spots), highlighting the relevance of considering both aspects of biodiversity (richness and rarity) when planning for conservation.

Biogeography and macroecology aim to describe and understand spatial patterns of biodiversity and their results can provide primary information for conservation assessments and planning (Whittaker et al. 2005, Villalobos et al. 2013b). However, many biogeographical and macroecological studies still focus on single response variables and do not consider the multifaceted nature of biodiversity. In my thesis, I showed how the use of primary biogeographical information (presence–absence) and the simultaneous consideration of species richness and geographical distribution allow more informative description of biodiversity patterns, potentially providing stronger inference on causal processes. Additionally, such a multiple-pattern approach, coupled with stochastic simulation models including specific processes,

can help investigate the relative influence of these processes. Applying this approach, I found that geographical association among species and similarity among sites of the bat family Phyllostomidae are driven by a combination of factors beyond simple geometric and geographical constraints and not limited to climatic conditions or historical contingency. I also showed that integrating different biodiversity features better describes complex biogeographical patterns and helps conduct informed conservation assessments.

Finally, I would like to point out that all patterns and approaches described and developed in my thesis can be easily extended to other taxonomic groups and geographical regions, facilitating the comparison among different data sets. I hope these methods will provide a more comprehensive understanding of geographical patterns of biodiversity and contribute to conservation of that biodiversity.

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