



Range–diversity plots for conservation assessments: Using richness and rarity in priority setting

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ABSTRACT

Current claims of biodiversity crisis call for immediate conservation actions. These require the identification of priority sites for conservation based on an assessment of biodiversity patterns. Patterns of species richness are crucial in such endeavor. Also rarity, measured by the size of species' geographical ranges, is often used as a single or complementary criterion. For instance, hotspots for conservation have been defined using either one or the other criterion. We apply a novel tool, range–diversity plots, which simultaneously analyze species richness and range size from a presence–absence matrix to identify sites and species with potential conservation value. We applied this tool to the Mexican avifauna and show how it can be readily used to conduct broad-scale conservation assessments. Mexican birds showed congruent patterns between richness and rarity, richer sites harbor small-ranged species. Also, we identified Mexican ecoregions harboring richness–rarity sites and compared our assessment with an exhaustive prioritization procedure. A range–diversity approach can be useful when fine-scale information is lacking, such as in poorly studied regions. We demonstrate that spatial congruence between richness and rarity can be easily identified and interpreted using range–diversity plots based solely on a presence–absence matrix, providing a transparent, robust and explicit application for conservation assessments.

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1. Introduction

Current claims of an unprecedented biodiversity crisis, namely species extinctions, call for effective conservation measures (Barnosky et al., 2011). Spatial assessments involving the identification of important areas or species for conservation represent the first step towards adequate conservation planning and implementation (Cowling et al., 2004; Knight et al., 2008). Further, limited funding demands prioritization of those areas or species to ensure efficient use of resources and effective conservation action (Wilson et al., 2007). However, the identification of priority areas or species is not free of difficulties, especially regarding the criteria used to define them.

Common criteria in assessing priority areas broadly referred as “hotspots” or “crisis ecoregions” include total species richness, number of threatened and endemic or narrow-ranged species (Brooks et al., 2006; Wilson et al., 2007). In parallel, priority species are usually defined using the latter two criteria, threat level and rarity, based on either range size or abundance (Gauthier et al.,

2010). Total species richness represents a simple and obvious target of any conservation effort. In contrast, determining the number of threatened species requires a case-by-case evaluation of species and their threats, implying huge amounts of data and time (e.g., IUCN's RedList). A common and straightforward way to define species as threatened is to consider their geographical range sizes (Gaston, 1994). Species with geographically restricted distributions are deemed either rare or endemic. Such restrictedness can be defined by political units or biomes delimiting the domain of interest or, more broadly, as the lower percentiles of a range size frequency distribution (Jetz et al., 2004; Orme et al., 2006).

Contention around “hotspot” assessments relies on the potential spatial congruence of such priority areas when defined by different criteria. Although the issue remains controversial, several lines of evidence suggest that there is little congruence at least for two of the criteria: species richness and rarity/endemism. First, empirical data show that hotspots of richness and endemism do not have the same spatial distribution (Ceballos and Ehrlich, 2006; Grenyer et al., 2006; Orme et al., 2005). Second, widespread species seem to exert a disproportional effect on patterns of species richness, as compared with restricted taxa (Jetz and Rahbek, 2002; Lennon et al., 2004).

Here we apply a novel methodological framework and visual analytical tools, called the Range–Diversity (RD) plots (Arita et al., 2012), for a conservation assessment of areas and species.

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Our purpose is to show how congruent patterns of species richness and rarity, measured by range size, can be readily used to inform conservation actions. We used Mexican birds as case study and previous prioritizations within Mexico to exemplify the usefulness and applicability of RD plots. Based solely on primary biodiversity information (i.e., species presence–absence data) under a conservation biogeography approach (Whittaker et al., 2005), RD plots provide a straightforward application for broad-scale conservation assessments.

2. Materials and methods

2.1. Distributional data

Bird distribution maps were obtained from the Mexican Commission for Biodiversity (CONABIO), generated by expert groups (Navarro-Sigüenza and Peterson, 2007) and based on the “Atlas of the Birds of Mexico” database (Navarro-Sigüenza et al., 2003). These ranges were generated using the Genetic Algorithm for Rule-set Prediction (GARP) at a resolution of 1 km² and then “trimmed” on the basis of experts’ knowledge (see Lira-Noriega et al., 2007 and Navarro-Sigüenza and Peterson, 2007; for details on this process). We restricted our analyses to 655 terrestrial and resident species. We overlaid an equal-area hexagonal grid (256 km² per cell) onto the distribution maps and constructed a presence–absence matrix of $N = 7887$ sites \times $S = 655$ species. This grid was chosen to allow comparison between our approach and previous prioritizations of the Mexican territory using the same grid (see Section 2.4). We repeated the analyses including only those species entirely restricted to Mexico, hereafter endemics. In this case, we considered 98 species and constructed a presence–absence matrix of 7834 sites \times 98 species.

2.2. Analytical framework

Each type of information, distribution and diversity, is usually treated separately to describe and analyze patterns of either range size (Arita et al., 1997; Orme et al., 2006) or species richness variation (Hillebrand, 2004; Willig et al., 2003). Here we simultaneously obtained information from both variables, species richness and range size, using a recently described macroecological approach called Range–Diversity (RD) plots, to conduct conservation assessments under biogeographic analyses (Arita et al., 2012; Whittaker et al., 2005).

Range–Diversity (RD) plots are scatter-plots depicting information on range size and species richness simultaneously. There are four vectors of numbers used to construct RD plots: (i) the proportional (to S) species count in every one of $j = 1, 2, \dots, N$ sites, that we denote by \mathbf{s} and (ii) the proportional (to N) size of the range of every one of $i = 1, 2, \dots, S$ species, denoted by \mathbf{n} . The mean value of any of these two vectors gives the inverse value of Whittaker’s multiplicative beta diversity (Arita et al., 2008), and represent fairly well known quantities. (iii) The mean proportion of species inhabiting every site in the range of species i is called the “diversity field” (Arita et al., 2008), denoted by \mathbf{D} . The numbers in \mathbf{D} are less well-known quantities that measures how rich in species are the localities composing the range of a species. Finally, (iv) the mean proportional (to N) range of distribution of the species inhabiting a site is called the “dispersion field” (Graves and Rahbek, 2005), denoted by \mathbf{R} . It measures how widespread are the species living on a given site. These four vectors, plotted in pairs, constitute the by species (\mathbf{n} vs \mathbf{D}) and by sites (\mathbf{s} vs \mathbf{R}) RD plots, respectively (details in Arita et al., 2012; Soberón and Ceballos, 2011).

In RD plots by species, axes correspond to the mean proportional range richness and the proportional range sizes of species,

in the abscissas and ordinates, respectively. In RD plots by sites, axes represent the mean proportional per-site range size and the proportional species richness of sites, in the abscissas and ordinates, respectively. Location of points within RD plots is limited by biological and mathematical constraints determined by the minimum and maximum richness and range size, while the central tendency is determined by Whittaker’s beta diversity of the system (i.e. the proportional fill of the PAM; Arita et al., 2008). Furthermore, the detailed dispersion of points within those limits depends on the overall covariance among species or sites, which is ultimately determined by the patterns of species’ co-occurrence. Specifically, the covariance of a species with respect to the rest of species depends on the number of species with which it shares its distribution, whereas the covariance of a site depends on the number of sites with which it shares species (Arita et al., 2008). In general, points arranging to the left side of the plot’s vertical line represent negative covariances whereas points to the right correspond to positive covariances (see Fig. 1 for a simplified version of RD plots and interpretation of point dispersion within them).

2.3. Congruence between diversity and distribution

We examined the spatial congruence between species richness and rarity of the Mexican avifauna using a RD plot by sites. We described the assemblages (in terms of per-site range size) present in each site and determined if sites harboring a high number of species were inhabited by restricted or more widespread species. We focused our exploration on the extreme values of species richness (i.e., higher) and per-site range size (i.e., smaller). To do this, we followed a quartile approach commonly used as a pragmatic criterion to define richness hotspots and rarity of species (e.g., Jetz et al., 2004; Orme et al., 2005, 2006). We divided the RD plot axes in quartiles defining regions representing distinct assemblages. For instance, we defined a region where sites harbor species assemblages of high richness and small ranges (i.e., fourth quartile of richness and first quartile of per-site range size, hereafter richness–rarity quartile). Separation of points within the RD plot, when performed linked to a map, immediately identifies regions with different combinations of richness and degree of rarity. Accordingly, we also described the spatial distribution of richness–rarity sites within Mexico.

In addition, we explored the pattern by species. Using a RD plot by species, we examined the species’ co-occurrence patterns describing the geographic association among species (Villalobos and Arita, 2010). In this case, we were interested in the diversity field of species with restricted ranges in order to describe their tendency to coexist with either low or high numbers of species. We present distribution maps of four species, along with their correspondent species richness frequency distribution (SRFD) within individual ranges, to exemplify species’ patterns. The SRFD and its skew value (g_1) describe the variation of species richness within a species’ range and, with the aid of range maps, they help inspecting the richness structure at different parts of the focal species’ range.

2.4. Mexican ecoregions and priority sites

At global and regional scales, priority areas such as ecoregions or hotspots represent templates to guide conservation efforts and attract further attention (Brooks et al., 2006). To evaluate the usefulness of our richness–rarity sites in providing such a template, we compared them with previous regionalization and prioritizations of the Mexican territory. We used Level I Mexican ecoregions representing a coarse-scale regionalization of North American ecosystems (CEC, 1997; INEGI et al., 2007) and a recently proposed set of priority sites for Mexico produced by an exhaustive gap analysis

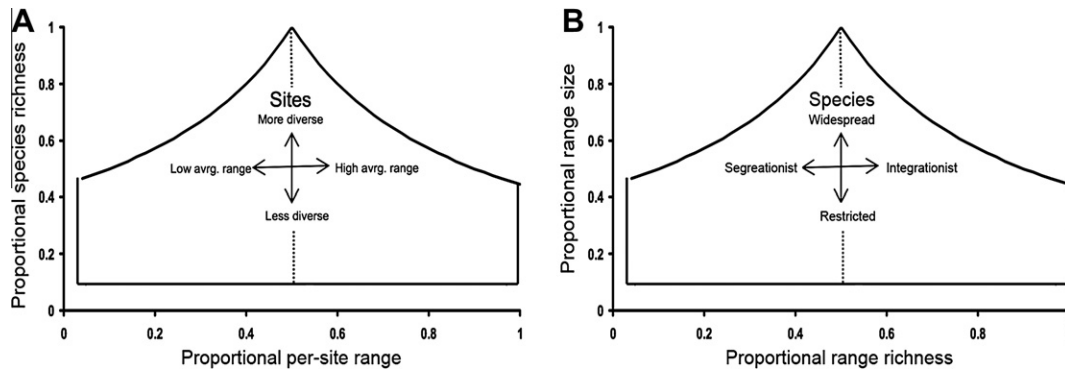


Fig. 1. Range–diversity plots (A) by sites and (B) by species. In both plots, the solid curved lines mark the upper theoretical limit for points; the vertical dashed line corresponds to the mean proportional (A) range size and (B) range richness.

based on different vertebrate and plant taxa and pressure factors (Urquiza-Haas et al., 2009). We explored the position within the RD plot of sites belonging to ecoregions (ERs) and priority sites (PSs), and quantified the number and proportion of sites within the richness–rarity quartile overlapping the PS set and present at different ecoregions. Mapping of sites within the RD plot and their geographic distribution was performed with ArcGIS 9.3 (ESRI, 2009).

3. Results

3.1. Distribution of bird diversity and range-size assemblages

3.1.1. Total bird species

The largest concentration of species occurs from the lowlands of the Gulf of Mexico through the Isthmus of Tehuantepec to the highlands of Chiapas, peaking at 354 species (54.05%) in a single grid-cell (Fig. 2A). On the other hand, the lowest concentration of species is in the central–northern regions of the country characterized by the presence of large desert areas harboring widespread bird species (Fig. 2B).

Range-size assemblages, sites with different per-site mean range size, showed an opposite geographic pattern to that of species richness. Sites harboring, on average, widespread species locate at central–northern parts of Mexico whereas sites inhabited by more restricted species, on average, are located towards south-eastern regions (Fig. 2B). Altogether, the Mexican avifauna had a Whittaker's beta of 4.97, which is equal to the reciprocals of the average proportional species richness and the average proportional range size in the system ($S/Beta = 131.87$; $N/Beta = 1587.89$), meaning that sites contain, on average, 20.13% of the species (131.87), and that the average bird species occurs in 20.13% of the sites (1587.89).

3.1.2. Endemic birds

Endemic species richness peaked at western, central and southern highlands of Mexico and was lower at the lowlands of Tabasco, northern Chiapas, both peninsulas (Yucatan and Baja California), and the Chihuahuan desert (Fig. 2C). Richest sites in endemics hold almost 50% of these species, whereas a few sites were not occupied by any endemic species.

Range-size endemic assemblages occupied mostly by restricted species were distributed at western, central and southern highlands whereas sites harboring mostly widespread endemic species were located at northern–central, northeastern and parts of the gulf lowlands (Fig. 2D). Spatial turnover of endemic species, measured by Whittaker's beta, is greater than the total species value ($Beta = 7.95$). In this case, an average site contains 12.58% of ende-

mic species and an average endemic bird occurs on 12.58% of the territory ($S/Beta = 12.33$; $N/Beta = 985.89$).

3.2. Range–diversity plot by sites

3.2.1. Total bird species

Points (i.e., sites) arranged to the left side of the RD plot with a right-side tail (Fig. 3A). All points fell to the right side of the proportional fill value indicating that, on average, all sites covaried positively with the rest of sites. Sites with low richness had high mean per-site range size values whereas richer sites had low mean per-site range size values. There was an overall correspondence between high species numbers and low mean per-site range sizes, confirmed by a negative linear correlation between species richness and per-site range size ($r = -0.928$).

Sites in the upper–most left corner of the RD plot (i.e. those with the highest richness and lowest mean per-site range size) were spatially arranged over southern parts of the country comprising a region from central Veracruz to the north east of Chiapas, crossing the Isthmus of Tehuantepec (Figs. 2B and 3A), whereas sites in the lower–right corner (those with the lowest richness and highest mean per-site range size) were distributed at the north–central part of the country (Figs. 2B and 3A).

3.2.2. Endemic birds

In general, point dispersion within the RD plot by sites followed a similar structure between the endemic avifauna and total bird species. There was a negative linear correlation between richness and per-site range size ($r = -0.582$). Difference between endemics and all species relied on sites with low species richness. For endemics, sites with low richness attained both low and high values of per-site range size, arranging on both sides of the plot's vertical, dashed line (Fig. 3C). Hence, although most sites had positive covariance with the rest of sites, some sites showed negative covariance.

Sites in the lower–left corner of the RD plot (low richness and range size) were spatially arranged at the eastern part of the Yucatan peninsula and northeast Chiapas, whereas sites in the lower–right corner (low richness and high range size) were located at the north–central and northwestern parts of the country, following the pattern observed for the total avifauna (Figs. 2D and 3C).

3.3. Range–diversity plot by species

3.3.1. Total bird species

Species were arranged in both sides of the vertical, dashed line but clumped towards the right side of the plot, implying a positive covariance among species (Fig. 3B). In fact, the majority of species

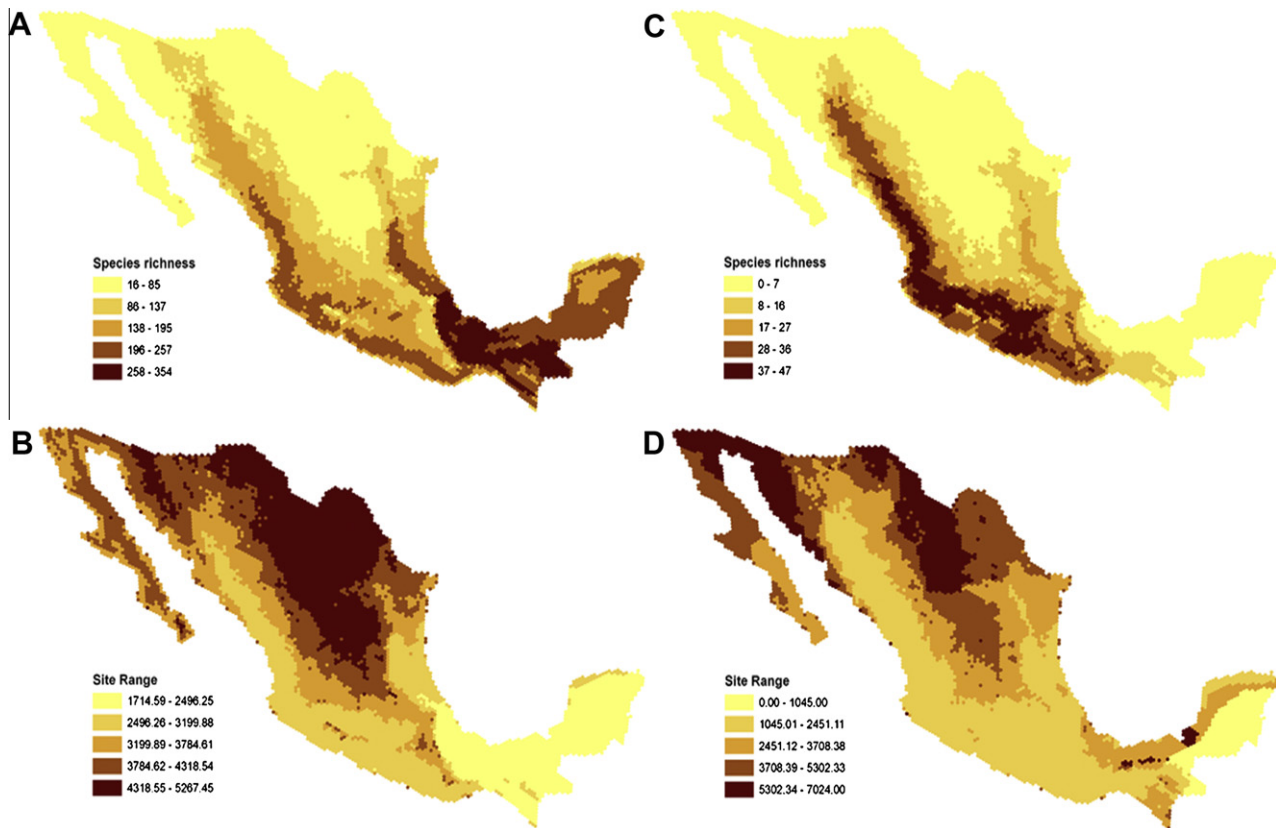


Fig. 2. Geographic patterns of Mexican avifauna. Total avifauna species richness (A) and per-site range size (B). Endemic birds species richness (C) and per-site range size (D). Units are number of species (A) and number of grid-cells (B), respectively.

(85.3%) had average within-range richness equal or higher than the overall mean species richness (131.87 species), whereas only few species (14.7%) had within-range richness values lower than the overall mean and negative covariance with the rest of species. Range-size frequency distribution (RSFD) of Mexican birds showed the common right-skewed pattern observed in regional assemblages with many narrow-ranged species, most of which occupied less than 20% of all grid cells, and some widespread species with at least one species occupying the whole territory (Fig. 3B, right-hand histogram).

Species with contrasting diversity field patterns were located at different parts of the country. For instance, the two species with the highest mean within-range richness (Nava's wren, *Hylorchilus navai* and Sumichrast's wren, *Hylorchilus sumichrasti*) were geographically restricted and distributed over the richest regions of the country (Fig. S1A and B). On the other hand, the two species with the lowest mean within-range richness (Belding's yellowthroat, *Geothlypis beldingi* and Xantus's humminbird, *Hylocharis xantusii*) were also restricted but distributed over the southern Baja California, where only few bird species occur (Fig. S1C and D).

3.3.2. Endemic birds

Endemic bird species followed a similar pattern to that of the total avifauna. Species arranged in both sides of the vertical, dashed line with most species (81.63%) clumping towards the right side and few species (18.37%) to the left side of the RD plot (Fig. 3D). Hence, most endemic species had a positive covariance with the rest of endemics, whereas only a few species covariate negatively with the rest. RSFD for endemic birds was also highly right-skewed, with most endemics (83%) being restricted to less than 20% of the territory and only three species being present in more than half of it.

As with the total avifauna, endemic birds with contrasting diversity field patterns occurred at different parts of the country. For instance, the two species with the highest mean within-range richness (White-tailed hummingbird, *Eupherusa poliocerca* and Short-crested coquette, *Lophornis brachylophus*) were restricted and distributed over western-central Mexico where most of the endemics occur (Fig. S2A and B). In contrast, the two species with the lowest mean within-range richness (Yucatan wren, *Campylorhynchus yucatanicus* and Belding's yellowthroat, *G. beldingi*) were also restricted but each one distributed at one of the two Mexican peninsulas, Yucatan and Baja California, respectively (Fig. S2C and D).

3.4. Richness–rarity sites, ecoregions and priority sites

Richness–rarity quartiles comprised 1674 sites for the total avifauna set and 1397 for the endemic birds set (21.22% and 17.83% of respective domains). Sites within the richness–rarity quartiles were located mainly to the southeast and along both coasts for the total avifauna and to the central and western regions along the pacific coast of Mexico for endemic birds (Fig. 4). These richness–rarity sites, for both total and endemic birds, were distributed exclusively within three of the seven Level I Mexican ecoregions; Wet Tropical Forests, Dry Tropical Forests and Temperate Sierras (Fig. 4). The most important ecoregion for the total Mexican avifauna was the Wet Tropical Forests followed by the Temperate Sierras, representing 58% and 25% of the richness–rarity sites, respectively. In contrast, the Temperate Sierras was the most important ecoregion for the endemic avifauna followed by the Dry Tropical Forests representing 52% and 41% of richness–rarity sites, respectively. Priority sites coincided with 25.75% and

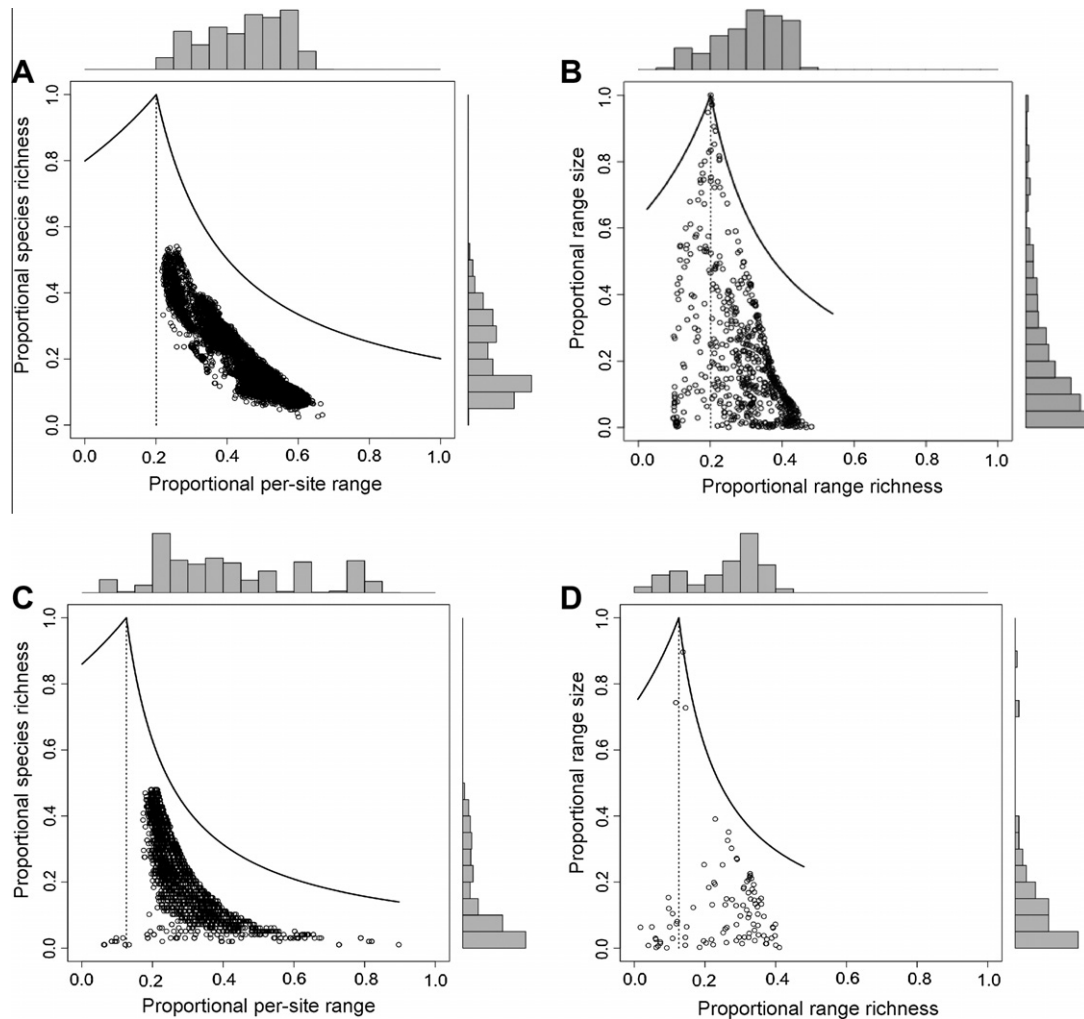


Fig. 3. Range–diversity plots by sites and by species, for the total Mexican avifauna (A and B) and endemic birds (C and D), respectively. Histograms on top and on the right-hand side show the frequency distribution of those variables; the solid curves and the vertical dashed lines are as indicated in Fig. 1.

18.47% of sites within the richness–rarity quartile of total avifauna and endemic birds, respectively.

4. Discussion

4.1. Range–diversity plots for conservation assessments

Conservation assessments are needed to identify and prioritize areas that inform resource allocation to particular biodiversity elements and locations (Knight et al., 2006). Such spatial assessments are critical for implementing effective conservation actions through conservation planning (Knight et al., 2008; Margules and Sarkar, 2007). Here, we showed the usefulness of a macroecological approach based on primary biodiversity information (i.e., species presence–absence data) to conduct broad-scale conservation assessments (i.e., conservation biogeography; Whittaker et al., 2005). Results from our range–diversity approach, simultaneously analyzing diversity (species richness) and distribution (range sizes), can be used to select geographical templates where further attention towards specific locations can be directed.

Straightforward identification of sites and species with characteristics of conservation interest is possible with range–diversity plots. For instance, sites harboring high number of species averaging restricted geographic ranges can be easily identified as well as restricted species occurring at species-poor regions. Both aspects

are relevant in prioritizing sites and species for conservation actions (Arponen, 2012; Wilson et al., 2009). Moreover, a simultaneous assessment of richness and rarity through RD plots can enable critical readings of alternative conservation assessments (e.g., Ecoregions, Priority Sites) regarding the representation of these important biodiversity elements.

4.2. Richness and rarity of Mexican birds

Spatial variation of bird diversity is highly structured within Mexico and differs considerably between all bird species and species entirely restricted to it (endemics). Although contrasting patterns between total and endemic species richness of Mexican birds has been widely acknowledged (e.g., Escalante et al., 1993; Koleff et al., 2008; Navarro-Sigüenza et al., 2009), a thorough inspection of such patterns had been surprisingly lacking from the literature (Sánchez-González et al., 2008). This is true especially for range-size assemblages, a site's property just recently being considered in continental analyses (e.g., Hawkins and Diniz-Filho, 2006; Whitton et al., 2012) and implemented in range–diversity plots by sites.

Mexican highland regions, like the Sierra Madre Oriental and the Mexican Transvolcanic Belt comprising humid and temperate forests, have been considered priority areas for bird conservation owing to their high diversity (Hernández-Baños et al., 1995; Nav-

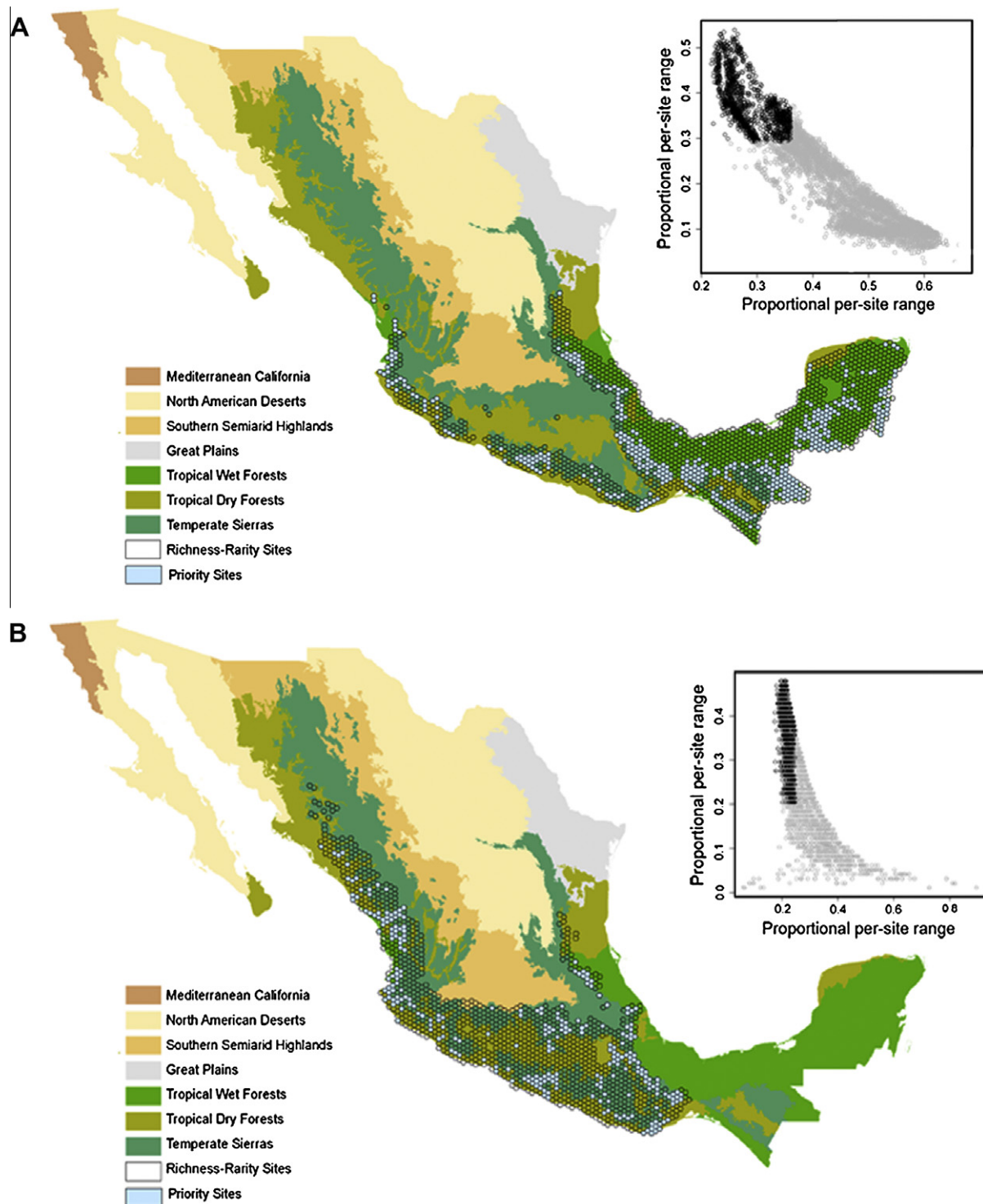


Fig. 4. Maps depicting the geographic location of Level I Mexican ecoregions, richness–rarity quartiles, and priority sites contained in these quartiles for the total Mexican avifauna (A) and endemic birds (B). Insets: RD plots by sites, highlighting richness–rarity quartiles.

arro-Sigüenza et al., 2007; Peterson et al., 2003). Our results identified these and other specific regions as potentially important for bird conservation not only for their overall diversity but also for the presence of restricted species. Indeed, our richness–rarity sites were distributed mostly over mountainous regions where high numbers of bird species co-occur, with many of them having restricted geographic ranges.

Considering other aspects of biodiversity such as rarity of species inhabiting different sites could reveal patterns hidden when

looking at richness alone. For instance, species-poor sites may not be considered as conservation targets even if those sites are inhabited mostly by restricted species (e.g., “Coldspots”, see Kareiva and Marvier 2003 for a thoughtful comment on this topic). Fortunately, this seems not to be the case for the total Mexican avifauna. However, for the Mexican endemic birds, we identified some “coldspots” sites having low numbers of mostly restricted species. Such sites are the most unique and unrelated, in terms of species composition, to the rest of sites. This means that conser-

vation actions should consider such idiosyncratic sites for an effective conservation of a region's biota. These "coldspots", however, may not be distinguished if attention is focused on total species richness without looking separately at endemics or range-size assemblages.

A positive relationship between richness and rarity is characteristic of nested assemblages, in which sites occupied by restricted species are usually species-rich and represent a subset of sites occupied by widespread species (Arita et al., 2012). Although nestedness has been mostly studied in species occurrences and species interactions patterns (Ulrich et al., 2009); they can have direct implications for conservation actions (Patterson, 1987). For example, the observed positive relationship between richness and rarity found for Mexican birds could in fact optimize site selection (in terms of pattern description) since either one of these attributes, richness or rarity, can be used to identify priority sites with much the same results.

4.3. Species geographic associations

Our study of Mexican avifauna showed a high degree of co-occurrence among bird species, with most birds sharing at least part of their ranges with many other bird species. Thus, there is an elevated level of geographic association among species resulting from high numbers of species aggregating over specific regions. This pattern would also suggest that conservation of species-rich regions could potentially ensure the conservation of widespread, restricted and endemic species altogether. However, not all bird species tend to occur in species-rich regions.

We identified a few restricted species that occur exclusively on species-poor regions sharing their geographic distribution with only a few other birds. These idiosyncratic species are endemics located at the extremes of the country over both peninsulas (Baja California and Yucatan), where only few species of birds occur. As mentioned above, such species-poor regions may not score high under simple prioritization procedures based on species numbers even though these regions harbor species not present in any other part of the country. Therefore, potentially leaving those idiosyncratic species out of conservation action. Moreover, the fact that these idiosyncratic species are all true endemics stresses the importance some "coldspots" (i.e., species-poor regions) can have in the conservation of particular species (Kareiva and Marvier, 2003).

4.4. Conservation assessments for the Mexican avifauna

Conservation assessments at large geographic scales have gained strong support from non-governmental organizations and government agencies (Brooks et al., 2006). One of the most employed assessments is the one based on ecoregions (Olson et al., 2001), which have been considered as the largest operational units where decisions can actually be taken and implemented (Loyola et al., 2009). Our results identified three Mexican ecoregions representing the totality of richness–rarity sites for the Mexican avifauna (all birds and endemics). Ecoregions represent distinct geographical units sharing common physiographic and biotic features within them (Olson et al., 2001), which may explain the observed richness–rarity patterns of the Mexican avifauna. For instance, the mountainous nature of the Mexican humid and temperate forests (e.g., Wet Tropical Forests and Temperate Sierras ecoregions) with large tropical rain and cloud forests, and river basins throughout their entire altitudinal gradient favor the co-occurrence of widespread species over lowlands and endemic and narrow-ranged species restricted to highlands (Hernández-Bañón et al., 1995; Peterson et al., 2003).

At finer spatial scales, area prioritization requires more detail information on biological features as well as socio-economic data to guide implementation of conservation actions (Bottrill et al., 2012; Knight et al., 2011). Gathering and guarantying the quality of such amount of biological information further requires the participation of different experts before considering socio-economic aspects such as governance and stakeholder opinion (Knight et al., 2006). Indeed, many prioritization exercises rely on continuous meetings and workshops among experts to identify relevant areas for the conservation of specific taxa. This has been the case in Mexico, where important efforts to prioritize regions for the conservation of different plant and vertebrate taxa in general (Urquiza-Haas et al., 2009) and for birds in particular (Navarro-Sigüenza et al., 2011) have been undertaken (Koleff and Urquiza-Haas, 2011). Our range–diversity approach is not intended as an alternative to such important efforts. Instead, the comparison of our approach to some of these prioritizations (e.g., priority sites) was aimed at showing its simplicity and usefulness for initial assessments at broad spatial scales.

Spatial congruence between Mexican priority sites produced by an exhaustive prioritization procedure and our richness–rarity sites highlights the usefulness of the range–diversity approach. Mexico is a megadiverse, developing country that contrasts with other such countries owing to the fairly good knowledge of its biodiversity patterns (Sarukhán et al., 2009) and prioritization exercises undertaken (Koleff and Urquiza-Haas, 2011). Thus, our findings of richness–rarity patterns supported by more detailed prioritizations within Mexico suggest a wider applicability of the range–diversity approach to other regions and taxa. Ours is a quantitatively rigorous approach that requires only species distributional data at geographic scales. This kind of data can be obtained from low-resolution maps (e.g., Atlas information) or, at higher resolutions, by modeling species-occurrence data. Nowadays much of these data can be obtained from online, publicly available resources (e.g., NatureServe, Global Biodiversity Information Facility). This can facilitate application of our range–diversity approach in different regions where no other information is yet available and broad-scale biodiversity patterns need to be described, which is sadly the case of many species-rich but poorly explored developing countries (Soberón and Peterson, 2009).

5. Conclusions

Richness and rarity are positively related in the Mexican avifauna, with richer sites harboring assemblages of species averaging restricted ranges. Such relationship can be readily analyzed and depicted using range–diversity plots, allowing identification of specific regions potentially relevant for conservation of particular assemblages or individual species. Such regions, once identified, could be given priority over other regions and used to conduct finer assessments of specific locations worthy of protection. Finally, we envision our approach as a first, broad-scale assessment of biodiversity elements with conservation value that can guide initial stages of conservation planning, especially in situations where detailed, fine-scale information is lacking. We hope that our approach and methodology foster more informed conservation assessments within the broader planning framework leading to effective conservation action.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2012.10.002>.

References

- Arita, H.T., Figueroa, F., Frisch, A., Rodríguez, P., Santos del Prado, K., 1997. Geographical range size and the conservation of Mexican mammals. *Conserv. Biol.* 11, 92–100.
- Arita, H.T., Christen, J.A., Rodríguez, P., Soberón, J., 2008. Species diversity and distribution in presence–absence matrices: mathematical relationships and biological implications. *Am. Nat.* 112, 519–532.
- Arita, H.T., Christen, J.A., Rodríguez, P., Soberón, J., 2012. The presence–absence matrix reloaded: the use and interpretation of range–diversity plots. *Global Ecol. Biogeogr.* 21, 282–292.
- Arponen, A., 2012. Prioritizing species for conservation planning. *Biodivers. Conserv.* 21, 875–893.
- Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., 2011. Has the Earth's sixth mass extinction already arrived? *Nature* 471, 51–57.
- Bottrill, M.C., Mills, M., Pressey, R.L., Game, E.T., Groves, C., 2012. Evaluating perceived benefits of ecoregional assessments. *Conserv. Biol.* 26, 851–861.
- Brooks, T.M., Mittermeier, R.A., da Fonseca, G.A.B., Gerlach, J., Hoffmann, M., Lamoreux, J., Mittermeier, C.G., Pilgrim, J.D., Rodrigues, A.S.L., 2006. Global biodiversity conservation priorities. *Science* 313, 58–61.
- Ceballos, G., Ehrlich, P.R., 2006. Global mammal distributions, biodiversity hotspots and conservation. *Proc. Natl. Acad. Sci. USA* 103, 19374–19379.
- CEC, 1997. Ecological Regions of North America – Toward a Common Perspective. Commission for Environmental Cooperation, Montreal.
- Cowling, R.M., Knight, A.T., Faith, D.P., Ferrier, S., Lombard, A.T., Driver, A., Rouget, M., Maze, K., Desmet, P.G., 2004. Nature conservation requires more than a passion for species. *Conserv. Biol.* 18, 1674–1676.
- Escalante, P., Navarro-Sigüenza, A.G., Peterson, A.T., 1993. A geographic, historical, and ecological analysis of avian diversity in Mexico. In: Ramamoorthy, T.P., Bye, R., Lot, A., Fa, J. (Eds.), *Biological Diversity of Mexico: Origins and Distribution*. Oxford University Press, New York, pp. 281–307.
- ESRI (Environmental System Research Institute), 2009. ArcView GIS Ver. 9.3.1. Environmental Systems Research Institute, Inc., Redlands, California, USA.
- Gaston, K.J., 1994. *Rarity*. Chapman & Hall, London, UK.
- Gauthier, P., Debussche, M., Thompson, J.D., 2010. Regional priority setting for rare species based on a method combining three criteria. *Biol. Conserv.* 143, 1501–1509.
- Graves, G.R., Rahbek, C., 2005. Source pool geometry and the assembly of continental avifaunas. *Proc. Natl. Acad. Sci. USA* 102, 7871–7876.
- Grenyer, R., Orme, C.D.L., Jackson, S.F., Thomas, G.H., Davies, R.G., Davies, T.J., Jones, K.E., Olson, V.A., Ridgely, R.S., Rasmussen, P.C., Ding, T., Bennet, P.M., Blackburn, T.M., Gaston, K.J., Gittleman, J.L., Owens, I.P.F., 2006. Global distribution and conservation of rare and threatened vertebrates. *Nature* 44, 93–96.
- Hawkins, B.A., Diniz-Filho, J.A.F., 2006. Beyond Rapoport's rule: evaluating range size patterns of New World birds in a two dimensional framework. *Global Ecol. Biogeogr.* 15, 461–469.
- Hernández-Baños, B.E., Peterson, A.T., Navarro-Sigüenza, A.G., Escalante-Plegio, P., 1995. Bird faunas of the humid montane forests of Mesoamerica: biogeographic patterns and conservation priorities. *Bird Conserv. Int.* 5, 251–277.
- Hillebrand, H., 2004. On the generality of the latitudinal diversity gradient. *Am. Nat.* 163, 192–211.
- INEGI, CONABIO, INE, 2007. Ecorregiones terrestres de México, escala 1:1,000,000. Instituto Nacional de Estadística y Geografía, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad e Instituto Nacional de Ecología, México. <<http://www.conabio.gob.mx/informacion/gis/>>.
- Jetz, W., Rahbek, C., 2002. Geographic range size and determinants of avian species richness. *Science* 297, 1548–1551.
- Jetz, W., Rahbek, C., Colwell, R.K., 2004. The coincidence of rarity and richness and the potential signature of history in centres of endemism. *Ecol. Lett.* 7, 1180–1191.
- Kareiva, P., Marvier, M., 2003. Conserving biodiversity coldspots. *Am. Sci.* 91, 344–351.
- Knight, A.T., Driver, A., Cowling, R.M., Maze, K., Desmet, P.G., Lombard, A.T., Rouget, M., Botha, M.A., Boshoff, A.F., Castley, J., 2006. Designing systematic conservation assessments that promote effective implementation: best practice from South Africa. *Conserv. Biol.* 20, 739–750.
- Knight, A.T., Cowling, R.M., Rouget, M., Balmford, A., Lombard, A.T., Campbell, B.M., 2008. Knowing but not doing: selecting priority conservation areas and the research–implementation gap. *Conserv. Biol.* 22, 610–617.
- Knight, A.T., Cowling, R.M., Boshoff, A.F., Wilson, S.L., Pierce, S.M., 2011. Walking in STEP: lessons for linking spatial prioritisations to implementation strategies. *Biol. Conserv.* 144, 202–211.
- Koleff, P., Urquiza-Haas, T. (coords.), 2011. *Planeación para la conservación de la biodiversidad terrestre en México: retos en un país megadiverso*. Conabio-Conanp, México.
- Koleff, P., Soberón, J., Arita, H.T., Dávila, P., Flores-Villela, O., Golubov, J., Halffter, G., Lira-Noriega, A. et al. 2008. Patrones de diversidad espacial en grupos selectos de especies, in *Capital natural de México, Conocimiento actual de la biodiversidad*, vol. I. Conabio, México, pp. 323–364.
- Lennon, J.J., Koleff, P., Greenwood, J.J.D., Gaston, K.J., 2004. Contribution of rarity and commonness to patterns of species richness. *Ecol. Lett.* 7, 81–87.
- Lira-Noriega, A., Soberón, J., Navarro-Sigüenza, A.G., Nakazawa, Y., Peterson, A.T., 2007. Scale-dependency of diversity components estimated from primary biodiversity data and distribution maps. *Divers. Distrib.* 13, 185–195.
- Loyola, R.D., Kubota, U., da Fonseca, G.A.B., Lewinsohn, T.M., 2009. Key Neotropical ecoregions for conservation of terrestrial vertebrates. *Biodivers. Conserv.* 18, 2017–2031.
- Margules, C., Sarkar, S., 2007. *Systematic Conservation Planning*. Cambridge University Press, Cambridge.
- Navarro-Sigüenza, A., Peterson, A.T. 2007. Mapas de las aves de México basados en web. Informe final SNIB-CONABIO, Proyecto CE015, México.
- Navarro-Sigüenza, A., Peterson, A.T., Gordillo-Martínez, A., 2003. Museums working together: the atlas of the birds of Mexico. *Bull. Brit. Orn. Club* 123A, 207–225.
- Navarro-Sigüenza, A.G., Lira-Noriega, A., Peterson, A.T., Oliveras de Ita, A., Gordillo-Martínez, A., 2007. Diversidad, endemismo y conservación de las aves. In: Luna-Vega, I., Morrone, J.J., Espinosa, D. (Eds.), *Biodiversidad de la Faja Volcánica Transmexicana*. UNAM, pp. 461–483.
- Navarro-Sigüenza, A.G., Gordillo-Martínez, A., Peterson, A.T., 2009. Mapeando la diversidad de las aves de México. *TIP Revista Especializada en Ciencias Químico-Biológicas* 12, 91–95.
- Navarro-Sigüenza, A.G., Lira-Noriega, A., Arizmendi, M.C., Berlanga, H., Koleff, P., García-Moreno J., Peterson, A.T. 2011. Áreas de conservación para las aves de México: integrando criterios de priorización. In: Koleff, P., Urquiza-Haas, T. (Coords.), *Planeación para la conservación de la biodiversidad terrestre en México: retos en un país megadiverso*. Conabio-Conanp, México.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Kassem, K.R., 2001. Terrestrial ecoregions of the World: a new map of life on Earth. *BioScience* 51, 933–938.
- Orme, C.D.L., Davies, R.G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V.A., Webster, A.J., Ding, T.S., Rasmussen, P.C., Ridgely, R.S., Stattersfield, A.J., Bennett, P.M., Blackburn, T.M., Gaston, K.J., Owens, I.P.F., 2005. Global hotspots of species richness are not congruent with endemism or threat. *Nature* 436, 1016–1019.
- Orme, D.L., Davies, R., Olson, V.A., Thomas, G.H., Ding, T.-S., Rasmussen, P.C., Ridgely, R.S., Stattersfield, A.J., Bennett, P.M., Owens, I.P.F., Blackburn, T.M., Gaston, K.J., 2006. Global patterns of geographic range size. *PLoS Biol.* 4, 1276–1283.
- Patterson, B.D., 1987. The principle of nested subsets and its implications for biological conservation. *Conserv. Biol.* 1, 323–334.
- Peterson, A.T., Navarro-Sigüenza, A.G., Hernández-Baños, B.E., Escalona-Segura, G., Rebón-Gallardo, F., Rodríguez-Ayala, E., Figueroa-Esquivel, E.M., Cabrera-García, L., 2003. The Chimalapas region, Oaxaca, Mexico: a high-priority region for bird conservation in Mesoamerica. *Bird Conserv. Int.* 13, 227–254.
- Sánchez-González, L.A., Morrone, J.J., Navarro-Sigüenza, A.G., 2008. Distributional patterns of the Neotropical humid montane forest avifaunas. *Biol. J. Linn. Soc.* 94, 175–194.
- Sarukhán, J., Koleff, P., Carabias, J., Soberón, J., Dirzo, R., Llorente-Bousquets, J., Halffter, G., González, R., March, I., Mohar, A., Anta, S., de la Maza, J. 2009. *Capital natural de México. Síntesis: conocimiento actual, evaluación y perspectivas de sustentabilidad*. Conabio, México.
- Soberón, J., Ceballos, G., 2011. Species richness and range size of the terrestrial mammals of the World: biological signal within mathematical constraints. *PLoS ONE* 6, e19359. <http://dx.doi.org/10.1371/journal.pone.0019359>.
- Soberón, J., Peterson, A.T., 2009. Monitoring biodiversity loss with primary species-occurrence data: toward national-level indicators for the 2010 target of the convention on biological diversity. *AMBIO* 38, 29–34.
- Ulrich, W., Almeida-Neto, M., Gotelli, N.J., 2009. A consumer's guide to nestedness analysis. *Oikos* 118, 3–17.
- Urquiza-Haas, Kolb, M., Koleff, P., Lira-Noriega, A., Alarcón, J. 2009. Methodological Approach to Identify Mexico's Terrestrial Priority Sites for Conservation. *Gap Analysis Bulletin* 16. USGS.
- Villalobos, F., Arita, H.T., 2010. The diversity field of New World leaf-nosed bats (Phyllostomidae). *Global Ecol. Biogeogr.* 19, 200–211.
- Whittaker, R.J., Araújo, M.B., Jepson, P., Ladle, R.J., Watson, J.E.M., Willis, K.J., 2005. Conservation biogeography: assessment and prospect. *Divers. Distrib.* 11, 3–23.
- Whitton, F.J.S., Purvis, A., Orme, C.D.L., Olalla-Tárraga, M.Á., 2012. Understanding global patterns in amphibian geographic range size: does Rapoport rule? *Global Ecol. Biogeogr.* 21, 179–190.
- Willig, M.R., Kaufman, D., Stevens, R.D., 2003. Latitudinal gradients in biodiversity: pattern, process, scale, and synthesis. *Ann. Rev. Ecol. Syst.* 34, 273–309.
- Wilson, K.A., Underwood, E.C., Morrison, S.A., Klausmeyer, K.R., Murdoch, W.W., Reyers, B., Wardell-Johnson, G., Marquet, P.A., Rundel, P.W., McBride, M.F., Pressey, R.L., Bode, M., Hoekstra, J.M., Andelman, S., Looker, M., Rondinini, C., Kareiva, P., Shaw, M.R., Possingham, H.P., 2007. Conserving biodiversity efficiently: what to do, where and when. *PLoS Biol.* 5, e223. <http://dx.doi.org/10.1371/journal.pbio.0050223>.
- Wilson, K.A., Carwardine, J., Possingham, H.P., 2009. Setting conservation priorities. *Ann. NY Acad. Sci.* 1162, 237–264.