Sobre Diversidad Biológica: el Significado de las Diversidades Alfa, Beta y Gamma

ABSTRACTS

Prefacio

Gonzalo Halffter, Patricia Koleff, Jorge Soberón & Antonio Melic

PARTE GENERAL

CAPÍTULO 1:

Biological meaning of alpha, beta and gamma diversity

Gonzalo Halffter & Claudia E. Moreno

Abstract: In this study we attempt to determine the biological meaning of three terms that are widely used in the context of species richness: alpha or local diversity, beta diversity or species turnover, and gamma or landscape diversity. The spatial and temporal scales on which these three expressions of species richness occur are discussed, as are the relationships between them. This leads to an analysis of the influence of the historical (biogeographical) and ecological factors that affect these three different expressions of species richness. In addition, some of the effects of habitat fragmentation caused by human activities on species diversity are presented.

Key words: Alpha diversity, beta diversity, gamma diversity, community fragmentation, species richness indicator groups, tourist species.

CAPÍTULO 2:

Concepts and measurements of beta diversity

Patricia Koleff

Abstract: Beta diversity captures a fundamental aspect of species diversity: spatial replacement in species identity between any two or more areas. However, diverse concepts have been linked, such as turnover along gradients, turnover through space, a measure of the difference between samples, ecological distance, a function of changing habitat, the degree of species distributions overlap and complementarity in species composition, which has led to suggestions for a number of methods and measures to estimate it, and has made strict comparison of studies impossible.

We evaluated 25 published measures of beta diversity based on presence/ absence data, expressing them in common terms in order to compare some of their basic properties, and exemplified, by means of empirical analyses, some implications of the spatial patterns of species turnover.

This study suggests a new perspective on assessing and expressing beta diversity patterns to test important hypotheses that may contribute to a better understanding of the structure of species assemblages across space.

Key words: Aves, birds, beta diversity, species turnover, Britain, South Africa.

CAPÍTULO 3:

Beta diversity as an integrative element of several macroecological patterns

Pilar Rodríguez & Héctor T. Arita Watanabe

Abstract: Several hypotheses attempt to explain the latitudinal gradient of species diversity, but some basic aspects of the pattern remain insufficiently explored, including the effect of scales and the role of beta diversity. To explore such components of the latitudinal gradient, we tested the hypothesis of covariation, which states that the gradient of species diversity should show the same pattern regardless of the scale of analysis. The hypothesis implies that there should be no gradients of beta diversity, of regional range size within regions, or of the slope of the species-area curve, and that a linear LR relationship should be expected.

For the fauna of North American mammals, we found contrasting results for bats and non-volant species. We could reject the hypothesis of covariation for non-volant mammals, for which the number of species increases towards lower latitudes, but at different rates depending on the scale. Also, for this group, beta diversity is higher at lower latitudes, the regional range size within regions is smaller at lower latitudes, *z*, the slope of the species-area relationship, is higher at lower latitudes, and a saturating (Type II) LR relationship was produced.

Contrarily bats did not show any significant deviations from the predictions of the hypothesis of covariation: at two different scales, species richness shows similar trends of increase at lower latitudes, and no gradient can be demonstrated for beta diversity, for regional range size or for the slopes of the species-area curve, and a linear LR (Type I) relationship was produced.

Our results show that the higher diversity of non-volant mammals in tropical areas of North America is a consequence of the increase in beta diversity and not of higher diversity at smaller scales. In contrast, the diversity of bats at both scales is higher at lower latitudes. These contrasting patterns suggest different causes for the latitudinal gradient of species diversity in the two groups that are ultimately determined by differences in the patterns of geographic distribution of the species.

Key words: Beta diversity, regional range size, continental range size, regional diversity, local diversity, mammals, North America.

CAPÍTULO 4:

Similarities and differences between the concepts and patterns of beta diversity and genetic differentiation: an application to Mexican coniferous forests

Daniel Piñero

Abstract: The paper discusses the conceptual relations between beta diversity and genetic differentiation. Four differences are proposed between them, but a basic correlation was found. These ideas were used to explore the relations between estimates of β diversity and F_{ST} in two ecosystems that have been traditionally studied in Mexico, the Transmexican Volcanic Belt (TVB) and the Sierra Madre Oriental (SMOr) using studies from different plants and animal species but particularly using Mexican pine taxa.

Results show patterns of change that suggest a clear correlation between β diversity and genetic differentiation (F_{ST}), which for the SMOr point at higher diversity around 20º and 25º of latitude, while for the TVB a higher degree of diversity was found around its center. These results are discussed in order to make generalizations that in the future may help uncover the causes of biodiversity both at the species and the genetic level and considering the scale of the analysis.

Key words: Beta diversity, genetic differentiation, forest ecosystems, Mexico.

CAPÍTULO 5:

Spatial statistics as a biodiversity analysis tool

Miguel Murguía

Abstract: Spatial statistics is a consolidated science that has measurement tools with reliable interpretative and structural properties. As these instruments are for generic application, i. e., valid not just for biodiversity variables, there are many examples both of their application in the literature and of its strengths, weaknesses and interpretation. In this paper some ways in which spatial statistics can be applied to biodiversity analyses are explained and exemplified. The spatial mean, spatial autocorrelation and the semivariogram are presented with schematic examples. The benefits of using spatial statistics as a descriptive and analytical tool for biodiversity are discussed.

Key words: Spatial analysis, spatial autocorrelation, geographic data bases, spatial statistics, MAUP, spatial mean, semivariogram, geographical information systems.

CAPÍTULO 6:

Interpolating, extrapolating, and comparing incidende-based species accumulation curves

Robert K. Colwell, Chang Xuan Mao & Jing Chang

Abstract: A general binominal mixture model is proposed for the species accumualtion function based on presence-absence (incidence) of species in a sambple of quedrats or other sampling units. The model covers interpolation between zero and the observed numbers of samples, as well as extrapolation beyond the observed sample set. For interpolation (sample based rarefaction) easily calculated, closed-form expressions for both expected richness and its confidence limits are developed (using the method of moments) that completely eliminate the need for resampling methods and permit direct statistical comparison of richness between sample sets. An incidence-based form of the Coleman (ramdom-placement) model is developed and compared with the moment-based interpolation method. For extrapolation beyond the empirical sample set (and simultaneously, as an alternative method of interpolation), a likelihood-based estimator with a bootstrap confidence interval is described that relies on a sequential, AIC-guided algorithm to fit the mixture model parameters. Both the moment-based and likelihood-based estimators are illustrayed with data sets for temperate birds and tropical seeds, ants, and trees. The moment-based estimator is confidently recommended for interpolation (sample-based rarefaction). For extrapolation, thelikelihood-based estimator performs well for doubling or tripling the number of empirical samples, but it is nor reliable for estimating the richness asymptote. The sensitivity of individual-based and sample-based rarefaction to spatial (or temporal) patchiness is discussed.

Key words: binomial mixture model, Coleman curve, EstimateS, ramdom placement, rarefaction, richness estimation, richness extrapolation, species accumulation curve, species richness.

CAPÍTULO 7:

A new statistical approach for assessing similarity of species composition with incidence and abundance data

Anne Chao, Robin L. Chazdon, Robert K. Colwell & Tsung-Jen Shen

Abstract: The classical Jaccard and Sørensen indices composotopnal similarity (and others indices that depend upon the same variables) are anotoriously sensitive to sample size, especially for assemblages with numerous rare species. Furthers, because these indices are based solely on presence-absence data, accurate estimators for them are unattainable. We provide a probabilistic derivation for the classic, incidende-based forms of these indices and extend this approach to formulate new Jaccerd-type of Sørensen-type indices based on species abundance data. We then propose estimators for these indices thatinclude the effect of unseen shared species, based on either (replicated) indicende- or abundance- based sample data. In sampling simulations, these new estimator prove to be considerably less biased than classic indices when a substantial proportion od species are missing from samples. Based on species-rich empirical datasets, we show how incorporating the effect of unseen shared species not only increases accuracy but also can change the interpretation of results.

Key words: Abundance data, beta diversity, biodiversity, complementarity, indicence data, shared species, similarity stimators, similarity index, species overlap, succession.

CAPÍTULO 8:

Lower limits of the alpha diversity of birds in Mexico, and contributions made by the study of low diversity communities

Héctor Gómez de Silva

Abstract: Ecologists studying species diversity tend to focus on high diversities. To study their causes, we usually compare communities which we expect to be similar or contrast communities which we expect to be different. Here, I discuss the interesting possibilities of studying communities with low species diversity and of looking for similarities between communities which are not expected, beforehand, to be similar. These approaches have the potential to help us understand the concept of community, to provide a context for the similarities and differences we find between communities, and because it is in species-poor communities that it is easier to study the influence of abiotic factors in community assembly, among other reasons. The study of bird communities in Mexico using these approaches revealed that there tend to be one or more species from each food guild in every community, which places a lower limit on the alpha diversity of communities

Key words: Bird communities, community ecology, alpha diversity, community assembly rules, Mexico.

ANALISIS DE CASOS

CAPÍTULO 9:

An analysis of the diversity of Mexican tropical dry forests

Irma Trejo

Abstract: The tropical dry forest is the most widespread tropical vegetation in Mexico. It is characterised by its floristic composition, its structural pecularities and its seasonal phenology. The broad spectrum of environmental conditions in which it develops promotes its diversity, which reaches higher levels compared to similar neotropical forests. It is possible to find an average of 74 species with DBH ≥ 1cm in 0.1 ha. The most outstanding characteristic of the tropical dry forest is the great species turnover (β diversity), as 72% of the species from 20 selected sites are only found in one of the samples. The similarity indexes are under 15% in 85% of the cases. The high diversity can be related to endemicity hotspots and a complex biogeographic history. In spite of its importance, the tropical dry forest shows a high deforestation rate, and at present less than 30% of its original surface remains in a relative good state of conservation.

Key words: Diversity analysis, tropical dry forest, Mexico.

CAPÍTULO 10:

β-diversity and floristic differentiation in a complex seasonally dry tropical landscape of southern Mexico

Eduardo A. Pérez-García, Jorge A. Meave del Castillo & José A. Gallardo-Cruz

Abstract: In the study of β-diversity, the emphasis on the numerical attributes of the differentiation between biotic communities has often left aside the analysis of the underlying biological factors. This issue is examined in this paper by means of the succinct presentation of four study cases conducted in the region of Nizanda (Isthmus of Tehuantepec, Oaxaca), in the dry tropical zone of southern Mexico. Given their analogous objectives, these studies shared a common methodological basis, particularly concerning the use of analytical tools, and were supported by a solid knowledge of the regional flora, which resulted from almost ten years of floristic survey. In case study I the effect of two topographic variables (elevation and slope aspect) on the floristic composition on the Cerro Verde hill, one of the major topographical features in the area, was analyzed; the relevance of elevation as an axis of floristic differentiation was demonstrated, although its influence varied between slopes. Case study II took advantage of the fragmented configuration of the xerophytic vegetation associated to limestone outcrops, in order to analyze the spatial distribution of the floristic diversity in this system of habitat islands; its results evidenced the role of both spatial separation and habitat heterogeneity (edaphic gradient) in β-diversity, and that their effects may be additive. Case study III contrasted the two most widespread systems in the region (tropical dry forest and savanna) both in terms of their floristic composition across the taxonomic hierarchy, and in their life form, growth form and growth habit patterns; the magnitude of the differences indicated that these communities' respective floristic sets are not exchangeable in space, particularly because of the large divergences in morphological adaptations of each community's plants. Case study IV showed that floristic differentiation between all plant communities conforming Nizanda's landscape is not limited to the species level, but that it persists across the taxonomic hierarchy, reaching as high as the family level. The four case studies showed jointly that no single factor explaining β-diversity at any level (including from geological substrate, through soil characteristics, to the biogeographical history of each community's flora) is by itself capable of generating the very large γ-diversity recorded in the region (*ca*. 860 species). In fact, the large degree of biological differentiation between some communities suggests that this phenomenon may be very ancient.

Key words: Altitudinal gradient, environmental heterogeneity, xerophytic scrub, vegetational mosaic, spatial turnover, savanna, tropical dry forest, edaphic variability, Oaxaca, Isthmus of Tehuantepec, Mexico.

CAPÍTULO 11:

Latitudinal and longitudinal variation of richness and beta diversity for the Mexican herpetofauna

Oscar Flores Villela, Leticia Ochoa Ochoa & Claudia E. Moreno

Abstract: An analysis of six transects set up in Mexico is presented. Three of them run along a north-south axis (Baja California, Sierra Madre Occidental, Sierra Madre Oriental), the other three along a west-east one (Transvolcanic Axis, Sierra Madre del Sur, Yucatan). A study was made of beta diversity along these transects in the sense of species turnover in adjacent samples for amphibians and reptiles. In the comparison of mean values of beta, Sierra Madre Occidental and Yucatan presented the highest values, while species richness was higher on the Transvolcanic Axis and Sierra Madre del Sur. We did not observe any significant correlation between the number of squares per transect and the number of species in each of them (r^2=0.18, P=0.72), nor did we find a significant correlation between the number of squares per transect and the number of records per square (r^2=0.44, P=0.37). A significant relation was observed between the number of records and richness in each square for all transects (r^2=0.90, P=0.014). Also, a significant correlation was observed between decrement in latitude and increment of species richness for the transects of Baja California and Sierra Madre Oriental, and there was a significant relation between the decrement in longitude and species richness for the Transvolcanic Axis. There was no significant correlation between beta diversity and latitude, but there was a correlation between the increment of beta diversity and longitude for the Transvolcanic Axis and Yucatan.

We conclude that beta diversity of amphibians and reptiles in Mexico does not coincide with the regions of maximum species richness and endemism, although these results may be influenced by the unevenness of the collecting effort in different parts of the country.

Key words: Amphibia, Reptilia, herpetofauna, beta diversity, latitudinal gradient, longitudinal gradient, Mexico.

CAPÍTULO 12:

Complementarity and nestedness patterns of tree species in a cloud forest landscape in central Veracruz (Mexico)

Guadalupe Williams-Linera, Ana María López-Gómez & Miguel Angel Muñiz-Castro

Abstract: Sites representing the regional landscape were selected nearby Xalapa, Veracruz: cloud forest fragments (10) connected by active (4) and abandoned (4) shaded coffee plantations, and old fields derived from pastures abandoned 0.25 to 80 years ago (12). Richness and density of species of trees $\geq$ 5 cm diameter were determined. A total of 153 tree species was recorded: 125 were natives (71 primary, 54 secondary) and 28 non-natives. Forest and old fields had the lowest number of non-native species (2-3), and active coffee plantations had the highest number (25). Non-parametric estimators of species richness indicated that a bigger sampling effort would be necessary to complete inventories (12 to 36 additional tree species). Every site in each land use category displayed a different species composition; therefore, they were highly complementary at the landscape level (50 to 100%). Nestedness patterns were analyzed using the T metric (system temperature) to determine whether the flora in each land use is a subset of a whole regional flora. Species from all sites and land uses were distributed in nested subsets (T = 20.2, P <0.001). Old fields are formed by nested species assemblages because they are part of the same successional process (T = 29.0, P < 0.001). Likewise, coffee plantations had nested native species assemblages (T = 28.4, P < 0.001). In contrast, species assemblages of forest fragments are not nested (T = 45.3, P = 0.41); the cloud forest shows a great heterogeneity in species composition over short geographical distances. In conclusion, different land uses influence species composition in a distinctive way at the landscape level, but each landscape element acts as a repository of part of the regional diversity. Given the high complementarity of forest fragments, coffee plantations, and old fields, a regional conservation approach will require focusing on the integrity of the landscape.

Key words: Old fields, nestedness, trees, cloud forest, coffee plantations

CAPÍTULO 13:

Cloud forest fragmentation and frog diversity in a montane landscape in Mexico

Eduardo Pineda & Gonzalo Halffter

Abstract: Alpha (within-patch species richness), beta (spatial turnover between patches) and gamma (landscape) diversities of frogs were evaluated in a tropical montane cloud forest (TMCF) in central Veracruz, Mexico in order to assess (1) the influence of forest fragmentation on frog assemblages, (2) the importance for species diversity of the various elements of the landscape matrix, and (3) to identify the frog guilds most affected by habitat transformation. Between May 1998 and November 2000 ten sites were sampled: five TMCF fragments and five anthropogenic habitats (three shaded coffee plantations and two cattle pastures). For the entire landscape, 21 species belonging to six families and nine genera were recorded. 100% of these species were found in the TMCF fragments and 62% in the surrounding mosaic of transformed habitats. Gamma diversity is determined to a greater extent by species exchange (beta diversity) than by local species richness (alpha diversity). The degree of conservation of the vegetation canopy, fragment size and altitudinal variation appear to determine the species diversity of this landscape. Large species, terrestrial species, those whose eggs develop outside water and those whose larvae develop in the water seemed to be most affected by habitat transformation. On its own even the largest and most species-rich cloud forest fragment is not capable of preserving the current anuran diversity, neither are the intervening shaded coffee plantations that link the patches of TMCF. However, together they form a diverse system of habitats crucial to species conservation in this landscape.

Key words: Alpha, beta and gamma diversity, cloud forest, shaded coffee plantations, frog assemblages, nestedness, Mexico.

Capítulo 14:

Transformation of cloud forest into coffee agroecosystems: changes in alpha and beta diversity for three faunal taxa

Eduardo O. Pineda Arredondo, Gonzalo Halffter, Claudia E. Moreno & Federico Escobar

Abstract: The alpha and beta diversities of frogs, copronecrophagous beetles (Scarabaeinae) and bats in tropical montane cloud forest (original vegetation) and shaded coffee plantations were compared for a landscape in central Veracruz, Mexico. Three tropical montane cloud forest fragments and three coffee plantations with traditional polyculture shade were sampled between 1998 and 2001. The three animal groups responded differently to the transformation of tropical montane cloud forest into shaded coffee plantations. The species richness (alpha diversity) of frogs decreased by one fifth and there was two thirds of dissimilarity (beta diversity) in the species composition between forest fragments and coffee plantations. In contrast, the number of beetle species and their abundance was notably greater in coffee plantations than in the forest fragments, whereas the species richness and species composition of bats were virtually the same in both habitats. Most of the abundant species remained as such in both communities, but species that were less abundant did not remain scarce in both habitats. The differences in the species assemblages can be attributed to the differing degrees of penetrability of the borders of the two habitat types and to the differences in natural history traits between species. Shaded coffee plantations form a matrix that envelops the remaining fragments of cloud forest and connects them with the other habitats of the landscape. Forest fragments and shaded coffee plantations act complementarily as a highly functional resource for the preservation of biodiversity in a notably modified landscape.

Key words: Copronecrophagous beetles, bats, frogs, alpha and beta diversity, indicator groups, tropical montane cloud forest, shaded coffee plantations, habitat transformation, Mexico.

Capítulo 15:

Amphibian and reptile exchange along the pasture-edge-interior gradient at los Tuxtlas, Veracruz, Mexico

José Nicolas Urbina-Cardona & Víctor Hugo Reynoso-Rosales

Abstract: Based on 672 hours of sampling carried out in 126 transects set up in pasture, forest edge and forest interior at the Los Tuxtlas Selva Alta Perennifolia, a total of 21 amphibian and 33 reptile species were found. Amphibian and reptile richness increased at the forest edge. Towards the interior of the forest the number of species of reptiles with larger size and arboreal habitats increased, as did the amphibians with direct embryo development and with fossorial and arboreal habitats. The greatest species exchange was forest in pastures and forest interior for both amphibians and reptiles. To understand the patterns of species diversity it is important to considerer the natural history of the species, which offers useful information for species conservation.

Key words: Amphibians, reptiles, species diversity, conceptual groups, forest edge, Los Tuxtlas, Mexico.

Capítulo 16:

Alpha and beta diversity of dung beetles (Scarabaeinae) at Los Tuxtlas, Mexico

Mario E. Favila

Abstract: Knowledge of insect diversity at landscape level is analyzed in Los Tuxtlas Veracruz, Mexico, on the northernmost Amazon Forest remnant. In Los Tuxtlas, 2240 insect species, 85 families, and 9 orders of insects have been recorded. However, it is possible that with an intensive sampling effort, the number of species could triple. Given the difficulty of doing such an inventory and determining the conservation status of all species in the region, some insect groups have been proposed as indicators to evaluate the effects of forest fragmentation on biodiversity. One example of biodiversity analysis at landscape level in the region focuses on coprophagous and necrophagous beetles of the subfamily Scarabaeinae. In the entire region, 44 species of Scarabaeinae were identified, 26 of which were found exclusively on forest fragments. According to estimates from accumulation curves, the number of species in the region could reach 51. Classification and ordination analyses of sites as a function of the species found there separated patches of forest (less than 40 ha) and pastureland from small (60 to 90 ha), medium (100 to 300 ha), and large (over 500 ha) forest fragments. Thus, a loss in species is being observed as vegetation fragments become smaller. Such fragments do serve as refuges for some forest species but are also invaded by pasture species. Vegetation fragments of at least 90 ha preserve a good proportion of forest species, but larger fragments are preferable; furthermore, to conserve coprophagous and necrophagous beetle populations in Los Tuxtlas in good ecological and genetic conditions, fragments should be connected.

Key words: biodiversity, tropical rain forest, Los Tuxtlas, indicator groups, dung beetles, Scarabaeinae.

Capítulo 17:

Alpha and beta diversity in *Opuntia* and *Agave*

Jordan Golubov, M. C. Mandujano & F. Mandujano

Abstract: The genera *Agave* and *Opuntia* have important ecological, economic, social and biological implications in Mexico. We used bioclimatic modeling (GARP) and information from electronic-format herbaria housed in the National System of Biotic Information to generate the maps of potential distribution for each species at a scale of 1:4,000,000. From the maps generated for each species, we calculated alpha and beta diversity for the 20,932 cells found in Mexico. Alpha diversity was calculated as the sum of the presence of each species in each cell. To calculate Sorensen's beta diversity, an algorithm was implemented with Matlab. The results indicate areas of high alpha and beta diversity in certain areas of Mexico that do not necessarily coincide. We can however identify 6

ecoregional areas where most of the alpha and beta diversity of these two genera is found. Even though the use of bioclimatic models has been important recently, only now has it been possible to apply these models at a large scale, not without considering the problems associated with modeling species occurrences.
Key words: *Agave*, *Opuntia*, bioclimatic modeling, diversity indices, Mexico.

CAPÍTULO 18:

An estimate of the Beta component of the number of species of the Papilionidae and the Pieridae (Insecta: Lepidoptera) of Mexico by indirect methods

Jorge Soberón M., Jorge Llorente Bousquets & Armando Luis M.

Abstract: The concept of "beta diversity", proposed by Whittaker (1960), is applied to subdivisions of a region from which inventories are obtained. Therefore it has always been difficult to estimate beta, since in principle inventories for each subregion in the region are required. In this paper we discuss the biological meaning of the beta component of a region's species richness and show how to estimate beta without going through subregional inventories. We do this by empirically estimating the average alpha diversity and the regional (gamma) diversity and then calculating beta using Whittaker's equation. An example is shown using data on the Papilionidae and the Pieridae (Insecta: Lepidoptera) of Mexico.
Key words: Lepidoptera, Papilionidae, Pieridae, beta diversity, indirect estimate, Mexico.