Gayana 79(2): 167-172, 2015. ISSN 0717-652X

Scale analysis of carabids richness (Coleoptera: Carabidae) in southern South America

Análisis de escala de la riqueza de carábidos (Coleoptera: Carabidae) en América del Sur austral

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ABSTRACT

The southern South America presents a complex history of geomorphological and climatic events, which have modulated and fragmented the southwestern part of the Andes mostly. Given the complexity of the southern landscape, the analysis of the hierarchical components alpha-α, beta-β and gamma-γ on carabid diversity allows exploring the responses of species to spatial changes patterns according to the scales of the landscape. In order to understand how spatial scales influence the carabid diversity in southern South America, we used an approach at multiple spatial scales of multiplicative diversity partitioning. We included four spatial scales in our analysis: among 0.25° quadrats, 0.5° quadrats, provinces and biogeographic sub-regions. The results showed that the pattern of carabid distribution is not random, and varies according to the spatial scale. At larger scales β-diversities are observed to be higher than expected, but lower than expected at smaller scales. This suggests that carabid ensembles are more homogenous than expected, particularly at the scale of 0.5° quadrats. As explanatory factors, glacial/post-glacial events and historical processes may have had an impact on the present species patterns. Furthermore, due to the importance of beta-β diversity on local and regional scales, a promising approach for future studies is to investigate which biogeographic mechanisms seem to determine the species distribution in different provinces.

Keywords: Beta diversity, Multiplicative partitioning, Island Systems, Chile.

RESUMEN

La compleja historia geomorfológica y climática de Sudamérica austral ha modulado y fragmentado particularmente el sector sur de los Andes. Dada la complejidad del paisaje austral, un análisis de los componentes de diversidad alfa-α, beta-β and gamma-γ de carábidos, permite explorar los cambios de los patrones espaciales considerando las escalas de paisaje. Para analizar el efecto de la escala espacial sobre la diversidad de carábidos en Sudamérica austral, realizamos un particionamiento multiplicativo de diversidad. Para nuestro análisis incluimos cuatro escalas espaciales, cuadrículas de 0,25°, cuadrículas 0,5°, provincias biogeográficas y sub-regiones biogeográficas. Nuestros resultados muestran que el patrón de distribución de carábidos no es aleatorio. A gran escala se observa que las diversidades beta son mayores a lo esperado, mientras a baja escala son menores a lo esperado. Lo anterior sugiere que los ensambles de carábidos son más homogéneos, principalmente entre cuadrículas de 0,5°. Discutimos el efecto de procesos históricos en el patrón actual de especies. Debido a la importancia de la diversidad beta-β a escala local y regional, es que se da pie a una interesante línea de investigación para entender que mecanismos biogeográficos parecen determinar la distribución de especies en diferentes provincias.

Palabras Claves: Diversidad beta, Particionamiento multiplicativo, Sistemas insulares, Chile.

INTRODUCTION

The carabids (Coleoptera: Carabidae) are one of the most diversified animal groups in the terrestrial ecosystems of southern South America (Roig-Juñent & Domínguez 2001). Associated mainly with the Valdivian Forest and sub-Antarctic forests (Kuschel 1960), they are characterized by presenting endemic tribes (e.g. Migadopini, Ceroglossini), monotypic genera and species with relict distribution (Darlington 1965). These insects are good indicators of past terrestrial environments (Elias 2007), since they are highly mobile and thereby able to respond rapidly to environmental change by rapidly shifting its distribution patterns; they are also very abundant and have a well-preserved fossil record, since it is feasible to find almost all current species in ensembles of the Quaternary (Ashworth *et al.* 1991; Ashworth 2007).

Moreover, carabid beetles are ideal candidates to study nonrandom species distributions (Magura *et al.* 2001), manifested as particular metacommunity structures that represent the dynamics of diversity at local and landscape scales (Fournier & Loreau 2001). The scale dependence of carabid diversity has broad implications for biogeography, where the contemporary distribution patterns reflect biological and physical processes operating at multiple spatial scales, over both evolutionary and ecological time scales (Holling 1992). This is particularly interesting if we consider highly fragmented areas such as southern South America. This sector was broadly impacted by geological and paleoclimatic events which dramatically altered the landscape of southern Patagonia, and have impacted the abundance and distribution of the biota (Hinojosa & Villagrán 1997; Ashworth 2007).

In order to understand the currently uneven spatial distribution of species and how spatial scales influence the carabid diversity in southern South America, a focus at multiple scales it is required to study hierarchical/nested systems (Holling 1992). The hierarchical approximation proposed by Whittaker (1960, 1972) relates the composition and variability of local communities to that of regional ensembles. This author recognized a connection between the spatial scale and species richness in the hierarchical components of alpha (α, local or intra-site), beta (β, between sites) and gamma (γ, regional) diversity. The importance of this approximation lies in the definition of β-diversity as a measure of the variation in species composition between ensembles (Whittaker 1960). Whittaker (1972) suggested that gamma is the product of alpha and beta ($\gamma = \alpha * \beta$), considering β-diversity to be a comparison of the number of species at different spatial scales ($\beta = \gamma / \bar{\alpha}-1$).

One of the main approaches to conceptualize spatial variation in β-diversity it is the partitioning of species diversity (γ) into alpha and beta components (Crist *et al.* 2003; Chao *et al.* 2012). Partitioning the regional diversity of carabids into its average $\bar{\alpha}$ -diversity (local diversity) component and the amount of variation between ensembles (β-diversities) across multiple scales of sampling (i.e. sampling units that are progressively aggregated upwards), can give insight into the scales at which β-diversity might be higher or lower (Barton *et al.* 2013). This is important especially in fragmented environments, given that the responses of species to spatial changes may vary depending on the scales of the landscape (Pardini *et al.* 2010). The objectives of our study are to partitioning gamma diversity components of carabid beetles across hierarchical spatial scales in the highly fragmented landscape in southern South America, and to determine which spatial scale contributes the most to the species richness.

MATERIALS AND METHODS

Carabid beetles database

Our database included a total of 3955 geo-referenced records for 180 species of Carabidae. Thus, we worked with the complete distribution of those species that inhabit areas that were affected by the Last Glacial Maximum (LGM) and that are endemic to the Andean Region. The information was obtained by a review of five institutional collections. In Chile: Museo Nacional de Historia Natural (MNNC); Museo Entomológico Luis Peña (MEUC); Instituto de Entomología de la Universidad Metropolitana de Ciencias de la Educación (UMCE); Museo de Zoología, Universidad de Concepción (UCCC) and Instituto de la Patagonia (IPUM). In Argentina: Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA).

We also compiled information on locality recordings from scientific publications (Jeannel 1962; Straneo 1979; Niemelä 1990; Roig-Juñent 1993, 2000, 2004; Roig-Juñent & Domínguez 2001; Jiroux 2006; Allegro *et al.* 2008; Elgueta *et al.* 2013, among others) and from a number of samplings we performed: Región de Los Lagos: Parque Katalapi, Isla de Chiloé. Región de Aysén: valleys of the Aysén, Cóndor, Cuervo, Blanco, Baker and Pascua Rivers. Región de Magallanes: Parque Nacional Bernardo O'Higgins (PNBO), Reserva Nacional Alacalufes (sector Canal de las Montañas), Área Marina Costera Protegida Francisco Coloane (AMCP), Brunswick Península (Sector de San Juan), Parque Karukinka (Tierra del Fuego) and Parque Etnobotánico Omora (Isla Navarino).

Diversity partitioning

In order to rank the different spatial scales in terms of their importance to carabid species, we performed a multiplicative diversity partitioning (Jost 2007) based on Hill numbers (^{q}D) (Hill 1973). In this case, the parameter q determines the sensitivity of the index to the relative frequencies of the species (Chao *et al.* 2012). The advantage of this approximation is that ^{q}D is a measure of "true diversity" (effective number of communities), assuring independence between α and β, and allows the quantification of the heterogeneity of a region (Jost 2007; Chao *et al.* 2012). Since we worked with species records, we used a q value of order 0 ($^{q}D = 0$). Thus, we performed a partitioning of total richness ($^{0}D_{\gamma}$) into local $\bar{\alpha}$-diversity ($^{0}D_{\bar{\alpha}}$) and β-diversities ($^{0}D_{\beta}$) components, using an unbalanced sampling design that involves different spatial scales.

According to our geographical context, we divided the area into quadrats, recording the presence of each species and information on the province and biogeographic sub-region (according to Morrone 2006) with which the quadrats intersects. Hence, the geographic system was divided into four hierarchical scales: quadrats of 0.25°, quadrats of 0.5°, biogeographic provinces and biogeographic sub-regions. Carabid diversity was determined as ${}^0D_\gamma = {}^0D_{\bar{\alpha}1}$ (average diversity within of 0.25° quadrats) x ${}^0D_{\beta 1}$ (among 0.25° quadrats) x ${}^0D_{\beta 2}$ (among 0.5° quadrats) x ${}^0D_{\beta 3}$ (among provinces) x ${}^0D_{\beta 4}$ (among subregions).

To evaluate if the observed diversity components differ from those expected by chance, we generated a null model using a randomization process of individuals among samples of all the hierarchical levels (Crist *et al.* 2003). We selected this model since it allows the identification of how the inter-specific spatial aggregation patterns may modulate the partitioning (Crist *et al.* 2003). To generate the frequency distribution of null data we performed 10,000 iterations. This allows estimating the probability that the observed diversity component is greater, equal to or less than expected by chance. This analysis was performed in the PARTITION 3.0 program (Veech & Crist 2009).

RESULTS

The total γ-diversity (${}^0D_\gamma$) of the southern South America was mainly attributed to β-diversity. The beta components (${}^0D_\beta$) explained 75.81% (Table 1) among its different spatial scales (Fig. 1). The 0.25° quadrats (${}^0D_{\beta 1}$) explained 7.84%; the 0.5° quadrats (${}^0D_{\beta 2}$) 47.6%; the biogeographic provinces (${}^0D_{\beta 3}$) 11.49% and among biogeographic regions (${}^0D_{\beta 4}$) 8.89%. Although the greatest source of diversity was at the scale of 0.5° quadrats (β_2), both at this level and at the finer scale (β_1), the observed values were significantly lower than expected under the null distribution (Fig. 1). However, at the scale of provinces and sub-regions the observed values were significantly greater than expected by chance. The ᾱ-diversity was also significantly greater than expected by chance; it explained 24.19% of the total diversity with a mean of 4.38 species per 0.25° quadrat (Table 1).

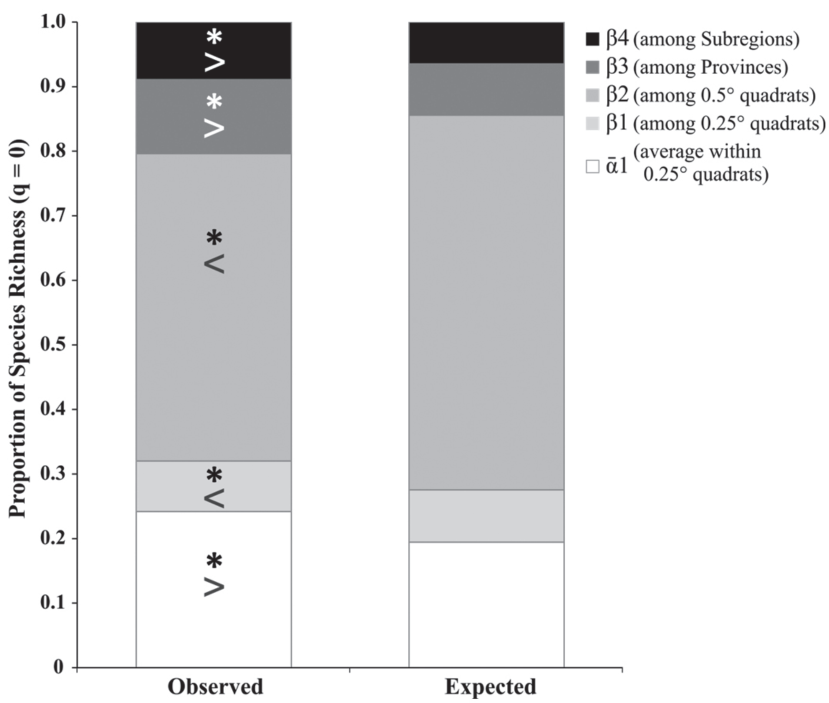

Figure 1. Multiplicative diversity partitioning of carabids based on species richness (q=0) at the Andean Region scale. Asterisks (*) indicate proportions with significant values (p < 0.001) in all cases. Symbols >/< represent greater or lower values than expected.

Figura 1. Particionamiento multiplicativo de la diversidad de carábidos basado en la riqueza específica (q=0) a escala de la Región Andina. Asteriscos (*) representan proporciones con valores significativos (p < 0,001). Símbolos >/<, representan valores mayores o menores a lo esperado respectivamente.

TABLE 1. Multiplicative diversity partitioning of carabids based on species richness (q=0) at the Andean region scale.

TABLA 1. Particionamiento multiplicativo de la diversidad de carábidos basado en la riqueza específica (q=0) a escala de la Región Andina.

q = 0		OBSERVED	%	EXPECTED	
				MEAN	INTERVAL
$\bar{\alpha}$ 1	average within 0.25° quadrats	4.38*	24.19	4.03	3.96 - 4.11
β 1	among 0.25° quadrats	1.42*	7.84	1.68	1.65 - 1.71
β 2	among 0.5° quadrats	8.62*	47.60	12.04	11.43 - 12.63
β 3	among Provinces	2.08*	11.49	1.65	1.57 - 1.73
β 4	among Subregions	1.61*	8.89	1.34	1.27 - 1.41
γ	Andean region	1.0		1.0	1.0 - 1.0

* $p < 0.001$

DISCUSSION

Our analysis of hierarchical components showed that the pattern of carabid distribution in southern South America is not random, and varies according to the spatial scale. Gering *et al.* (2003) have detected these scale dependent differences in spatial patterns of diversity for beetles. These authors found that a significant percentage of total species richness was attributed to β-diversity between ecoregions and, to a lesser extent, among sites. Likewise, our results shown that at larger scales (province and biogeographic sub-region) observed β-diversities were higher than expected (from a random distribution), but lower than expected at smaller scales (0.25° and 0.5° quadrats). It is well established that different factors affect community assembly at different scales (Holling 1992). For instance, diversity at large scales is expected to be relatively different due to historical-geographical factors (Magura *et al.* 2001). Climatic filters and limited connectivity could be responsible for demographic isolation in some areas with an important number of unshared species (Fournier & Loreau 2001).

We highlight the observed patterns of β-diversities at scales of 0.25° and 0.5° quadrats. Both components contributed over 55% to total diversity, but were lower than the expected by chance. This indicates that carabid species within each biogeographic province are a subsample of the same meta-community. Our result suggests the existence of continuous events of species immigration that would act as a homogenizing force among ensembles (Loreau & Mouquet 1999; Fournier & Loreau 2001). At lower scales, it seems that carabid beetles are not affected by the geographical fragmentation of southern South America. This could be explained because of the existence of habitat generalist carabids (Magura *et al.* 2001) and high dispersal trait is selected in unstable environments (Den Boer 1970). Other factors that could have contributed to carabids dispersion were the glacio-eustatic changes in sea level during quaternary. For instance, during LGM the lower sea level exposed the shelf around the Pacific Patagonian fjords (Ashworth *et al.* 1991) and later, post-glacial isostatic rebound caused land mass elevations along shoreline terraces (Stern *et al.* 2011). Therefore, such areas probably served as land bridges allowing the movement of carabid beetles among the mainland and islands.

All the mentioned factors could explain why the $\bar{\alpha}$-diversity was higher than expected, since species immigration between spatial units raises the local diversity. This agrees with the suggestions of Massol *et al.* (2011) who indicated that the structure of local ensembles is influenced by regional processes. We propose that a source-sink meta-community dynamics (Mouquet & Loreau 2003) or post-glacial dispersion would explain the pattern of greater richness at the local scale and less differentiation among quadrats than expected. This pattern suggests new hypotheses to account for the processes that explain the distribution pattern of carabids in southern South America. Moreover, we propose that regional processes (e.g. colonization, extinction) would be limiting factors in the replacement of species at large spatial scales (Massol *et al.* 2011; Barton *et al.* 2013), especially in fragmented environments (Magura *et al.* 2001) in which the meta-community dynamics determines the pattern of species distribution.

We emphasize the utility of partitioning diversity into its α and β components, since this analysis allows new approximations to the study of diversity and explore the conceptual underpinnings of the spatial scaling in order to provide a better understanding of the ecological processes that sustain a widely distributed pattern.

ACKNOWLEDGEMENTS

The authors thank the Corporación Nacional Forestal (CONAF), especially Jovito González, for support in the expedition to the Canal de las Montañas (R.N. Alacalufes). We thank the Centro de Estudios del Cuaternario (CEQUA), for their invitation and support in the expedition in the Parque Nacional Bernardo O´Higgins and the AMCP Francisco Coloane. We thank the Fundación Omora for collaboration and support in sampling of the Parque Etnobotánico Omora, and the Wildlife Conservation Society for their support in the sampling of Parque Karukinka (Tierra del Fuego), Dr. Lafayette Eaton and Javiera Alfaro who helped translating earlier versions of this manuscript. Finally C. Muñoz-Escobar is a student in the Doctoral Program in Systematics and Biodiversity and was supported by UdeC and CONICYT Doctoral Fellowships. This work was funded by project DIUC 212.113.080-1.0.

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Recibido: 27.06.14
Aceptado: 06.08.15