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Assessing the relative contribution of functional divergence and guild aggregation to overall functional structure of species assemblages

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ABSTRACT

The study of functional structure in species assemblages emphasizes the detection of significant guild aggregation patterns. Thus, protocols based on intensive resampling of empirical data have been proposed to assess guild structure. Such protocols obtain the frequency distribution of a given functional similarity metric, and identify a threshold value (often the 95th percentile) beyond which clusters in a functional dendrogram are considered as significant guilds (using one-tailed tests). An alternative approach sequentially searches for significant differences between clusters at decreasing levels of similarity in a dendrogram until one is detected, then assumes that all subsequent nodes should also be significant. Nevertheless, these protocols do not test both the significance and sign of deviations from random at all levels of functional similarity within a dendrogram. Here, we propose a new bootstrapping approach that: (1) overcomes such pitfalls by performing two-tailed tests for each node in a dendrogram of functional similarity after separately determining their respective sample distributions, and (2) enables the quantification of the relative contribution of guild aggregation and functional divergence to the overall functional structure of the entire assemblage. We exemplify this approach by using long-term data on guild dynamics in a vertebrate predator assemblage of central Chile. Finally, we illustrate how the interpretation of functional structure is improved by applying this new approach to the data set available.

1. Introduction

One way to understand the behavior of complex systems such as biotic communities is to study their aggregate variables (Inger and Colwell, 1977; Pianka, 1980; Thomson and Rusterholz, 1982; Winemiller and Pianka, 1990; Maurer, 1999). In particular, the functional structure of assemblages, and its potential consequences, has received a renewed attention in the last 15 years (Walker, 1992; Jaksic et al., 1996; Tilman et al., 1997; Loreau, 1998; Diaz and Cabido, 2001; Loreau et al., 2001; Petchey and Gaston, 2002; Naeem and Wright, 2003). We can define functional structure as the non-random distribution of species on the functional space of interest (e.g. the trophic, spatial or temporal niche axes). Functional structure thus synthesizes all pairwise niche relationships displayed by a set of species, and may vary between different species subsets that constitute the assemblage under study (Pianka, 1980). This structure could have major implications for system functioning because it implies the aggregation of species in guilds or in functional groups (Wilson, 1999; Blondel, 2003) and it may

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provide redundancy to the system, thus increasing its resilience to eventual disturbances (Walker, 1992, 1995; Jaksic et al., 1996; Naeem, 1998; Rosenfeld, 2002; Jaksic, 2003).

On the other hand, significant divergence (niche differentiation or complementarity; Mason et al., 2005) of individual species or of whole guilds in functional space could enhance ecosystem functioning (Tilman et al., 1997; Loreau, 1998; Diaz and Cabido, 2001; Loreau et al., 2001; Rosenfeld, 2002; Naeem and Wright, 2003). Because species tend to interact more strongly with their functionally closest associates, the relative importance of functional aggregation or divergence should covary with the rank of functional similarity. Thus, functional structure should be independently assessed at each of such ranks to provide a complete description of the study system (Inger and Colwell, 1977; Pianka, 1980).

Traditional approaches to the study of functional structure have emphasized guild identification and ignored explicit descriptions of functional divergence patterns (Rosenfeld, 2002). The original guild concept assigns functional identity to species groups based on their similarity in resource use (Root, 1967; Jaksic, 1981; Simberloff and Dayan, 1991), and has sometimes been extended to include functions not necessarily related to resource consumption (Wilson, 1999; Blondel, 2003). Nevertheless, it opens for consideration the practical problem of determining the level of similarity at which a given number of species could be recognized as clustered (Simberloff and Dayan, 1991; Terborgh and Robinson, 1986). Many different approaches have been used to cope with this issue, ranging from subjective *a priori* definitions of guilds to objective *post hoc* assessments of statistically significant species clusters (Pianka, 1980; Terborgh and Robinson, 1986; Jaksic and Medel, 1990; Wilson, 1999; McKenna, 2003).

Jaksic and Medel (1990) faced the problem of significant guild recognition by assessing a threshold value beyond which the occurrence of a node in a dendrogram of functional similarity resulted statistically unlikely, and thus all the species clustered together may consequently be assumed to constitute a single guild. The proposed threshold value was the 95th percentile of the distribution of a similarity metric obtained after intensively re-sampling the observed resource use matrices. Unfortunately, this approach did not test for significant functional divergence, nor did it examine functional structure at each rank of functional similarity. Another related approach – developed to compare species composition between assemblages (McKenna, 2003) – sequentially tests for significant divergence among clusters at each rank of similarity until significance is reached, assuming that all subsequent nodes in the corresponding branch of the dendrogram must also be significant. The major advantage of this approach is its ability to detect difference in the rank of similarity at which significance is detected on different branches of a given dendrogram. Nevertheless, it is unable to distinguish significant aggregation (i.e. guilds) from random expectations. In sum, none of the already existing approaches simultaneously tests for both significant aggregation and divergence at every rank of functional similarity in a dendrogram.

Here, we extend the approach of Jaksic and Medel (1990) to simultaneously detect guild structure and functional divergence, and to estimate their relative contribution to the overall functional structure. By assigning both upper and lower threshold values to each node, this new approach independently examines all hierarchical levels in the dendrogram of functional similarity. We illustrate its use by applying it to empirical long-term data on a vertebrate predator assemblage in central Chile, and show how previous approaches may have neglected information about its functional structure, where the importance of functional divergence seems to override that of guild aggregation.

2. Materials and methods

2.1. Source of empirical data

We used real data from a long-term project on the food-niche dynamics of a vertebrate predator assemblage at Las Chinchillas National Reserve (31° 30′ S, 71° 06′ W), 300 km north of Santiago, Chile. This area is characterized by a rugged topography and semiarid climate. The annual precipitation averages ca. 200 mm concentrated during the austral winter (June–August), and varies greatly from year to year in relation to El Niño–Southern Oscillation phenomena (Jaksic, 2001). The dominant vegetation is thorn-scrub, consisting primarily of shrubs, terrestrial bromeliads, and cacti (Jaksic et al., 1993). In rainy years, major flushes of grasses and herbs occur, supplying sudden productivity pulses that trigger subsequent increases in prey availability (mainly rodents and arthropods) for vertebrate predators. Detailed descriptions of the study area and community dynamics are reported elsewhere (Jimenez et al., 1992; Jaksic et al., 1993, 1996; Jaksic and Lazo, 1999; Lima et al., 1999, 2002a,b; Jaksic, 2004; Arim and Jaksic, 2005; Farias and Jaksic, in press).

The assemblage under study is composed by six predator species: the culpeo fox (*Pseudalopex culpaeus*), the American kestrel (*Falco sparverius*), and four owls (horned owl *Bubo magellanicus*, barn owl *Tyto alba*, austral pigmy owl *Glaucidium nanum*, and burrowing owl *Athene cunicularia*). The diets of these species were recorded after dissecting regurgitated pellets or feces, for each biological season (non-breeding: April–September, breeding: October–March) of each year from 1987 to 2004 (35 biological seasons). The level of taxonomic resolution of prey was order for invertebrates and species for vertebrates. Pairwise diet overlap values among predator species were calculated for each biological season using Pianka's niche overlap index (Pianka, 1973):

$$Ov_{jk} = \frac{\sum p_i q_i}{(\sum p_i^2 \times \sum q_i^2)^{1/2}} \quad (1)$$

where p_i and q_i are the relative occurrences of prey category i in the diets of predators j and k, respectively. This index ranges between 0 and 1 (0 and 100% of diet similarity). Then, a matrix of functional distances (with entries $1-Ov_{jk}$) was constructed, and used as input for a cluster analysis using the unweighted pair-group method with arithmetic averaging (UPGMA; Sneath and Sokal, 1973; Jaksic and Medel, 1990; Jaksic et al., 1993; Farias and Jaksic, in press). To satisfy the requirements of the software used, dissimilarity values were used instead of Ov_{jk} values. Thus, results are shown in terms of functional distances between species and, consequently, a