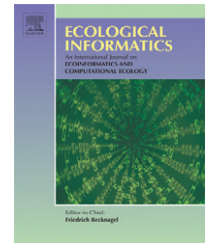


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Assessing the relative contribution of functional divergence and guild aggregation to overall functional structure of species assemblages

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ARTICLE INFO

Article history:

Received 7 June 2006

Received in revised form

14 September 2006

Accepted 16 September 2006

Keywords:

Functional structure

Guild structure

Functional divergence

Bootstrapping

Null model

Cluster analysis

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.

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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

dendrogram of functional dissimilarity was obtained for each biological season of each year. From each dendrogram the corresponding assemblage functional structure was evaluated.

2.2. Testing of functional structure

Following Jaksic and Medel (1990), the observed diets were resampled 1000 times for each biological season of each year according to a probability distribution function defined *a priori*, recalculating the pairwise diet overlap values in each iteration step. Differences between this re-sampling procedure and that proposed by McKenna (2003) have some implications for data requirements that are discussed below. To exemplify our approach, we used the simplest randomization algorithm (RA1) proposed by Lawlor (1980). This algorithm resamples for each predator species all prey categories with an equal probability (i.e. uniform sampling probability distribution for prey categories), keeping fixed only the observed number of predator species and prey categories, and the observed sample sizes. Therefore, this is a completely random null model for assemblage functional structure. At each iteration step, the cluster analysis was repeated using the new functional distance pseudovalues ($1 - Ov_{jk(r)}$, where $Ov_{jk(r)}$ is the dietary overlap between species j and k in the iteration step r). In each case, node values of the corresponding functional dissimilarity dendrogram were preserved, and ranked in increasing order of functional dissimilarity. Then, the distribution of 1000 pseudovalues for each n -th rank of functional dissimilarity (where n is the number of nodes in the dendrogram) was obtained for each biological season of each year. Using those frequency distributions, three different approaches for assessing functional structure were performed, and their results were compared.

A1 is the simplest approach, equivalent to that of Jaksic and Medel (1990), but here we used node pseudovalues instead of pairwise overlap pseudovalues to build the reference sampling distributions. This approach assigns a single threshold level in the dendrogram of functional similarity (one-tailed test) corresponding to the 5th percentile of the joint distribution of nodes through all ranks of functional dissimilarity (i.e. the combined sampling distribution of all nodes in the dendrogram, Fig. 1), and is assumed to detect species clusters whose probability of occurring by chance is very low (i.e. guilds).

A2 assesses both an upper and a lower threshold level of functional dissimilarity (two-tailed test) corresponding to the quantiles 97.5% and 2.5% of the distribution of node pseudovalues, obtained as in A1 (Fig. 1). This approach is able to detect both significant guild aggregation and significant functional divergence.

A3 (the approach favored by us) relies on the independent analysis of the distribution of node pseudovalues for each rank of functional dissimilarity (i.e. the respective sampling distribution of each node in the dendrogram). Then, it assesses their corresponding upper and lower threshold levels (97.5%–2.5% quantiles, respectively; Fig. 1). It detects those ranks of functional dissimilarity where aggregation or divergence is statistically significant. Under this approach, a given species cluster is defined as a guild if all nodes comprised within it show dissimilarity values significantly lower than expected by chance. This avoids ambiguities on guild definition that cannot be resolved using A1 or A2 (see Discussion).

2.3. Quantification of functional structure

Two complementary indices were used to quantify the functional structure of the vertebrate predator assemblage. The first index estimates the magnitude of the overall functional

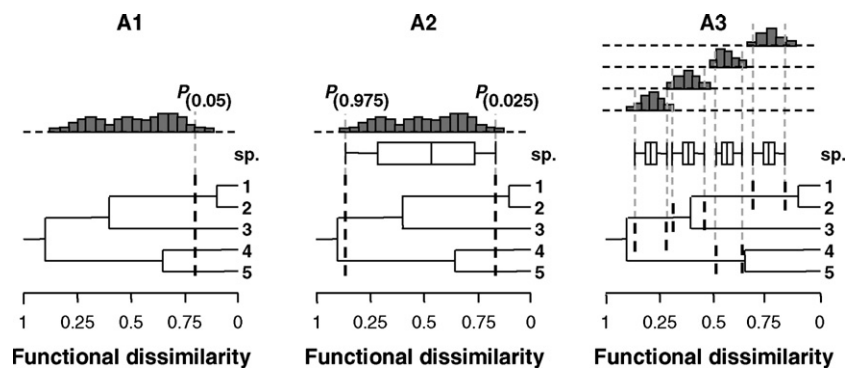


Fig. 1 – Three approaches to determine functional structure. In each case, the sample distribution of node values is obtained by bootstrapping the observed data. From the corresponding functional dissimilarity dendrogram, A1 defines as guilds those species clusters where observed values of all nodes are lower than the 5th percentile (vertical dotted line) of the combined sample distribution of all nodes (histogram). In the artificial example illustrated here, only the cluster comprising species 1 and 2 matches this condition. A2 assesses functional structure by determining both the 97.5% and 2.5% quantiles of the combined sample distribution of all nodes (whiskers in the box-plot and the respective dotted vertical lines) to detect both significantly high or low node values. In the example, it identifies significant segregation between two species clusters (species 1 to 3, and species 4 and 5). A3 contrasts each observed node value with the 97.5% and 2.5% quantiles (whiskers in the box-plots and the respective dotted vertical lines) of its own sample distribution (histogram). This approach detects the existence of another significant guild formed by species 4 and 5, ignored by A1 and A2.

structure. It corresponds to the average square deviations of dendrogram node values from their expected values:

$$\text{FSt} = \sum_{r=1}^n (x_{o(r)} - x_{e(r)})^2 / n \quad (2)$$

where n is the number of nodes in the dendrogram, and $x_{o(r)}$ and $x_{e(r)}$ are the observed and expected node values for the r -th rank of functional dissimilarity. For A1 and A2, $x_{e(r)}$ is the same for all nodes: the mean of the joint distribution of node pseudovalues through all ranks of functional dissimilarity. Instead, for A3 $x_{e(r)}$ it represents the mean node pseudo-value for the r -th rank of functional dissimilarity. Further, for A1 only the negative square deviations were summed in the numerator of Eq. (2) (i.e. those implying functional aggregation, $x_{o(r)} < x_{e(r)}$). In this case, FSt increases either by an increment in the magnitude of deviations or in the number of nodes showing significant values.

The second index was calculated only for A2 and A3 (all symbols as in Eq. (2)), and represents the relative importance of guild aggregation and functional divergence to the functional structure. It was calculated as the difference between the relative contribution of positive and negative square deviations to FSt:

$$\text{FDv} = \frac{\frac{1}{n} \times \left(\sum_{r=1}^n (x_{o(r)} - x_{e(r)})^2 - \sum_{r=1}^n (x_{o(r)} - x_{e(r)})^2 \right)}{\text{FSt}} \quad (3)$$

Thus, FDv measures the total degree of functional divergence in the assemblage, yielding values between 0 and 1

when functional divergence prevails over guild aggregation, and between -1 and 0 otherwise (note that terms in the numerator must be reversed if the dendrogram has been constructed using functional similarities). All calculations were done for each biological season of each year, and the resulting time series were plotted for qualitative examination (see below). All simulations were performed using the R 2.2.0 software (R Development Core Team, 2005).

2.4. Comparison of the statistical power of algorithms

Dissimilarity values within the range delimited by the lower and upper tail of the corresponding sampling distribution of nodes (or just by the lower tail in the case of A1) represent an area of statistical uncertainty with regard to ecological structure. That is, an area where deviations of observed node values from random expectations can be ascribed neither to functional divergence nor to guild aggregation, and nodes falling within such limits are treated as non-significant. The smaller the area of uncertainty and the magnitude of node deviation needed for significance to be detected, the higher the probability to detect significant structure (i.e. power; Manly, 1998, p. 80). Then, the power of the three algorithms we are comparing will depend on the extent of such areas of statistical uncertainty and, consequently, on the magnitude of the minimal deviation from random expectations needed to treat a given node as significant.

Because A3 tests the significance of each node from their respective sampling distribution, which is included within the

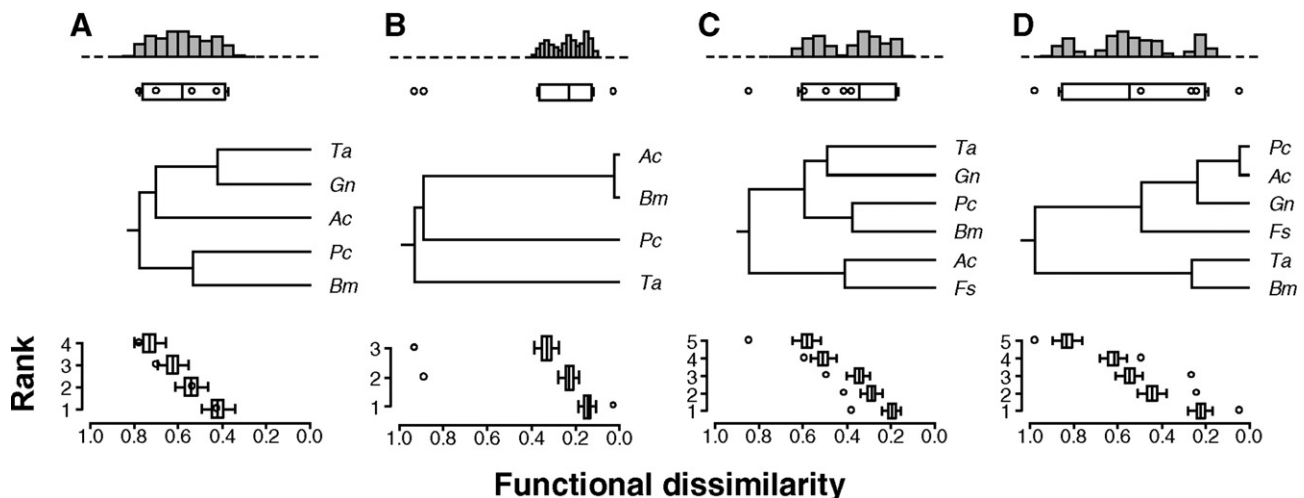


Fig. 2 – Four real examples to illustrate the observed patterns of differentiation in the information given by each approach about the functional structure of the vertebrate predator assemblage at Las Chinchillas National Reserve (LCNR). In the middle of each panel is the respective dendrogram of functional dissimilarity between predator species (*Ta*: *Tyto alba*, *Gn*: *Glaucidium nanum*, *Pc*: *Pseudalopex culpaeus*, *Bm*: *Bubo magellanicus*, *Ac*: *Athene cucularia*, *Fs*: *Falco sparverius*). Histograms represent the combined sample frequency distribution for all nodes, obtained by resampling the observed prey use matrices (1000 iterations per biological season). Upper box-plots show the quantiles 2.5%, 97.5% (whiskers), 5% and 95% (boxes) of such sample distributions, and the observed node values (open dots). The right margin of the boxes corresponds to the threshold value for A1, while whiskers represent threshold values for A2. Lower box-plots display the threshold values for each node (whiskers: 2.5% and 97.5% quantiles; boxes: 25% and 75% quantiles) used in A3 and the observed node values (open dots), ordered by rank of functional dissimilarity. The four panels represent: (A) No clear differentiation (non-breeding season of 2002); (B) A2 detects a high degree of functional divergence while A3 adds no new information (breeding season of 1996); (C) A3 detects significant functional divergence for most nodes, not detected by A1 and A2 (breeding season of 2003); (D) A3 detects significant guild aggregation for most nodes, not detected by A1 and A2 (non-breeding season of 1987).

joint distribution of all nodes used by A1 and A2 (Fig. 1), we propose that the former algorithm may detect more significant node values than the other two and may constitute a more powerful test for functional structure. Further, the larger the magnitude of deviation from randomness needed for significance, the higher the relative contribution of non-significant nodes to FSt values. Thus, we expect such contribution to be lower for A3 than for the other two algorithms. Accordingly, the statistical power of the three algorithms was compared using the difference between the FSt values obtained using all nodes (Eq. (2)) and those obtained using only significant nodes in the numerator of Eq. (2) (FSt*). This approach is better than just comparing the number of significant nodes identified by each algorithm, because it also quantifies the amount of variation that they cannot confidently ascribe to functional structure.

Then, for each algorithm, the relative discrepancy between FSt and FSt* values was estimated as $(FSt - FSt^*)/FSt$, and their mean values for the whole study period were contrasted using randomization tests (Manly, 1998). In each case, the observed

discrepancies were randomly reassigned between the samples to be compared (fixing sample sizes) and then all the pairwise differences of means were calculated. This was iterated 1000 times, and the observed pairwise differences of means were compared with their respective sampling distributions. Subsequently, the probability of obtaining such differences by chance (P_D) was estimated as the ratio between the number of resampled differences of means higher than the observed one and the number of iterations done. Significance levels were Bonferroni-adjusted for the number of pairwise comparisons done in between-algorithms tests ($\alpha_c = 0.05 \div 3 = 0.017$; Manly, 1998). Observed differences of means were considered significant whenever $P_D < \alpha_c$, and marginally significant whenever $\alpha_c < P_D < 0.05$. Thus, significantly lower values of mean discrepancy were interpreted as lower contribution of non-significant node deviations to FSt, and higher statistical power for functional structure identification. Values for non-breeding and breeding seasons were tested separately. Randomisation tests were performed using the Poptools 2.5.8 application for Excel (Hood, 2003).

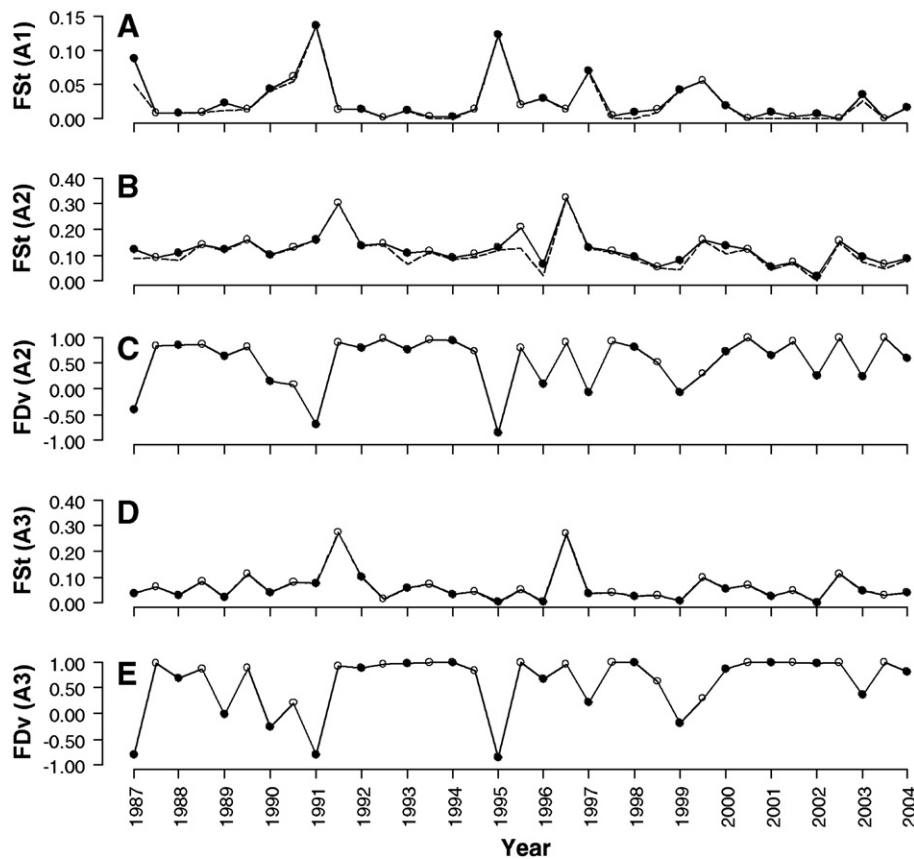


Fig. 3 – (A) Fluctuations in the overall functional structure (FSt) of the predator assemblage at LCNR through the entire study period, following A1. (B) Fluctuations in FSt and (C) degree of functional divergence (FDv) of the predator assemblage, following A2. Because nodes come from dendrograms of diet dissimilarity (Figs. 1 and 2), positive values in panel C indicate higher relative contribution of functional divergence to overall functional structure, while negative values indicate higher contribution of guild aggregation. (D) Fluctuations in FSt and (E) in FDv of the predator assemblage, following A3. Positive and negative values indicate the same as in C. All values were calculated for the respective non-breeding (filled dots) and subsequent breeding (open dots) biological seasons of each year. In A, B and D, values of FSt were calculated using all the observed node values (solid line) or only those that were significantly different from random (segmented line). However, note that the very small differences shown by them in D, make both dynamics to collapse.

3. Results

3.1. Information provided by each approach

Important differences were obtained in the information provided by the three approaches. The 35 biological seasons comprised in this study can be classified in four broad categories, each exemplified by an arbitrarily chosen case in Fig. 2.

The first set (5.7% of biological seasons) corresponded to those in which neither A2 nor A3 substantially increased the information given by A1. In the particular case of the non-breeding season of 2002 (Fig. 2A) none of the three approaches detected guilds. With the A2 two-tailed test, the dissimilarity value of the fifth node seemed to be higher than expected by chance, but with a marginal probability ($P_{[\text{obs}>\text{exp}]}=0.025$). Similarly, A3 node values fell fairly within their respective confidence intervals, with the exception of the marginal dissimilarity showed by the third one ($P_{[\text{obs}>\text{exp}]}=0.023$). Therefore, in spite of these rather subtle differences, there was no major conflict between the information supplied by the three approaches.

The second set of biological seasons comprised those (20%) in which A2 allowed detection of functional divergence, but A3 did not increase substantially the information given by the former. In most of such cases, divergence seemed to be the main component of functional structure. This is exemplified by the breeding season of 1996 (Fig. 2B), where A1 detected only one significant species grouping: *A. cucularia* and *B. magellanicus*. Instead, A2 revealed significant differences from the expected values for all nodes. Further, judging from the number of nodes involved (2 out of 3) and the magnitude of their deviations, functional divergence seemed to be the main determinant of overall functional structure. Identical conclusions were reached from A3.

The third category of biological seasons (25.7%) grouped cases in which A1 detected no functional structure, but A3 revealed a high degree of functional divergence, partially ignored by A2. Particularly, in the breeding season of 2003 (Fig. 2C) A1 did not detect guilds, while A2 showed significant dissimilarity only for the basal node of the dendrogram. Nevertheless, results from A3 revealed significant structure for all nodes, and suggest that it was completely due to divergence.

Finally, the commonest situation (48.8%) was that in which both A1 and A2 captured some of the functional structure, but A3 resulted more informative. For example, in the non-breeding season of 1987 (Fig. 2D), A1 detected a guild comprised by *A. cucularia* and *P. culpaeus*, and A2 showed functional divergence at the basal node. A3, in turn, extended the number of guilds to two (one made up by *A. cucularia*, *P. culpaeus*, *F. sparverius* and *G. nanum*, another made up by *T. alba* and *B. magellanicus*), revealing structure at all nodes in the dendrogram of functional dissimilarity. In this particular case, both the magnitude of deviations and the number of nodes involved suggest that guild aggregation explained most of the functional structure, but the relative contribution of aggregation and divergence vary throughout the study period (see below).

In sum, during ca. 75% of the biological seasons A3 conveyed information ignored by the other two approaches,

while in the remaining cases A3 did not contradict the conclusions reached by A1 and A2.

3.2. Interpretation of the dynamics of functional structure

Our perception of the dynamics of functional structure in this assemblage varied depending on the approaches used. Following A1, its magnitude appeared highly variable (mean=0.05, CV=0.91) due to episodic increases of otherwise low values of FSt (Fig. 3A). Such peaks decreased in magnitude with time, and tended to disappear when only significant negative deviations were considered, suggesting a temporal reduction in variability (Fig. 3A). This view changed as A2 accounted for the degree of functional divergence. First, we found an increase in both mean functional structure and its variability (mean=0.12; CV=2.08), which is expected for considering both negative and positive deviations. Second, there were qualitative changes such as long-term trends disappearing and only two peaks occurring (Fig. 3B). The highest FSt values from A1 and A2 rarely corresponded, and functional divergence contributed more to functional structure than guild aggregation in most biological seasons (Fig. 3C). A1 obviated this information, performing better in the few cases in which A2 yielded low values for FSt. This suggests that changes in functional structure were more tightly linked to fluctuations in functional divergence than in guild aggregation.

Results from A3 were qualitatively similar to those from A2, showing no clear long-term trends (Fig. 3D). But by using the sampling distribution of each node it reduced the magnitude of deviations, rendering FSt values lower and less variable (mean=0.06; CV=1.03). While the relative contribution of functional divergence continued prevailing over guild aggregation, the importance of the latter notoriously increased in some cases (Fig. 3E). Further, while A3 detected structure for more nodes and showed higher statistical power than the

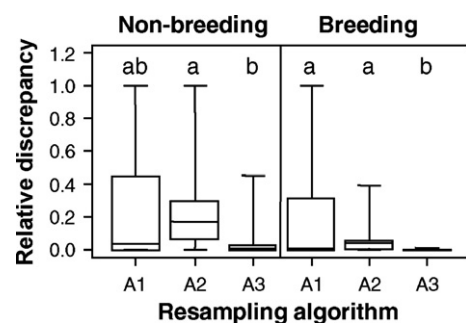


Fig. 4 – Differences in statistical power of three algorithms as estimated by the relative discrepancy between the overall functional structure values obtained from all observed nodes values (FSt) and those obtained only from significant node values (FSt*). Box-plots show the distribution of relative discrepancy values [calculated as $(FSt - FSt^*)/FSt$] obtained for all the non-breeding and breeding seasons (midline: median, box: 1st and 3rd quartiles, whiskers: range). Letters above the box-plots show if differences of means were significant (a vs b: $P_D < 0.017$), marginally significant (ab vs b: $P_D = 0.031$), or non-significant (a vs a, or a vs ab: $P_D > 0.05$) after randomization tests.

other two algorithms, no significant differences existed between A1 and A2 (Fig. 4). A closer examination makes clear that the small differences between FSt and FSt* values for A3 render their long-term dynamics undistinguishable (Fig. 3D), such differences being more clearcut for the other two algorithms (Fig. 3A and B). That is, non-significant nodes made almost no contribution to FSt values obtained after A3. In turn, because A1 and A2 were constrained to detect significance at both ends of the dendrogram of functional dissimilarity (Fig. 2), marked deviations at intermediate levels were frequently accountable for much of their FSt values (Fig. 4). Then, A3 was able to extract new information from the area of statistical uncertainty of A1 and A2, reducing the magnitude of the deviations needed to detect significant aggregation or divergence on this portion of the functional space. As a consequence, A3 seemed to be more informative about the functional structure of the assemblage under study than were A1 or A2.

4. Discussion

Methodological biases in the identification of assemblage functional structure may affect the study of the community patterns and processes of interest. In particular, the high attention paid to guild aggregation (Rosenfeld, 2002) is reflected on the conventional one-tailed statistical procedures developed for the study of functional structure (Jaksic and Medel, 1990; McKenna, 2003). Our results suggest that such approach may render an incomplete picture of the magnitude and direction of functional structure dynamics. We propose that the simultaneous consideration of guild aggregation and functional divergence offers a more accurate description of community functional organization. Our reasoning follows.

On the one hand, the one-tailed approach (A1) ignores all the structure attributable to the over-dispersion of species in functional space. This results not only in an underestimation of the total structure but also in a biased interpretation when the magnitude of guild aggregation and functional divergence vary independently of each other. This was the case here, where increases in guild aggregation (Fig. 3A) did not correspond with similar changes in functional structure (Fig. 3B and D), being more influenced by functional divergence (Fig. 3C and E). Thus, the observed long-term variability of functional structure was more strongly linked to fluctuations in the functional divergence of species and guilds than to the dynamics of guild aggregation. Due to its inability to distinguish between functional differentiation and lack of structure, A1 missed most of this information. Focused on the detection of significant divergence between samples or clusters, the algorithm proposed by McKenna (2003) faces the opposite problem: it is unable to distinguish significant aggregation from randomness, and thus may miss information in such cases in which functional structure is mainly driven by guild aggregation.

On the other hand, previous approaches assumed that all nodes in a branch of the dendrogram nested beyond a threshold value were statistically significant, either defining the same guild (Jaksic and Medel, 1990) or determining significant differentiation between samples or clusters

(McKenna, 2003). Jaksic and Medel (1990) obtained such threshold from a single sampling distribution for all nodes in the dendrogram, while McKenna (2003) did it by sequentially testing each node along a given branch in the dendrogram until significance was achieved, and then assuming that all subsequent nodes were also significantly divergent. The algorithm favored by us (A3), instead, simultaneously assesses the significance of each node and the magnitude and direction of their deviations from random according to their rank of functional similarity. This enables independent tests for any given cluster and for the sub-clusters included within. Thus, it can detect whether a significant aggregation at a given rank includes functionally divergent (or non-significant) clusters or samples at lower ranks, a pattern that cannot be accounted for by the two approaches described above. In such cases, guild identification becomes rather ambiguous, especially when the probability distribution function used in the randomization procedure of the observed data includes species-specific restrictions (i.e. when the consumption probability for different resource states varies between species). For example, a relatively high similarity between two species with similar behavior or handling capabilities could be nonetheless lower than expected by chance, while at the same time a relatively low similarity between them and other less similar species could be interpreted as significant closeness. Hence, A3 enables to unambiguously define guilds as species clusters within which all observed nodes display higher values of functional similarity than expected by chance. This seems to be more straightforward and convenient, even if one is only concerned about guild identification.

Another difference between A3 and the method proposed by McKenna (2003) is related to the randomization procedure. McKenna's method obtains the sampling distribution of each item (e.g. each prey category) from replicated samples of the units compared in the cluster analysis (e.g. predator diets). As consequence, this method is sensitive to replication because: (1) if there are no replicates for one or more units, the test cannot proceed for the first ranks of similarity; (2) the statistical power of the test depends on the rank of similarity at which nodes are evaluated, increasing as more samples are clustered together; (3) high variability between replicates may yield spurious clustering at low ranks. In turn, A3 resamples items according to probability distributions given by the operator, maintaining fixed the number of individual observations in each sample. Such distributions are grounded on theoretical, statistical or empirical basis, depending on the hypothesis to be tested, and thus they are independent on the observed data. Then, the statistical power of the test is constrained mainly by the number of individual observations per sample, determining how representative are the observed differences between samples or clusters, and not by replication. This renders it convenient to pool, whenever possible, all the information available for a species in the same sample, and is more straightforward when potential replicates are not – by themselves – representative of the real situation. For example, because single pellets or feces contain remains of just one or a few prey individuals, predator diets in our study site are better represented by pooling all of them into a single sample for each season of interest.

In our case, we gave the same sampling probability to all prey categories (i.e. uniform probability distribution), generating a completely random null model for community structure. Nevertheless, using A3 on alternative randomization algorithms accounting for different aspects of the study system (e.g. species selectivity; Lawlor, 1980) enable to simultaneously test the relative importance of various processes at different ranks of functional similarity. Thus, one could test the conditions, if any, under which species within a guild interact more strongly between them than with others, as has been proposed (Pianka, 1980). One could also analyze how deviations from random expectations in community organization patterns vary when more information about the assemblage and the environment is added to the model, or which groups of species are more affected. The latter may offer plausible explanations for the observed functional structure when hypotheses including the effects of different variables are contrasted. For example, an analysis of the functional structure of the assemblage at Las Chinchillas National Reserve suggests that it could be significantly reduced when including information about intrinsic functional constraints of predator species (Farias, 2006).

It must be emphasized that the approach proposed here does not take into account which species are grouped together, and hence does not test their pairwise relationships. Instead, it analyzes the probability of occurrence of the observed nodes values given their rank of functional similarity in the assemblage under study, and under the specified null model. Thus, it answers questions such as: What is the probability that the node corresponding to the highest level of similarity shows the observed value by chance if all species use all resource states with an equal probability? What is such probability for the second highest node?, and so on. In other words, this approach tests the observed functional configuration of the assemblage, without depending on the identity of its constituent species. It is the functional structure of the assemblage, as an aggregate variable, that is tested here.

Finally, the proposed functional structure (FSt) and divergence (FDv) indices provide complementary information about the magnitude and direction of the overall functional structure, respectively. Further, if the functional dendrogram is obtained using a metric of proportional niche overlap between species (such as Pianka's index), FDv represents an estimate of the degree of functional complementarity in the assemblage that is not explained by chance, and consequently serves as a statistical test for variations in this component of functional diversity (Mason et al., 2005). This approach may help build a connection between the processes that determine assemblage structure, and the current theoretical body linking functional diversity to ecosystem function (Tilman et al., 1997; Loreau, 1998; Diaz and Cabido, 2001; Loreau et al., 2001; Petchey and Gaston, 2002; Naeem and Wright, 2003).

In conclusion, we propose a relatively simple but powerful approach to the study of functional structure of species assemblages. This approach makes use of known methods of cluster analysis and intensive bootstrapping (Jaksic and Medel, 1990; McKenna, 2003). It expands the information rendered by previously proposed alternatives, by simultaneously considering the relative effect of guild aggregation

and of functional divergence. A balanced consideration of these two aspects of community structure may lead to a better understanding of the processes acting on ecological systems, and consequently of the plausible causes and consequences of species losses in ecosystems.

Acknowledgments

This research was funded through grant FONDAP-FONDECYT 1501-0001 to the Center for Advanced Studies in Ecology and Biodiversity. The A. W. Mellon Foundation also contributed to support the research at the study site. AF was supported by fellowships from DIPUC/VRAID. M. Lima and S. Navarrete made useful comments on previous drafts of this paper, and an anonymous reviewer made insightful contributions that enriched the original manuscript.

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