

# Effects of functional constraints and opportunism on the functional structure of a vertebrate predator assemblage

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## Summary

**1.** Within mainstream ecological literature, functional structure has been viewed as resulting from the interplay of species interactions, resource levels and environmental variability. Classical models state that interspecific competition generates species segregation and guild formation in stable saturated environments, whereas opportunism causes species aggregation on abundant resources in variable unsaturated situations.

**2.** Nevertheless, intrinsic functional constraints may result in species-specific differences in resource-use capabilities. This could force some degree of functional structure without assuming other putative causes. However, the influence of such constraints has rarely been tested, and their relative contribution to observed patterns has not been quantified.

**3.** We used a multiple null-model approach to quantify the magnitude and direction (non-random aggregation or divergence) of the functional structure of a vertebrate predator assemblage exposed to variable prey abundance over an 18-year period. Observed trends were contrasted with predictions from null-models designed in an orthogonal fashion to account independently for the effects of functional constraints and opportunism. Subsequently, the unexplained variation was regressed against environmental variables to search for evidence of interspecific competition.

**4.** Overall, null-models accounting for functional constraints showed the best fit to the observed data, and suggested an effect of this factor in modulating predator opportunistic responses. However, regression models on residual variation indicated that such an effect was dependent on both total and relative abundance of principal (small mammals) and alternative (arthropods, birds, reptiles) prey categories.

**5.** In addition, no clear evidence for interspecific competition was found, but differential delays in predator functional responses could explain some of the unaccounted variation. Thus, we call for caution when interpreting empirical data in the context of classical models assuming synchronous responses of consumers to resource levels.

*Key-words:* arid environments, community structure, El Niño/Southern Oscillation, niche dynamics, productivity.

*Journal of Animal Ecology* (2007) **76**, 246–257  
doi: 10.1111/j.1365-2656.2006.01202.x

## Introduction

A major goal of ecology is to assess the factors determining diversity (Ricklefs & Schluter 1993). One component of diversity that has attracted much attention in the last decade is functional diversity (Naeem & Wright 2003); that is, the extent to which species fill a given

functional space of interest (e.g. a multivariate space of traits associated with resource use or ecosystem function) (Díaz & Cabido 2001; Rosenfeld 2002). Consequently, an assemblage is said to be functionally structured if its component species are distributed non-randomly on such functional space (Wilson 1999). This structure can have two major implications for ecosystem function: (1) species aggregations in guilds or functional groups (Wilson 1999; Blondel 2003) may provide redundancy to the system, increasing its resilience to eventual disturbances that eliminate one or more species (Walker 1995; Jaksic, Feinsinger & Jiménez 1996; Naeem 1998);

and (2) species divergence (i.e. differentiation or segregation) in functional space may increase the complementarity of their individual effects on ecosystem processes, thus enhancing ecosystem function or interaction strength (e.g. the amount of prey removed by predators; Sih, Englund & Wooster 1998; Díaz & Cabido 2001; Loreau *et al.* 2001). Consequently, factors determining functional diversity could also affect the stability and function of ecosystems.

Functional structure has been viewed traditionally as a result of the interplay between species interactions, resource levels and environmental variability (Schoener 1982; Nudds 1983). In stable environments, competition should increase functional structure by increasing either species niche segregation or the formation of guilds (Pianka 1980; Schoener 1982). Conversely, in variable environments, where species cannot attain equilibrium densities, they should converge on the use of some profitable/abundant resource categories (Wiens 1977; Jaksic 1981). As a consequence, these views predict a directional gradient between divergent (or multiguild) stable systems and convergent variable systems (Nudds 1983).

However, the above model makes no explicit consideration of intrinsic functional differences between species. This is intriguing because it is well known that coexisting taxa differ in their ability to perceive, exploit and affect available resources due to functional constraints in their morphology, behaviour and physiology (e.g. Nudds 1983; Marti *et al.* 1993; Chalcraft & Reseraris 2003; Arim & Jaksic 2005; Van Son & Thiel 2006). Such constraints result from historical processes not necessarily associated with current interactive state (Connell 1980; Losos *et al.* 2003; Vitt & Pianka 2005). Consequently, the observed functional structure could result from a balance of two forces. First, a set of species could converge on the same available resources when the latter become more abundant or when competition decreases, thus improving correlations in their resource use. Secondly, intrinsic functional constraints may weaken such correlations by limiting the flexibility of species responses. Although some putative effects of functional constraints on assemblage functional structure have been documented (e.g. Joern & Lawlor 1980; Winemiller & Pianka 1990; Albrecht & Gotelli 2001), they are rarely considered before discarding opportunistic hypotheses in favour of resource competition. As far as we know, no attempt has been made to assess the relative contribution of functional constraints to the observed functional structure.

Since 1987, a long-term study has been in progress at Las Chinchillas National Reserve in central Chile. There, the diet of vertebrate predators and the abundance of their main prey (i.e. small mammals) have been recorded for 18 years, encompassing four marked pulses of productivity associated with El Niño/Southern Oscillation phenomena. Despite the high variability that characterizes the system (see Methods), previous studies have recorded a well-defined functional (guild) structure for the vertebrate predator assemblage that has remained

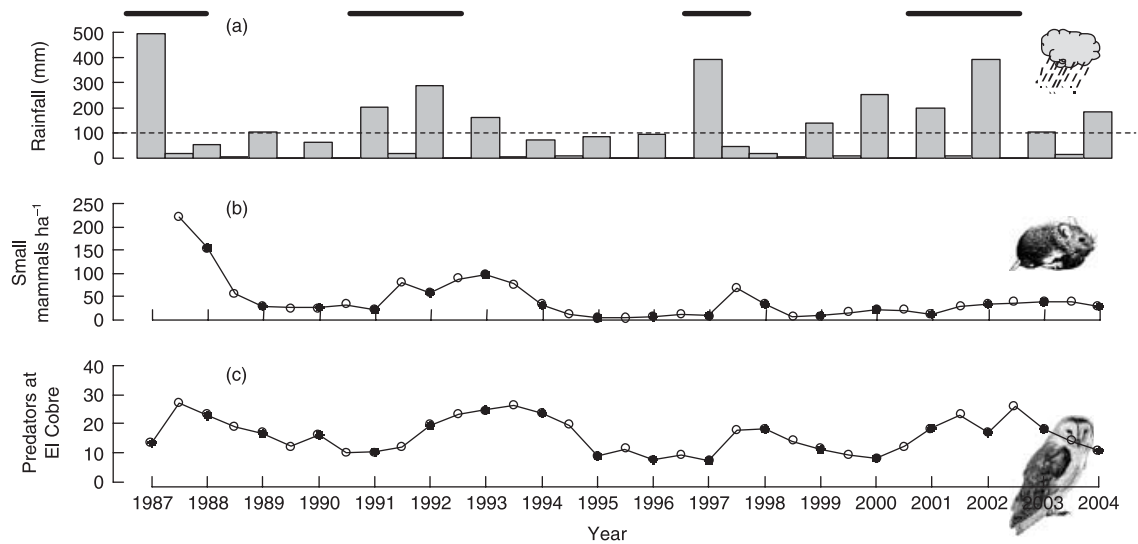
more or less constant over two decades (Jaksic, Feinsinger & Jiménez 1993, 1996; Farias & Jaksic in press). However, variations of this structure do not sustain the classical prediction made for highly variable ecosystems: an increased dietary overlap of predatory species when the main prey category becomes abundant, with a concomitant relaxation of guild structure (Wiens 1977; Schoener 1982). Plausible explanations for this discrepancy focus on prey dynamics (Jaksic *et al.* 1993), but the role of intrinsic functional constraints has yet to be assessed. Indeed, differences in the extent to which predatory species respond to fluctuations in prey levels (Jaksic *et al.* 1992; Arim & Jaksic 2005; Farias & Jaksic in press) suggest that functional constraints may be exerting an influence on the observed guild structure.

Our aim is to determine and quantify the importance of intrinsic functional constraints on the observed functional structure of a well-studied predator assemblage. To do that, we contrast the observed structure with that predicted by multiple null models (Gotelli & Graves 1996) that account for opportunistic convergence of predatory species and intrinsic functional constraints on prey use. Additionally, we apply a procedure designed to quantify the magnitude and direction of data deviations from null-model predictions. We use null models as benchmarks to map the observed functional structure on the space of plausible community configuration. Finally, we correlate the residual variability with predator and prey abundance to assess the plausibility of interspecific competition effects.

## Materials and methods

### STUDY AREA

Data came from El Cobre ravine at Las Chinchillas National Reserve (LCNR), near Aucó, Chile (31°30' S; 71°06' W), 300 km north of Santiago. The 4229-ha reserve is located in the coastal range, and has a rugged topography with numerous ridges bisected by deep ravines and few level areas. Elevations range from 400 to 1700 m. The climate is semi-arid, with rainfall concentrated during the austral winter (June–August). Annual precipitation averaged 190.3 mm in 1987–2003, but varied greatly from year to year (SD = 144.5 mm, Fig. 1a). The thorn-scrub vegetation consists primarily of shrubs, terrestrial bromeliads and cacti. Slopes that face north (equatorial) receive higher solar radiation than south-facing slopes (polar) and have sandy open soils with scattered gravel patches and rock outcrops. On the xeric north-facing slopes, grasses are scarce (mainly *Nassella* spp. and *Stipa* spp.), but cacti (*Trichocereus* spp., *Tephrocactus ovatus*), bromeliads (*Puya berteroniana*) and sclerophyllous shrubs (*Bahia ambrosioides*, *Cordia decandra*, *Bridgesia incisaeifolia*, *Flourensia thurifera*) are abundant. In contrast, the more mesic south-facing slopes support many grasses but few cacti and no bromeliads; further, a different assemblage of shrubs prevails (*Adesmia* spp., *Porlieria chilensis*, *Colliguaya odourifera*, *Proustia* spp.).



**Fig. 1.** Temporal dynamics of the study system at Las Chinchillas National Reserve. (a) Precipitation accumulated during each biological season from 1987 to 2004. Black bars at the top show the occurrence of El Niño events and the segmented line indicates mean rainfall throughout the study period. (b) Abundance of small mammals obtained from live trapping in two grids (1.1 ha each) at El Cobre ravine. (c) Minimum number of predator individuals at El Cobre ravine, estimated from the number of collected faeces and pellets (see Appendix S1). Filled and open dots are values for non-breeding and breeding seasons, respectively. Note that plots (b) and (c) differ in the scale of the y-axes.

#### SYSTEM DYNAMICS

Major prey categories for local predators (arthropods, birds, small mammals) fluctuate markedly in abundance at two different temporal scales. Seasonally, prey is more abundant during the warmer months. This is more noticeable for arthropods and birds, which increase markedly in abundance shortly after winter rainfalls, peaking in summer (Jaksic & Lazo 1999). Between years, outbreaks of small mammals (Fig. 1b) and insects, as well as increases in the abundance and richness of birds, follow vegetation blooms triggered by high winter rainfall, usually associated with El Niño events (Jaksic 2001; Fig. 1a). Whereas arthropods and birds respond almost instantaneously and decline quickly in abundance by the following autumn (Jaksic & Lazo 1999), small mammal irruptions carry over to the following winter (Jiménez, Feinsinger & Jaksic 1992; Lima, Stenseth & Jaksic 2002; Fig. 1b). The predatory assemblage responds numerically (Fig. 1c) and functionally to such fluctuations, with some species immigrating to or emigrating from the reserve, whereas a core of resident predators remain there (Jaksic *et al.* 1993; Arim & Jaksic 2005). In total, 14 predatory species have been observed at LCNR during this 18-year period (Jaksic *et al.* 1993; Jiménez *et al.* 1992; Martínez, Rau & Jaksic 1993), but our work concentrates on the six most abundant resident (core) species there: four owls (*Athene cunicularia*, *Glaucidium nanum*, *Bubo magellanicus* and *Tyto alba*), the American kestrel (*Falco sparverius*) and the culpeo fox (*Pseudalopex culpaeus*). The remaining species occur more sporadically, either being rare or foraging over a larger area than that encompassed in this study (Jaksic *et al.* 1993). In the case of sporadic

species, their functional responses could depend on the unknown dynamics of resources outside the reserve, and thus linked in an unpredictable manner to local fluctuations in the availability of prey.

#### DETERMINATION OF PREDATOR FUNCTIONAL RELATIONSHIPS

From March 1987 to February 2004, all available pellets and faeces at known roosts, perches or nests (raptors) and along permanent transects (foxes) were collected monthly. Pellets and faeces were teased apart under a dissecting microscope and prey were identified to the maximum achievable level of resolution (specific for vertebrates, ordinal for invertebrates). The minimum number of individual prey present in pellets or faeces was estimated by the number of paired or unique anatomical elements such as crania, mandibles, tooth rows, elytra and head capsules (Martí 1987). Data were pooled into two biologically relevant seasons per year: non-breeding (April–September) and breeding (October–March). Following Pianka (1973), we computed diet overlap between predator species pairs as:

$$O_{v_{jk}} = \frac{\sum p_{ik} p_{ij}}{\sqrt{\sum p_{ik}^2 \times \sum p_{ij}^2}} \quad \text{eqn 1}$$

where  $p_{ik}$  and  $p_{ij}$  are the relative occurrences of prey category  $i$  in the diets of two predators, respectively.  $O_{v_{jk}}$  ranges from 0 to 1 (0–100% similarity). Then, a matrix of functional dissimilarities (with entries  $1 - O_{v_{jk}}$ ) was constructed, and used as input in a cluster analysis employing the unweighted pair-group method with arithmetic averaging (UPGMA; Sneath & Sokal 1973).

Dissimilarity values were used instead of  $Ov_{jk}$  values to satisfy the requirements of the software used in the following analyses. Finally, a dendrogram of functional dissimilarity was obtained for each biological season of each year, and used in evaluating the respective assemblage functional structure.

#### QUANTIFICATION OF FUNCTIONAL STRUCTURE

The functional structure of the predatory assemblage was quantified by comparing the observed node values in the dendrogram of functional dissimilarity with those predicted by four alternative null models (Gotelli & Graves 1996), designed in an orthogonal fashion to account for either none, one or both factors of interest (i.e. functional constraints and opportunistic convergence). Models were constructed by resampling the observed diets 1000 times with replacement, for each biological season of each year, using the bootstrapping algorithms detailed below. In each iteration, pairwise  $Ov_{jk}$  values were recalculated and the cluster analysis was repeated, extracting and ranking in ascending order the node-pseudovalues obtained from the new dendrogram of functional dissimilarity. Subsequently, the 2.5% and 97.5% quantiles of the distribution of such pseudovalues at each rank of functional dissimilarity were determined. Any observed node value outside this confidence interval was considered as significantly different from random under the respective null model, and interpreted as evidence of significant functional structure. Nodes beyond the 2.5% or 97.5% quantiles implied significant aggregation or divergence at the corresponding rank of functional dissimilarity, respectively. We considered only those species clusters in which all included nodes show significant aggregation as guilds.

Two complementary indices were used to quantify the assemblage functional structure for each biological season of each year. One estimated the magnitude of the functional structure as the mean square-deviation of observed node values from those expected under the respective null model:

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

where  $n$  is the number of nodes in the dendrogram,  $x_{o(r)}$  and  $x_{e(r)}$  are the observed value and the expected (mean) pseudo-value for the node in the  $r$ th rank of functional dissimilarity, respectively. The other index depicted the relative importance of functional aggregation and divergence to the assemblage functional structure. It was calculated as the difference between the relative contribution of positive and negative square deviations to  $FSt$ :

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

(symbols as in eqn 2). Thus,  $FDv$  measures the degree of functional divergence in the assemblage, yielding values between 0 and 1 when divergence is prevalent over aggregation, and between -1 and 0 otherwise. All simulations were performed using R version 2.2.0 software (R Development Core Team 2005).

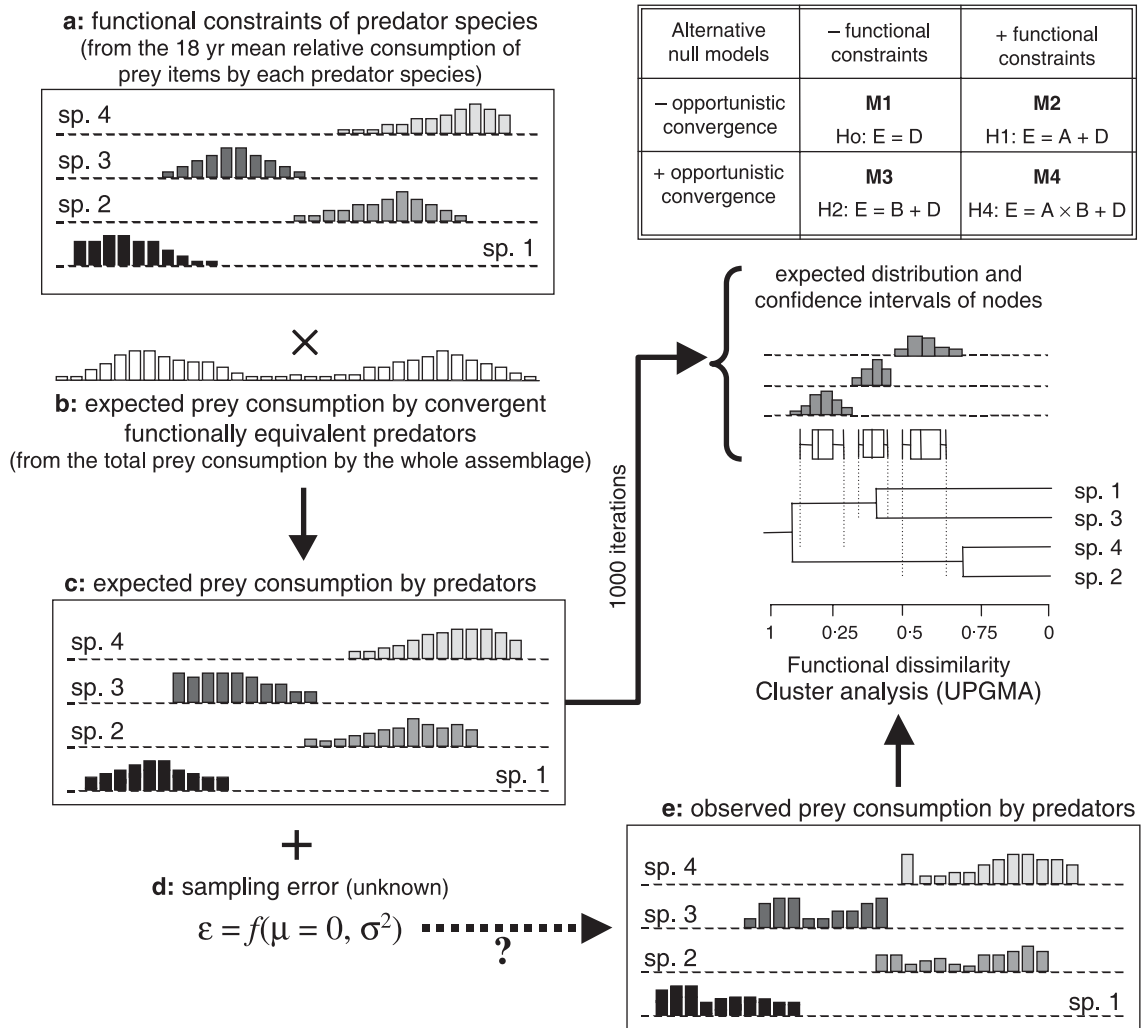
The obtained  $FSt$  and  $FDv$  values were compared between biological seasons and models using randomization tests (Manly 1998). In each case, the observed values were reassigned randomly between the samples to be compared (fixing sample sizes) and then all the pairwise differences of means were calculated. 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 performed. Significance levels were Bonferroni-adjusted for the number of pairwise comparisons performed in between-models within-season tests ( $\alpha_c = 0.05 \div 6 = 0.008$ , Manly 1998). Observed differences of means were considered significant whenever  $P_D < \alpha_c$ , and marginally significant whenever  $\alpha_c < P_D < 0.1$ . Randomization tests were performed using the Poptools version 2.5.8 application for Excel (Hood 2003).

#### RANDOMIZATION ALGORITHMS

Four randomization algorithms were developed (Fig. 2): M1 ignored both factors of interest by resampling with replacement all prey categories (for each predator) with an equal probability (fixing predator richness, number of prey categories and sample sizes). This was a completely random null model for functional structure, and serves as control in our experimental design.

M2, analogously to Lawlor's RA2 (Joern & Lawlor 1980), accounted for intrinsic functional constraints of predatory species (Fig. 2). For each predator species, prey categories were resampled according to a probability distribution vector obtained by: (1) averaging consumption records (percentage of diet) of each prey category eaten at least once by such predator during the study period, (2) assigning zeros to prey categories that were never consumed and (3) re-scaling all the vector elements to sum 1. Then, for a given predator, consistently rare prey items had a lower probability of being resampled than those that were consistently abundant. This emulated the general tendency for large-sized prey to be less frequently consumed than small-sized ones. It also avoided the overrepresentation of prey that are seldom expected to be consumed in high numbers due to their consistent scarcity in the field. Finally, it gave relatively low (or high) sampling probability to consistently avoided (or preferred) prey categories.

M3 accounted for opportunistic convergence of predators by assuming that if all of them were functionally equivalent (i.e. they did not differ in their functional



**Fig. 2.** Diagram of the steps followed in this paper. Table in the upper-right corner shows the orthogonal design used to construct the null models, alternatively following none, one or both steps a and b. c is the resulting probability distribution of prey use for the bootstrapping procedure (uniform for M1). The dotted arrow shows the unknown link between model and real data for the hypothetical case in which the former explained the latter.

constraints) and responded opportunistically to prey levels, they should be mutually correlated in their diet composition, differing only by chance (Fig. 2). Then, for any predator, the consumption probability of a given prey category  $i$  ( $\pi_i$ ) should be correlated with its observed relative consumption by the whole assemblage, the latter being a function of their relative consumption by each predator and its relative predation impact:

$$\pi_i = \frac{\sum_{k=1}^S p_{ik} \times RPI_k}{\sum_{i=1}^n \sum_{k=1}^S p_{ik} \times RPI_k} \quad \text{eqn 4}$$

where  $p_{ik}$  is the relative occurrence of prey category  $i$  in the diet of predator  $k$ ,  $S$  is the assemblage richness,  $n$  is the number of prey categories and  $RPI_k$  is the relative predation impact of predator  $k$ . The latter depends on the abundance and food requirements of each predator species, and because the assemblage comprised species

covering almost two orders of magnitude in body mass (thus largely differing in their food requirements, see Table S1 in Appendix S1; please refer to end of article for Supplementary material), we considered  $RPI_k$  to be a better weighting factor than abundance. Food requirements of predator species were estimated from their expected field metabolic rates (Nagy, Girard & Brown 1999), as detailed in Appendix S1. Thus, the resulting vector of  $\pi_i$  elements represented the resampling probability distribution of prey categories.

M4 simultaneously accounted for both factors of interest (i.e. functional constraints vs. opportunistic convergence), by resampling prey categories following a probability distribution vector obtained by the element-by-element product of the probability distribution vectors used in M2 and M3 (Fig. 2). This model assumes that both factors affected functional structure independently, and consequently their effects in the consumption probability distribution of prey items were multiplicative (i.e. for each predator:  $\pi_{i(M4)} = \pi_{i(M2)} \times \pi_{i(M3)}$ ).

## MODEL PERFORMANCE

We defined functional structure as a deviation of the observed pattern of dietary dissimilarities from that expected under a given null model. Thus, the model showing the lowest *FSt* values was assumed to account for more information about factors structuring the predatory assemblage. In particular, we were concerned with the performance of the three more informative models when compared to our control (M1). This relative performance was estimated for each model as:

$$RPf_{Mx} = \frac{FSt_{Mx} - FSt_{M1}}{FSt_{M1}} \quad \text{eqn 5}$$

where  $FSt_{Mx}$  and  $FSt_{M1}$  are the assemblage functional structure quantified by model  $x$  (M2, M3 or M4) and by M1, respectively.  $RPf < 0$  when the alternative model performed better than M1, and  $RPf > 0$  otherwise. Unity change in either direction represents 100% improvement (or impairment) in model fitting in relation to M1. To assess if any model differed significantly in performance from M1, we tested if their respective  $RPf$  values (pooled by biological season) differed significantly from zero using two-tailed  $t$ -tests ( $\alpha = 0.05$ ) on log-transformed data. Due to the existence of negative  $RPf$  values, the data were transformed to  $\log(x + c)$ , with constant  $c$  selected to improve normality as much as possible. Thus, the null hypothesis was:  $\mu_{\log(x+c)} = \log(c)$ . Differences in  $RPf$  values between biological seasons and models were tested by means of randomization tests (Manly 1998; see above). Significance levels were Bonferroni-adjusted for the number of pairwise comparisons performed in between-models within-season tests ( $\alpha_c = 0.05 \div 3 = 0.017$ ).

## ANALYSIS OF RESIDUAL VARIATION

After selecting the model(s) showing the best performance (lowest  $RPf$  value), the effect of the abundance of core and alternative prey categories and that of predators on functional structure was assessed by means of stepwise multiple regressions (Neter *et al.* 1996), using *FSt*, *FDv* and  $RPf$  as dependent variables. Three variables were tested as predictors: (1) the minimum number of predatory individuals present at El Cobre ravine (see Appendix S1 and Fig. 1c); (2) the abundance of the core prey category (small mammals) estimated as the minimum number of known alive individuals live-trapped in two 1.1-ha grids (see Jaksic *et al.* 1993 for details); and (3) the total precipitation accumulated during the respective non-breeding season (Fig. 1a), which correlates with productivity and with the abundance of alternative prey categories (Jaksic 2001). Classical models predict that an increase in the intensity of interspecific competition should be counteracted by a decrease in niche breadth of at least some of the species in the assemblage (Schoener 1982). Thus, to assess if variable (1) reflected the intensity of interspecific competition, the niche breadth of each predator (estimated

using the standardized version of Levins' index, Hurlbert 1978) was regressed against total predator abundance. Whenever necessary, variables were log-transformed to improve the distribution of residuals (Neter *et al.* 1996). These analyses were performed using R version 2.2.0 (R Development Core Team 2005) and STATISTICA version 5.1 (StatSoft Inc. 1997).

## Results

## COMPLETELY RANDOM NULL MODEL

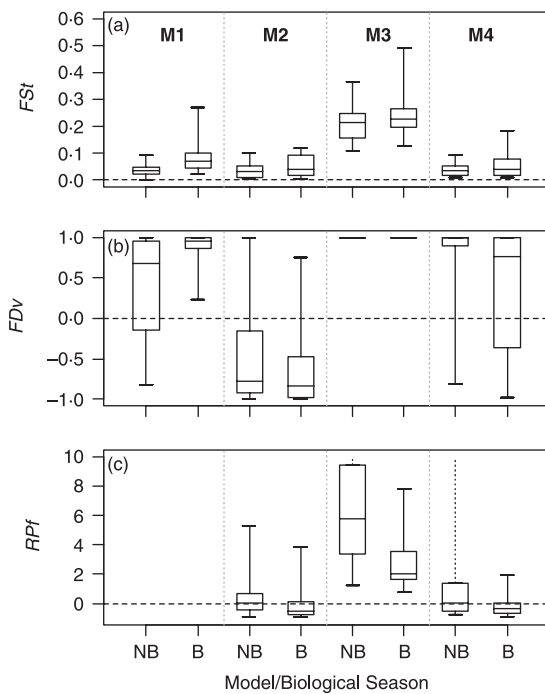
Overall, only our control model (M1) shows significant seasonal differences in functional structure (Table 1), *FSt* values being higher during the breeding seasons (Fig. 3a). *FDv* values were mainly positive (Fig. 3b), indicating the prevalence of functional divergence vs. aggregation for most biological seasons. Except for the breeding season of 1995, all cases showed significant divergence in at least one node of the dendrogram of functional dissimilarity. Most (88.6%) cases showed divergence at the basal node level, splitting the assemblage into two functionally divergent species-clusters: one made up of those predators that consumed mainly small mammals, and the other by those with a generalized diet dominated by arthropods. Superimposed upon this, significant divergence at one or more nodes at lower levels of functional dissimilarity indicated differences in the relative consumption of some prey categories or the sporadic inclusion of new prey items (e.g. amphibians) by one or a few predators. These species-clusters frequently involved at least one recognizable guild (Table 1). Specifically, *T. alba* and *B. magellanicus* formed a guild specialized on small mammals, mainly the rodent *Phyllotis darwini*. This guild remained unchanged during most of the non-breeding seasons and for half the breeding seasons between 1987 and 1995. Afterwards, the two owls were grouped again only during the non-breeding season of 2004. During the non-breeding season of 2003, *B. magellanicus* and the fox *P. culpaeus* formed a guild that diverged significantly from *T. alba* by consuming rodents bigger than *P. darwini* (i.e. *Octodon degus*), but preying mainly on small mammals. The other guild detected in our study consumed principally arthropods, but also a few birds, reptiles and mammals, and showed an irregular occurrence through time (c. 50% of biological seasons).

## ALTERNATIVE NULL MODELS

Both the magnitude and sign of functional structure differed according to the reference null model (Fig. 3). In general, the model accounting for opportunistic convergence (M3) showed higher functional structure (i.e. explained less variability) than the other three models during non-breeding seasons (Table 1). During the breeding seasons, *FSt* values for M1 and M3 were significantly higher than for the other two models; values for M3 were only marginally higher than those for

**Table 1.** Between-model/season comparisons of the functional structure (*FSt*) and functional divergence (*FDv*) of the vertebrate predator assemblage at *LCNR*, and relative performance (*RPf*) of null models. Differences are shown as absolute values, and are tested using randomization tests. Bonferroni-corrected significance levels are  $\alpha_c = 0.008$  for *FSt* and *FDv* in between-models within-season comparisons,  $\alpha_c = 0.017$  for *RPf* in between-models within-season comparisons and,  $\alpha_c = 0.05$  for all variables in between-seasons within-model comparisons. M1: completely random null model (control); M2: model accounting for functional constraints, M3: model accounting for opportunism; M4: model accounting for both factors. Significant and marginally significant differences are highlighted in bold type. The last two columns show for each model the percentage of cases showing guilds (%Gld) and significant divergence in at least one node (%Div).

Season/model	$\Delta FSt$	$P_D$	$\Delta FDv$	$P_D$	$\Delta RPF$	$P_D$	%Gld	%Div
Non-breeding season								
M1 vs. M2	0.04	0.22	<b>0.76</b>	<b>&lt; 0.01</b>				
M1 vs. M3	<b>0.14</b>	<b>&lt; 0.01</b>	<b>0.64</b>	<b>0.02</b>				
M1 vs. M4	0.03	0.29	0.36	0.17				
M2 vs. M3	<b>0.18</b>	<b>&lt; 0.01</b>	<b>1.40</b>	<b>&lt; 0.01</b>	<b>14.50</b>	<b>&lt; 0.01</b>		
M2 vs. M4	< 0.01	0.87	<b>1.12</b>	<b>&lt; 0.01</b>	1.43	0.85		
M3 vs. M4	<b>0.18</b>	<b>&lt; 0.01</b>	0.28	0.28	<b>13.06</b>	<b>&lt; 0.01</b>		
Breeding season								
M1 vs. M2	<b>0.12</b>	<b>&lt; 0.01</b>	<b>1.37</b>	<b>&lt; 0.01</b>				
M1 vs. M3	<b>0.08</b>	<b>0.04</b>	0.15	0.58				
M1 vs. M4	<b>0.11</b>	<b>&lt; 0.01</b>	<b>0.54</b>	<b>0.04</b>				
M2 vs. M3	<b>0.20</b>	<b>&lt; 0.01</b>	<b>1.52</b>	<b>&lt; 0.01</b>	<b>2.85</b>	<b>&lt; 0.01</b>		
M2 vs. M4	0.01	0.82	<b>0.83</b>	<b>&lt; 0.01</b>	0.17	0.81		
M3 vs. M4	<b>0.19</b>	<b>&lt; 0.01</b>	<b>0.69</b>	<b>&lt; 0.01</b>	<b>3.02</b>	<b>&lt; 0.01</b>		
Non-breeding vs. breeding seasons								
M1	<b>0.05</b>	<b>&lt; 0.01</b>	<b>0.49</b>	<b>0.01</b>			69	97
M2	0.03	0.11	0.12	0.64	0.66	0.27	71	63
M3	0.02	0.45	0	n.a.	<b>12.31</b>	<b>&lt; 0.01</b>	0	100
M4	0.03	0.18	0.41	0.10	<b>2.26</b>	<b>0.07</b>	26	86



**Fig. 3.** Summarized information about assemblage functional structure for non-breeding (NB) and breeding (B) biological seasons. Box-plots show the distribution of: (a) functional structure values (*FSt*), (b) functional divergence values (*FDv*) and (c) relative performance values of models (*RPf*, only for M2, M3 and M4). Whiskers, boxes and central line represent 2.5–97.5%, 25–75% and 50% (median) quantiles, respectively.

M1 (Table 1, Fig. 3a). Functional divergence was always lowest for the model that accounted for functional constraints (i.e. M2; Table 1, Fig. 3b). Although *FDv* values tended to be higher for M3 than for M1 during non-breeding seasons, those corresponding to both M3 and M1 tended to be higher than those for the model accounting simultaneously for the two factors of interest (M4) during breeding seasons (Table 1). In summary, the two models that did not consider functional constraints (M3 and M1) explained less variability, and showed more divergence than those that did.

For M2 in particular, there were no seasonal differences in either functional structure or divergence (Table 1), and *FDv* values were mainly negative (Fig. 3b). This suggests that functional aggregation explained most of functional structure (i.e. predators aggregated more than expected from their functional constraints). Concomitantly, the occurrence of significant divergence became less frequent than for M1, but the basic subdivision between generalist and small mammal specialist predators persisted and the occurrence of guilds remained almost unchanged (Table 1). This suggests a role for functional constraints in determining part of the observed divergence.

Functional divergence always explained all of the functional structure recorded from M3 (Fig. 3b). The latter variable showed no seasonal trends and no guild was detected with this model (Table 1, Fig. 3a). Consequently, vertebrate predators seemed to diverge

functionally more than expected from opportunistic convergence on the same set of resources. On the other hand, M4 showed no clear seasonal trends in functional structure, although functional divergence decreased marginally during the breeding seasons (Table 1). In this case, divergence prevailed over aggregation for most of the study period (Fig. 3b), and the occurrence of guilds became rare (Table 1). Thus, the assemblage seemed to be more divergent than expected from M4, but not as much as expected from M2.

#### RELATIVE PERFORMANCE

None of the three more informative models (M2, M3 and M4) performed consistently better than the control (M1; Fig. 3c). In contrast, M3 always showed a poorer performance (non-breeding:  $t_{17} = 23.29$ , breeding:  $t_{16} = 19.71$ ;  $P < 0.01$  for both) that improved only slightly during the breeding seasons (Table 1). The mean performances of M2 and M4 did not differ from that of M1 in non-breeding seasons (M2:  $t_{17} = 0.86$ ,  $P = 0.40$ ; M4:  $t_{17} = 0.26$ ,  $P > 0.8$ ), but were marginally ( $t_{16} = -2.06$ ,  $P = 0.06$ ) and significantly ( $t_{16} = -2.13$ ,  $P = 0.05$ ) better during breeding seasons, respectively. However, whereas M4 showed marginal seasonal differences in its performance, M2 behaved similarly in both seasons (Table 1).

Overall, the performance of M3 was always poorer than that of M2 and M4, which in turn did not differ

significantly among them (Table 1). Both M2 and M4 were sometimes capable of explaining more of the assemblage functional structure than did the control. However, this trend appeared only in breeding seasons, when the medians of  $RPf_{M2}$  and  $RPf_{M4}$  values corresponded to an improvement of 55% and 38% over M1, respectively (Fig. 3c). Therefore, no alternative model performed much better than M1, but M2 and M4 sometimes seemed to fit slightly better to the observed data, suggesting that the functional structure of this assemblage fell between that predicted by these two latter models.

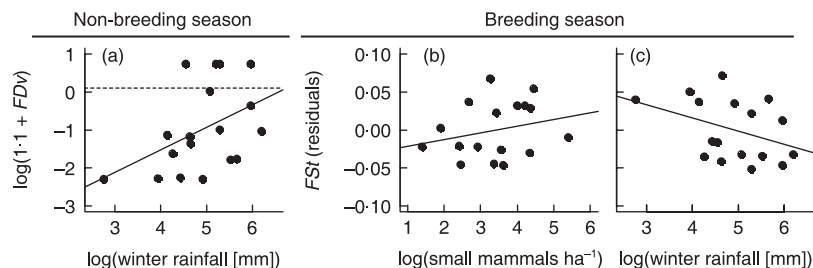
#### RESIDUAL VARIATION

The analysis of residual variation for the two fittest models showed that during non-breeding seasons the unexplained functional divergence by M2 was associated positively with winter rainfall (Table 2), and prevailed over aggregation only in rainy years (Fig. 4a). Simultaneously,  $FSI$  values for M4 also increased with rainfall, and the relative performance of this model improved with the abundance of small mammals (Table 2, Fig. 5). During breeding seasons,  $FSI$  values for M2 decreased with winter rainfall (Fig. 4), but this became evident only after including a non-significant ( $t_{14} = 1.26$ ,  $P = 0.23$ ) positive association with the abundance of small mammals in the regression model (Table 2). In turn, functional structure for M4 decreased with predator

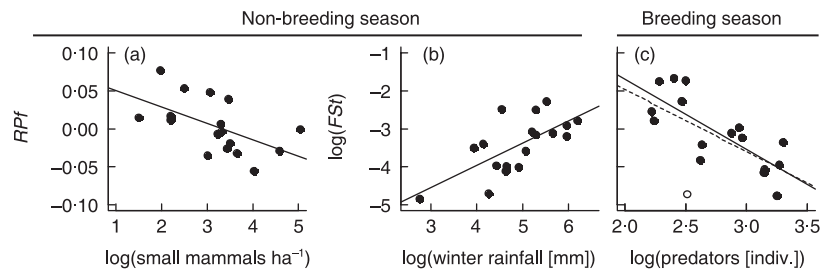
**Table 2.** Best linear regression models explaining the residual variability of the two fittest null-models (M2 and M4).  $R.X_{(Mx)}$ : residuals in the variable  $X$  not explained by null-model  $Mx$ .  $s.mamm.$  small mammals  $ha^{-1}$ ,  $pred.$  predators at El Cobre,  $w.rain.$  winter rainfall (mm). Significance level: 0.05.

Model	$R^2$	$F$ (d.f.)	$P$
Non-breeding season			
$\text{Log}(1.1 + R.FDV_{(M2)}) = \alpha + 0.49 \log(w.rain) + \epsilon$	0.20	4.03 (1,16)	0.06
$\text{Log}(R.FSI_{(M4)}) = \alpha + 0.69 \log(w.rain) + \epsilon$	0.47	14.14 (1,16)	< 0.01
$\text{Log}(R.RPf_{(M4)}) = \alpha - 0.55 \log(s.mamm.) + \epsilon$	0.30	6.51 (1,15)	0.02
Breeding season			
$R.FSI_{(M2)} = \alpha - 0.41 \log(w.rain) + \epsilon$	0.17	2.96 (1,15)	0.11
$R.FSI_{(M2)} = \alpha - 0.65 \log(w.rain) + 0.38 \log(s.mamm.) + \epsilon$	0.25	2.33 (2,14)	0.03
$\text{Log}(R.FSI_{(M4)}) = \alpha - 0.64 \log(pred.) + \epsilon$	0.41	10.34 (1,15)	< 0.01
$\text{Log}(R.FSI_{(M4)})^a = \alpha - 0.78 \log(pred.) + \epsilon$	0.60	21.25 (1,14)	< 0.01

<sup>a</sup>After removing an outlier (2000).



**Fig. 4.** Relationship between functional structure from M2 and environmental variables.  $FSI$ : functional structure,  $FDv$ : functional divergence. The segmented line in plot (a) represents the expected value for  $FDv = 0$  [i.e.  $\log(1.1)$ ]. Plots (b) and (c) depict partial regressions, and residuals are shown in the y-axis.



**Fig. 5.** Relationship between functional structure ( $FSt$ ) from M4, the relative performance of the latter ( $RPF$ ) and environmental variables. Segmented and continuous lines in (c) represent trends for all values and after removing an outlier (open dot), respectively.

**Table 3.** Relationship between the niche breadth of each vertebrate predator ( $y$ ) at *LCNR* and total predator abundance ( $x$ ). Selected linear regression models are shown in the second column to illustrate log-transformed variables and sign of regression coefficient (slope). Significant and marginally significant relationships are highlighted in bold type.

Species	Model	$R^2$	$F$	(d.f.)	$P$
<b>Non-breeding season</b>					
<i>Bubo magellanicus</i> <sup>a</sup>	$y = \alpha + \beta \log(x) + \epsilon$	0.15	2.83	(1,16)	0.11
<i>Tyto alba</i> <sup>b</sup>	$y = \alpha - \beta x + \epsilon$	0.08	1.21	(1,14)	0.29
<i>Athene cucularia</i>	<b><math>y = \alpha + \beta \log(x) + \epsilon</math></b>	<b>0.29</b>	<b>6.58</b>	<b>(1,16)</b>	<b>0.02</b>
<i>Glaucidium nanum</i>	<b><math>y = \alpha + \beta \log(x) + \epsilon</math></b>	<b>0.74</b>	<b>23.01</b>	<b>(1,8)</b>	<b>0.01</b>
<i>Falco sparverius</i> <sup>a</sup>	$y = \alpha + \beta \log(x) + \epsilon$	0.26	2.48	(1,7)	0.16
<i>Pseudalopex culpaeus</i>	$y = \alpha + \beta \log(x) + \epsilon$	0.02	0.35	(1,16)	0.56
<b>Breeding season</b>					
<i>Bubo magellanicus</i> <sup>c</sup>	<b><math>\log(y) = \alpha + \beta \log(x) + \epsilon</math></b>	<b>0.41</b>	<b>9.70</b>	<b>(1,14)</b>	<b>&lt; 0.01</b>
<i>Tyto alba</i>	$y = \alpha - \beta \log(x) + \epsilon$	0.12	1.79	(1,13)	0.20
<i>Athene cucularia</i>	<b><math>y = \alpha + \beta x + \epsilon</math></b>	<b>0.21</b>	<b>3.66</b>	<b>(1,14)</b>	<b>0.08</b>
<i>Glaucidium nanum</i>	$y = \alpha + \beta \log(x) + \epsilon$	0.03	0.21	(1,8)	0.66
<i>Falco sparverius</i>	$y = \alpha + \beta x + \epsilon$	0.15	1.04	(1,6)	0.35
<i>Pseudalopex culpaeus</i> <sup>d</sup>	<b><math>\log(y) = \alpha + \beta \log(x) + \epsilon</math></b>	<b>0.23</b>	<b>4.14</b>	<b>(1,14)</b>	<b>0.06</b>

Removed outliers: <sup>a</sup>1987; <sup>b</sup>1995; <sup>c</sup>1998; <sup>d</sup>1996.

abundance, especially after removing a single outlier (Table 2, Fig. 5c). Contrary to expectations, most predator species significantly increased their niche breaths with total abundance of predators for at least one biological season (Table 3). In turn, predator species with the lowest sample size (*F. sparverius*) showed non-significant positive associations, whereas *T. alba* was the only predator showing the expected negative (though non-significant) relationship.

## Discussion

### NON-RANDOM FUNCTIONAL STRUCTURE

Contrasting observed patterns of niche overlap with randomized null models is useful not only for determining the existence of functional structure in a given assemblage (Gotelli & Graves 1996), but also for quantifying the magnitude and form (divergence or aggregation) of the observed deviations from the random distribution of species in functional space. The significant deviations from pure randomness displayed by our data offer strong evidence that the predatory assemblage at *LCNR* is functionally structured. Consistent with previous findings (Jaksic *et al.* 1993; Farias & Jaksic in

press), our completely random null model identified two consistent divergent species groups; one which was more specialized, consuming mainly small mammals, and another with a generalized diet made up of a high proportion of arthropods and variable contributions of other prey categories (mammals, birds, reptiles and amphibians). *T. alba* and *B. magellanicus* were the species included more frequently in the former group, joined occasionally by *P. culpaeus* at the end of the study period. In turn, the latter group was represented mainly by *A. cucularia*, *F. sparverius*, *G. nanum* and *P. culpaeus*, and joined occasionally by *B. magellanicus* during the second half of the study period. Although guilds may be recognized within these species-clusters, functional aggregation explained less variability in functional structure than did divergence.

### ROLE PLAYED BY INTRINSIC FUNCTIONAL CONSTRAINTS

As our study system was highly variable, we expected that the opposed forces of intrinsic functional constraints and opportunism would explain some of the observed functional structure (Wiens 1977, 1993; Jaksic 1981; Nudds 1983). Accordingly, null models accounting for

at least one of such factors should have displayed less functional structure than the control (M1). However, none of our alternative models fitted the observed data much better than M1 (Fig. 3, Table 1). The model that accounted only for opportunism (M3) had the poorest fit and showed a high degree of functional divergence. However, as noted below, this result is insufficient to infer an effect of interspecific interactions, unless we account for functional constraints of the species and analyse how residual variation correlates with the abundance of both predators and prey.

Some degree of functional divergence could arise if coexisting species cannot use all the available resources in the same manner due to constraints in their foraging behaviour (Joern & Lawlor 1980). Therefore, the pertinent question should be whether functional structure persists after such intrinsic functional constraints are accounted for. The RA2 algorithm proposed by Joern & Lawlor (1980) can answer this partially by randomizing only those resources with a non-zero frequency of consumption for each consumer. Application of this approach reveals some effect of functional constraints on the functional structure of assemblages of ants (Albrecht & Gotelli 2001), grasshoppers (Joern & Lawlor 1980), fishes and reptiles (Winemiller & Pianka 1990). However, this method may be biased because it assigns indistinctly the same consumption probability to all non-zero prey categories. This is unlikely to happen because eco-morphological characteristics of both predator (size, hunting mode, energetic requirements) and prey (size, habitat–time use, antipredatory behaviour) could affect the consumption probability of any prey category (e.g. Marti *et al.* 1993; Chalcraft & Resetarits 2003).

Long-term data obtained under contrasting environmental contexts – as shown here – may help to determine which prey categories tend to be consistently more or less consumed by a given predator, and then allow estimation of predator constraints more accurately. Using this approach (M2) we recorded an improvement of model fitting for most (but not all) of the study period (Fig. 3). In addition, simultaneous accounting for opportunism (M4) did not lead to better fitting. Although under model M2 predators did not segregate as much as expected from their functional constraints, model M4 revealed functional divergence. Thus, the observed functional structure fell to an intermediate point between these two models (i.e. predators tended to diverge according to functional constraints, but not as much as expected).

Because small mammals constitute the core resource for the whole assemblage (Jaksic *et al.* 1992, 1993), functional constraints of predators should be more relevant for functional structure when the availability of alternative prey is higher, allowing predators to diverge (Tokeshi 1986). Thus, the marked seasonal dynamics of alternative prey could explain why null models accounting for functional constraints performed better during breeding seasons. Indeed, the residual variation un-

explained by M2 tended to be lower during breeding seasons of rainy years (Fig. 4c), when the availability of alternative prey categories was higher (Jaksic *et al.* 1993; Jaksic & Lazo 1999). However, this trend was more relaxed when core prey again became more available (Fig. 4b). In turn, predators may be forced to converge on core prey during non-breeding seasons, resulting in better performance of M4 at high abundances of small mammals (Fig. 5b). Convergence seemed strongest during the dry periods following the El Niño events (Fig. 1), most probably because small mammals remained abundant, contrary to alternative prey (Jaksic 2001).

Therefore, intrinsic functional constraints exerted certain effects on the functional structure of the vertebrate predator assemblage at LCNR, modulating the opportunistic response of predators to fluctuations in resource availability. This is in agreement with the idea that taxonomic composition of assemblages is reflected in historically determined functional constraints on species resource use, and these in turn affect community structure (Connell 1980; Losos *et al.* 2003; Vitt & Pianka 2005). Such constraints tended to decrease the expected correlation between the functional responses of coexisting predators, thus increasing the resulting functional diversity. As a consequence, an indirect positive link between taxonomic richness and functional complementarity emerges, with implications for system functioning (Díaz & Cabido 2001; Loreau *et al.* 2001). Further, the patterns we report are more complex than those predicted by previous models (Wiens 1977; Pianka 1980; Schoener 1982; Nudds 1983). We suggest that changes in the functional structure of this assemblage resulted from an interplay between species composition and both total and relative abundance of core and alternative prey categories. Because both types of prey show asynchronous dynamics, our system fell outside the domain of previous, more simplistic models (Jaksic *et al.* 1993; Wiens 1993; Farias & Jaksic in press).

#### WHAT ACCOUNTS FOR THE REMAINING FUNCTIONAL STRUCTURE?

Divergent deviations from random null models are usually attributed to the effect of interspecific interactions (Gotelli & Graves 1996). Classical models state that increased interspecific competition should cause a reduction in mean niche breadth and increased functional structure (Pianka 1980; Schoener 1982). Similarly, the abundance of competitors should be associated with decreased niche breadth and increased structure. However, we found the reverse situation (Fig. 5c, Table 3). In fact, *T. alba* was the only species that exhibited negative (but non-significant) associations between total predator abundance and niche breadth, perhaps because its low dietary flexibility rendered it more vulnerable to competition (Jaksic *et al.* 1993, 1992). Strengthening this view, Lima *et al.* (2002) found evidence of only intraspecific competition effects on the population dynamics of *B. magellanicus* at the study area, whereas

both intra- and interspecific competition were apparent in the dynamics of *T. alba*. Greater importance of intraspecific competition over interspecific competition would lead predators to increase their respective niche breadths as the *per capita* prey availability decreased (Schoener 1982), thus increasing their mean niche overlap. Thus, from the existing evidence, competitive interaction between species seems an unlikely explanation for the tendency of the assemblage to diverge more than predicted by M4.

An alternative explanation involves the performance of opportunistic, but none the less asynchronous, responses of predatory species to resource level fluctuations. As coexisting species may differ in their perception of environmental harshness, they could respond idiosyncratically to different resource levels (Nudds 1983; Arim & Jaksic 2005; Van Son & Thiel 2006; Farias & Jaksic in press). Then, following an increase in the abundance of a given prey category, members of the predatory assemblage may increase their consumption of that prey to differing extents, with more efficient or flexible consumers reacting first (but some of them not at all). Consequently, their resulting mean dietary overlap should be lower than that expected from all species converging simultaneously on an abundant prey category.

Consistent with this view, previous studies on the predatory assemblage at LCNR show that predator species differ in their dependence on small mammals and exhibit different functional responses to fluctuations in their prey abundance (Jaksic *et al.* 1992; Arim & Jaksic 2005). Further, species affiliation to the two main species-clusters is not static (Jaksic *et al.* 1993, 1996), but varies relative to the availability of core prey. Thus, most predators belonged to the mammal-specialized group when this prey was abundant, and shifted sequentially to the generalist group as mammals became more scarce (Farias & Jaksic in press). Only two predator species showed little change in their foraging behaviour: *T. alba* was always a strict mammal-specialist, emigrating from the study area when small mammals became too scarce, whereas arthropods were always the staple prey of *A. cucicularia* (Jaksic *et al.* 1992, 1993; Farias & Jaksic in press). In fact, the latter species showed a clear functional response to changes in the availability of small mammals. This prey category made up from 0% to 22% of the diet of this little owl, depending on its availability in the field, but always represented a minor portion of it. Thus, despite the observed functional response, the functional role of *A. cucicularia* as chiefly insectivorous remained more or less unchanged. In contrast, the diets of *B. magellanicus*, *P. culpaeus* and *G. nanum* varied widely in composition. They were dominated either by small mammals, by alternative prey categories (e.g. arthropods, birds and reptiles), or by similar proportions of both categories. Thus, these predators acted alternatively as small mammal specialists, insectivorous or generalized omnivorous, depending on the availability of the main prey. Consequently, the relative specialization of *A. cucicularia* and *T. alba* (or their lack of

flexibility) might have precluded the convergence of the whole assemblage, even when core prey became highly abundant. Then, the non-synchronous functional responses of predators became manifest in successive shifts between the two recognized species-clusters, and contributed to the unexplained functional structure.

Overall, we have no evidence of interspecific competition positively affecting the functional structure of the vertebrate predator assemblage at LCNR. Due to the high variability of the study system, this concurs with previous models relating functional structure to environmental variability and the intensity of competition (Wiens 1977; Schoener 1982; Nudds 1983). However, an increase in the abundance of local predators and in ensuing intraspecific competition seemed to be strong enough to force some convergence in our study system.

We propose that combining long-term data and comparing multiple alternative null models could be a powerful tool for disentangling the probable causes of functional structure of species assemblages. Quantifying the deviations from each of such models allows the simultaneous assessment of the relative contribution of different factors to the observed patterns. As a corollary, if this approach improves our understanding of the processes determining functional diversity, it will also contribute to illuminating the mechanisms regulating ecosystem functioning and stability (Naeem & Wright 2003).

### Acknowledgements

This research was funded through grant FONDECYT-FONDAP 1501-0001 to the Center for Advanced Studies in Ecology and Biodiversity. The A. W. Mellon Foundation also contributed to support research at the study site. A. F. was supported by a fellowship from DIPUC/VRAID. M. Arim, F. Labra, M. Lima and an anonymous reviewer made many useful comments on the manuscript.

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Received 5 June 2006; accepted 14 November 2006

## Supplementary material

The following supplementary material is available as part of the online article (full text) from

**Appendix S1.** Estimation of  $RPI_k$  values.

**Fig. S1.** Directed graph illustrating the Structural Equation Models used to estimate predator abundance from the number of pellets/faeces.

**Table S1.** Information used to estimate the daily food requirements of predators at El Cobre ravine.