



Geographical ecology of South American desert small mammals: consequences of observations at local and regional scales

DOUGLAS A. KELT¹, PABLO A. MARQUET² and JAMES H. BROWN³

¹*Department of Wildlife, Fish and Conservation Biology, University of California, Davis, CA 95616*

USA. E-mail: dakelt@ucdavis.edu ²*Facultad de Ciencias Biológicas, Departamento de Ecología, Universidad Católica de Chile, Casilla 114-D, Santiago, Chile. E-mail: pmarquet@genes.bio.puc.cl*

³*Department of Biology, University of New Mexico, Albuquerque, NM 87131 USA. E-mail: jhbrown@unm.edu*

ABSTRACT

Five major drylands in South American display very low levels of faunal similarity. The remarkable consistency of faunal structure, however, suggests that it may be possible to extend earlier conclusions based only on the mammal fauna of the

Altiplano and the Atacama Desert to all of South America's arid lands.

Key words biogeography, cross-scale patterns, desert small mammals, elevational gradient, latitudinal gradient, neotropics, South America, spatial scale, species–area relations

INTRODUCTION

In their analysis of regional faunas of five Neotropical aridlands, Ojeda *et al.* (2000; OBB hereafter) extended our earlier analysis of the small mammal fauna of two South American arid regions (Kelt *et al.*, 1996). We are pleased that our research has stimulated others to pursue further studies on the ecology and structure of small mammal faunas from arid lands in South America. It is evident to us, however, that our study and some of our conclusions have been misunderstood. Moreover, while OBB are critical of our methodology, and presumably our conclusions, their own data appear to support our approach and results. Finally, we encountered some miscalculations in OBB which substantially influence their interpretations of the relatedness of mammal faunas in Neotropical drylands. In the present note we wish to expand upon OBB's analysis and draw further conclusions based on a comparison of South American aridlands mammal faunas at disparate spatial scales.

RELATEDNESS OF SOUTH AMERICAN DRYLAND FAUNAS

Applying a metric of faunal similarity to the mammal faunas of five Neotropical aridlands, OBB reported that the standardized expected number of shared species among these faunas were all negative, suggesting that these faunas are quite distinct (see Table 1b). Additionally, four of the 10 comparisons were significant, and OBB emphasize that most of these significant coefficients (three of four) involved the Atacama Desert, underscoring 'the importance of the Andes as a biogeographic barrier'. They argue that the low degree of faunal similarity between the Atacama Desert and other South American drylands 'contrasts with statements by Kelt *et al.* (1996) regarding the importance of isolation between the South American drylands, particularly of the biogeographic effect of the Andean massif'. The quote that they provide from our paper, however, was not a conclusion regarding the influence of the Andean barrier; rather, it was a reference to

Table 1 Similarity between small mammal faunas of five South American drylands, as calculated by us (a) and Ojeda *et al.* (2000) (b). Numbers above the diagonal are the number of species that are shared between paired regions, with the expected number in parentheses. Below the diagonal is the standardized number of shared species using the metric of Connor & Simberloff (1978). The values presented are normalized similarity values (Connor & Simberloff, 1978), such that values > 1.96 (highlighted in bold) represent significantly disimilar ($P < 0.05$) pairwise comparisons. Along the diagonal are the number of species unique to each desert region, and the total number of species in each region are given in the right-hand column

	Atacama	Altiplano	Monte	Patagonia	Caatinga	Total no. of species
(a)						
Atacama	6	5 (5.26)	3 (3.94)	0 (2.63)	0 (1.75)	13
Altiplano	-0.16	27	5 (10.92)	3 (7.8)	0 (4.85)	36
Monte	-0.61	-2.77	16	6 (5.46)	0 (3.64)	27
Patagonia	-1.95	-2.29	0.31	11	0 (2.43)	18
Caatinga	-1.53	-3.05	-2.44	-1.86	11	12
(b)						
Atacama						
Altiplano	-2.92					
Monte	-3.28	-0.43				
Patagonia	-3.23	-2.40	-1.74			
Caatinga	-0.8	-1.77	-1.29	-1.09		

the fact that other authors (most recently, Caviedes & Iriarte, 1989; Marquet, 1989; Meserve & Kelt, 1990) have debated the relative magnitude of this effect. The unfortunate misrepresentation of this trivial point by OBB gives the reader the erroneous impression that their findings are at odds with those of Kelt *et al.* (1996). When we re-calculated the standardized expected number of shared species among these five regions, however (using data from OBB), our results differed from those reported by OBB. We also found four significant results (see Table 1a), but three of these involved the Altiplano (which shared significantly fewer species than expected with all regions except the adjacent Atacama Desert); the fourth involved the disjunct Monte and Caatinga regions. The Atacama and Patagonian faunas were marginally significant (Table 1), as were the Patagonian and Caatingan faunas. Additionally, we found one positive (but not significant) association, between the geographically abutting Patagonia and Monte regions.

This pattern of relatedness conforms very well to the general pattern of diversification of contemporary dryland mammals in South America. The species comprising these faunas are a complex mix of ancient marsupials and

caviomorph rodents as well as more recent sigmodontine rodents, which arrived in the late Pliocene as part of the Great American Biotic Interchange (GABI; Webb, 1991, 1999). It is generally thought that sigmodontine rodents underwent a massive radiation in the central Altiplano, with subsequent lesser radiations in south-eastern Brazil and in the southern Andes (Reig, 1981; Smith & Patton, 1999). Other immigrant taxa, such as the carnivores, underwent separate and smaller radiations at lower elevations. Evolution of these relatively recently radiating lineages stands in contrast to the caviomorph and marsupial faunas that likely had diversified long before the Pliocene. Our analysis suggests that geographical distance generally dictates resemblance in South American faunas, with the exception of the Altiplano and Monte, which are much less similar than might be expected.

HETEROGENEITY OF ARIDLANDS SMALL MAMMAL FAUNA

OBB appear critical that our 'analysis ... of the South American desert mammals draws general conclusions on community structure (α -diversity, β -diversity, co-existence, trophic structure) based

on information from only two biomes: Altiplano and Atacama'. The difficulty of finding data on local community composition for South American sites (see e.g. Marquet, 1989; Marquet & Cofré, 1999; Bakker & Kelt, in press) is underscored by the fact that OBB presented data on the species composition of five major arid regions of South America (the Altiplano, Atacama, Caatinga, Monte and Patagonia), and not data comparable to those of Kelt *et al.* (1996) on local communities. Although their analyses do not pertain to local composition (α -diversity) and therefore are not directly comparable to our paper, they do allow for insights into the importance of spatial scale in ecological studies. It is somewhat unfair, however, for OBB to criticize us for the limited geographical scope of our analysis ('without much consideration of the complexity and diversity of drylands'), when a principal conclusion of their own analysis is that trophic structure is remarkably similar across five Neotropical dryland faunas (log likelihood ratio = 5.7, $P > 0.3$), even in the light of impressive levels of regional endemism (0–15% faunal similarity by species, 0–36% for genera).

Similar concerns about regional heterogeneity in North America prompted Kelt (1999) to compare desert small mammal communities among four distinct desert regions (Sonoran, Chihuahuan, Mojave and Great Basin). Although Kelt's analysis documented significant variability in characteristics of local faunas among these deserts, this was trivial when compared to that existing between these desert regions and those of central Asia. In contradiction to OBB, therefore, it does appear justifiable to group data from the four deserts of North America *when the relevant comparison is with the fauna of another continent*. Similarly, in our 1996 paper we wished to compare desert small mammal communities among different continents; although they criticize us for doing so, OBB's analysis further supports our decision to group the faunas of the Altiplano and Atacama Desert. Furthermore, although we did not extend our results to dryland faunas elsewhere in South America, such extrapolation appears to be justified.

One of the primary concerns expressed by OBB, however, is the change in relative importance of omnivory and herbivory at different spatial scales of analysis. Whereas Kelt *et al.* (1996) concluded that omnivory was the predominant trophic strategy of South American

aridland small mammals (13 of 22 species = 59%), OBB argue that fully 70% (31 of 44 species) of the fauna of the Altiplano/Atacama are herbivorous (68% if the four fossorial *Ctenomys* are removed from consideration). This discrepancy reflects the addition to the species lists of 12 caviomorph and six sigmodontine rodents, and the reclassification of five (not six, as stated in OBB) species from omnivore to herbivore (these were *Auliscomys boliviensis*, *Calomys lepidus*, *C. sorellus*, *Eligmodontia puerulus* and *Phyllotis xanthopygus*). In fact, preliminary data from the northern Chilean Andes support the classification of *A. boliviensis*, *E. puerulus* and *P. xanthopygus* as omnivores; each of these species consumed 20–30% non-foilage material (insects, seeds, unidentified materials; S. Silva and P. Marquet, unpublished data). Whether herbivory is 'the dominant trophic strategy' (OBB, p. 9) remains dependent upon the definition of dominance as well as the definition of these trophic groups. If 'dominant' is defined in terms of the number of species in the regional pool that are characterized by this strategy, then we are pleased that OBB have increased our understanding of the ecology of this fauna. If, on the other hand, dominance is defined with respect to composition of local communities, then these results remain ambiguous, and depend on the metric used to define relative dominance — number of species, number of individuals, biomass, etc. For example, herbivory and carnivory are often defined by the consumption of $\geq 90\%$ plant or animal materials, respectively, other species being lumped as omnivores. Given the limited information on the diets of most Neotropical small mammals, and the potential for temporal and spatial variation in these, it may be too early to argue that the Neotropical drylands mammal fauna is dominated by herbivorous or omnivorous taxa. What is important here is that perspectives on ecological structure appear once again to be highly scale-dependent, and this constitutes a strong call for further research into ecological patterns at various spatial (and temporal) scales.

LOCAL VS. REGIONAL STRUCTURE

As noted above, OBB's data pertain to a broader spatial scale than that generally considered to

equate to α -diversity ('the species richness of a local ecological community' (Brown & Lomolino, 1998, p. 450)). Beta diversity 'refers to the change (or turnover) in species composition over a relatively small distance' (Brown & Lomolino, 1998, p. 450). OBB actually evaluate patterns and turnover of gamma diversity ('the total species richness of a large geographical area, such as a biome or continent' Brown & Lomolino, 1998, p. 450) between major biomes of South America. As such, their analyses and results are of great interest, but they are not directly comparable with those of Kelt *et al.* (1996). Although OBB evidently recognize this (see their conclusions), they make some inappropriate comparisons between their dataset (regional) and ours (local). Thus, the 'missing species' (p. 121) in our analysis were not missing at all; these were species that did not occur at sites sampled in our fieldwork and therefore never entered the dataset. The implication that our dataset was grossly incomplete is simply incorrect, and when OBB quote us to emphasize that we missed 'half ... of the total small mammal fauna for the Altiplano and Atacama' they evidently misunderstand both the methods and the objectives of our paper. The sites presented in Kelt *et al.* (1996) did not include all species found in the Altiplano and Atacama Desert (much less all of South America's drylands), because this was not the objective of our analysis.

NO MAJOR BIOGEOGRAPHIC PATTERNS?

OBB state that 'the drylands of South America show neither ... a species-area effect [nor] a latitudinal gradient in species richness'. They also claim that their data show no elevational gradients of species richness. The possibility that South American aridlands do not exhibit a latitudinal gradient in species diversity is intriguing (see also Meserve & Glanz, 1978; Marquet, 1994), but here again the coarse scale of analysis makes it difficult to draw meaningful conclusions. Data presented by Kaufman & Willig (1998; their Fig. 2c) show a clear and monotonic decline in richness across all latitudes in South America. Of course, data in Kaufman and Willig (1998) combine montane and lowland faunas; if OBB are correct and there is no latitudinal gradient

in South American aridland small mammal faunas, then the gradient reported by Kaufman and Willig (1998) must reflect a gradient in the Andean and/or precordilleran fauna. The aridland mammal fauna of Argentina (e.g. Chaco, Monte, and Patagonia) spans a sufficient latitudinal gradient ($> 45^\circ$) to confirm or refute this hypothesis.

Finally, using regional faunas over such a broad scale to evaluate elevational patterns of diversity seems excessively coarse. In contrast to OBB, other studies in South America have demonstrated strong relationships between species richness and elevation for small mammals (e.g. Pearson & Ralph, 1978; Marquet, 1994; for non-arid Andean gradients, Patterson *et al.*, 1989, 1998). Climatic patterns across elevations in arid regions (generally including decreases in mean and maximum temperatures, and increases in precipitation) often result in greater moisture availability at some intermediate elevation. The well-known relationship between available moisture and primary productivity for arid regions (e.g. Brown, 1975; Brown & Lomolino, 1998), and between primary productivity and mammalian species diversity (Brown, 1975; Owen, 1988), would predict a mid-elevation hump in diversity (e.g. Kelt, 1999), and we suspect that a finer scale of analysis would resolve such a pattern on both sides of the arid Andes.

CONCLUSIONS

The fauna of South America's aridlands is notably diverse and warrants greater consideration by biologists. Many species are known only taxonomically, and conclusions about other aspects of biology must often be regarded as tentative. Even basic natural history remains poorly documented for many species. Ojeda *et al.* (2000) criticized our earlier study (Kelt *et al.*, 1996) for combining two arid regions (Altiplano and Atacama), stating that they 'see no common denominator allowing one to combine these drylands in any analysis'. In fact, OBB concluded that although taxonomic composition varied among aridlands of South America, 'the trophic structure is consistent among drylands'. We (Kelt *et al.*, 1996) used trophic characteristics to emphasize functional rather than taxonomic relationships among these regions (see Kelt &

Brown, 1999). OBB's criticisms are either trivial or misdirected. Both their study and ours underscore the importance of functional characterizations of ecological communities and regional faunas. Of particular interest is the very different trophic composition that our two papers report (omnivore-dominated vs. herbivore-dominated). To what extent this reflects different levels of dietary resolution as opposed to spatial scale of analysis remains unclear with the data at hand. It is unfortunate that natural history is not 'in vogue' these days, as it is precisely such studies that are needed to improve understanding of the structure of the South American mammal fauna. Only when these are combined with additional studies at multiple spatial and temporal scales will we be able to place this fascinating biota in the context of a greater and evolving paradigm of desert community structure.

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