



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

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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

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 &

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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.

REFERENCES

- Bakker, V.J. & Kelt, D.A. (in press) Scale-dependent patterns in body size distributions of Neotropical mammals. *Ecology*, in press.
- Brown, J.H. (1975) Geographical ecology of desert rodents. *Ecology and evolution of communities*, (ed. by M.L. Cody & J.M. Diamond), pp. 315–341. Belknap Press, Cambridge, Massachusetts.
- Brown, J.H. & Lomolino, M.V. (1998) *Biogeography*, 2nd edn, 691 pp. Sinauer Associates, Inc., Sunderland, Massachusetts.
- Caviedes, C.N. & Iriarte, A.W. (1989) Migration and distribution of rodents in central Chile since the Pleistocene: the palaeogeographic evidence. *Journal of Biogeography*, **16**, 181–187.
- Connor, E.F. & Simberloff, D. (1978) Species number and compositional similarity of the Galápagos flora and avifauna. *Ecological Monographs*, **48**, 219–248.
- Kaufman, D.M. & Willig, M.R. (1998) Latitudinal patterns of mammalian species richness in the New World: the effects of sampling method and faunal group. *Journal of Biogeography*, **25**, 795–805.
- Kelt, D.A. (1999) On the relative importance of history and ecology in structuring communities of desert small animals. *Ecography*, **22**, 123–137.
- Kelt, D.A. (1999) Assemblage structure and quantitative habitat relations of small mammals along an ecological gradient in the Colorado Desert of southern California. *Ecography*, **22**, 659–673.
- Kelt, D.A. & Brown, J.H. (1999) Community structure and assembly rules: confronting conceptual and statistical issues with data on desert rodents. *Ecological assembly rules — perspectives, advances, retreats* (ed. by E. Weiher & P.A. Keddy), pp. 75–107. Cambridge University Press, Cambridge, UK.
- Kelt, D.A., Brown, J.H., Heske, E.J., Marquet, P.A., Morton, S.R., Reid, J.R.W., Rogovin, K.A. & Shenbrot G. (1996) Community structure of desert small mammals: comparisons across four continents. *Ecology*, **77**, 746–761.
- Marquet, P.A. (1989) Paleobiogeography of South American cricetid rodents: a critique to Caviedes Iriarte. *Revista Chilena de Historia Natural*, **62**, 193–197.
- Marquet, P.A. (1994) Diversity of small mammals in the Pacific Coastal Desert of Peru and Chile and in the adjacent Andean area: biogeography and community structure. *Australian Journal of Zoology*, **42**, 527–542.
- Marquet, P.A. & Cofré, H. (1999) Large temporal and spatial scales in the structure of mammalian assemblages in South America: a macroecological approach. *Oikos*, **85**, 299–309.
- Meserve, P.L. & Glanz, W.E. (1978) Geographical ecology of small mammals in the northern Chilean arid zone. *Journal of Biogeography*, **5**, 135–148.
- Meserve, P.L. & Kelt, D.A. (1990) The role of aridity and isolation on central Chilean small mammals: a reply to Caviedes and Iriarte (1989). *Journal of Biogeography*, **17**, 681–689.
- Ojeda, R.A., Blendinger, P.G. & Brandl, R. (2000) Mammals in South American drylands: faunal similarity and trophic structure. *Global Ecology and Biogeography*, **9**, 115–123.
- Owen, J.G. (1988) On productivity as a predictor of rodent and carnivore diversity. *Ecology*, **69**, 1161–1165.
- Patterson, B.D., Meserve, P.L. & Lang, B.K. (1989) Distribution and abundance of small mammals along an elevational transect in temperate rainforests of Chile. *Journal of Mammalogy*, **70**, 67–78.
- Patterson, B.D., Stotz, D.F., Solari, S., Fitzpatrick, J.W. & Pacheco, V. (1998) Contrasting patterns of elevational zonation for birds and mammals in the Andes of southeastern Peru. *Journal of Biogeography*, **25**, 593–607.
- Pearson, O.P. & Ralph, C.P. (1978) The diversity and abundance of vertebrates along an altitudinal gradient in Peru. *Memorias Del Museo de Historia Natural 'Javier Prado'*, **18**, 1–97.
- Reig, O.A. (1981) *Teoría del origen y desarrollo de la fauna de América del Sur*. Monografía Naturales 1, pp. 1–162. Museo Municipal de Ciencias Naturales 'Lorenzo Scaglia', Mar del Plata, Argentina.
- Smith, M.F. & Patton, J.L. (1999) Phylogenetic relationships and the radiation of sigmodontine rodents in South America: evidence from cytochrome *b*. *Journal of Mammalian Evolution*, **6**, 89–128.
- Webb, S.D. (1991) Ecogeography of the great American interchange. *Paleobiology*, **17**, 226–280.
- Webb, S.D. (1999) Isolation and interchange: a deep history of South American mammals. *Mammals of the neotropics*, vol. 3. *The central neotropics: Ecuador, Peru, Bolivia, Brazil* (ed. by J.F. Eisenberg & K.H. Redford), pp. 13–19. University of Chicago Press, Chicago.