

Diversity of Small Mammals in the Pacific Coastal Desert of Peru and Chile and in the Adjacent Andean Area: Biogeography and Community Structure

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Abstract

Species diversity patterns of small mammals (sigmodontine rodents) in the Chilean–Peruvian Pacific coastal desert and adjacent Andean area (Puna) were analysed by means of latitudinal and altitudinal transects. The statistical analyses of the patterns show: (1) a wide variation in latitudinal species diversity, with a peak in the region where the Puna reaches its greatest areal extent; (2) the differentiation of at least four groups of distinct faunal elements resulting from the interaction of large-scale biogeographic, geological and evolutionary processes; (3) a positive correlation between species richness and altitude for the altitudinal transects located within the Pacific coastal desert area and Puna; and (4) a highly individualistic pattern of community structure at a regional scale. These results are discussed considering biogeographic, palaeoclimatic and evolutionary processes, such as the establishment of the Pacific coastal desert, and the existence of a major centre of species diversification in the Puna area. Similarities and differences between these community-level patterns and those in North American deserts are discussed.

Introduction

A complete understanding of the determinants of species diversity patterns necessitates a consideration of processes acting at different scales in both time and space. On one hand, at a regional scale, biogeographic and evolutionary processes interact in shaping the pool of potential colonists of local communities. Key processes at this level are those affecting the dispersal and colonisation of species into a region, and those controlling their subsequent diversification and extinction dynamics (e.g. Ricklefs 1987). On the other hand, at local scales, biotic interactions and species' tolerances to environmental limiting factors will affect how regional diversity maps onto local species diversity (see Brown 1989 for a review).

The analysis of diversity patterns of small mammals (herein restricted mostly to sigmodontine rodents) in the Chilean–Peruvian Pacific coastal desert and adjacent Andean area provides a unique opportunity to evaluate how the above-mentioned processes controlling diversity interact. Although little studied, this area harbours a unique and conspicuous biota of Andean origin, descendants of the ancestral stock that, after their arrival in South America, used the Andes as one of its major dispersal routes (Webb 1978; Marshall 1979). As postulated by Reig (1984, 1986), subsequent to their arrival in South America these rodents underwent a tremendous adaptive radiation linked to the Andean orogeny and its palaeoclimatic history. Of particular interest to the understanding of the biogeographic history, as well as current patterns of diversity and community organisation within the Chilean–Peruvian Pacific coastal

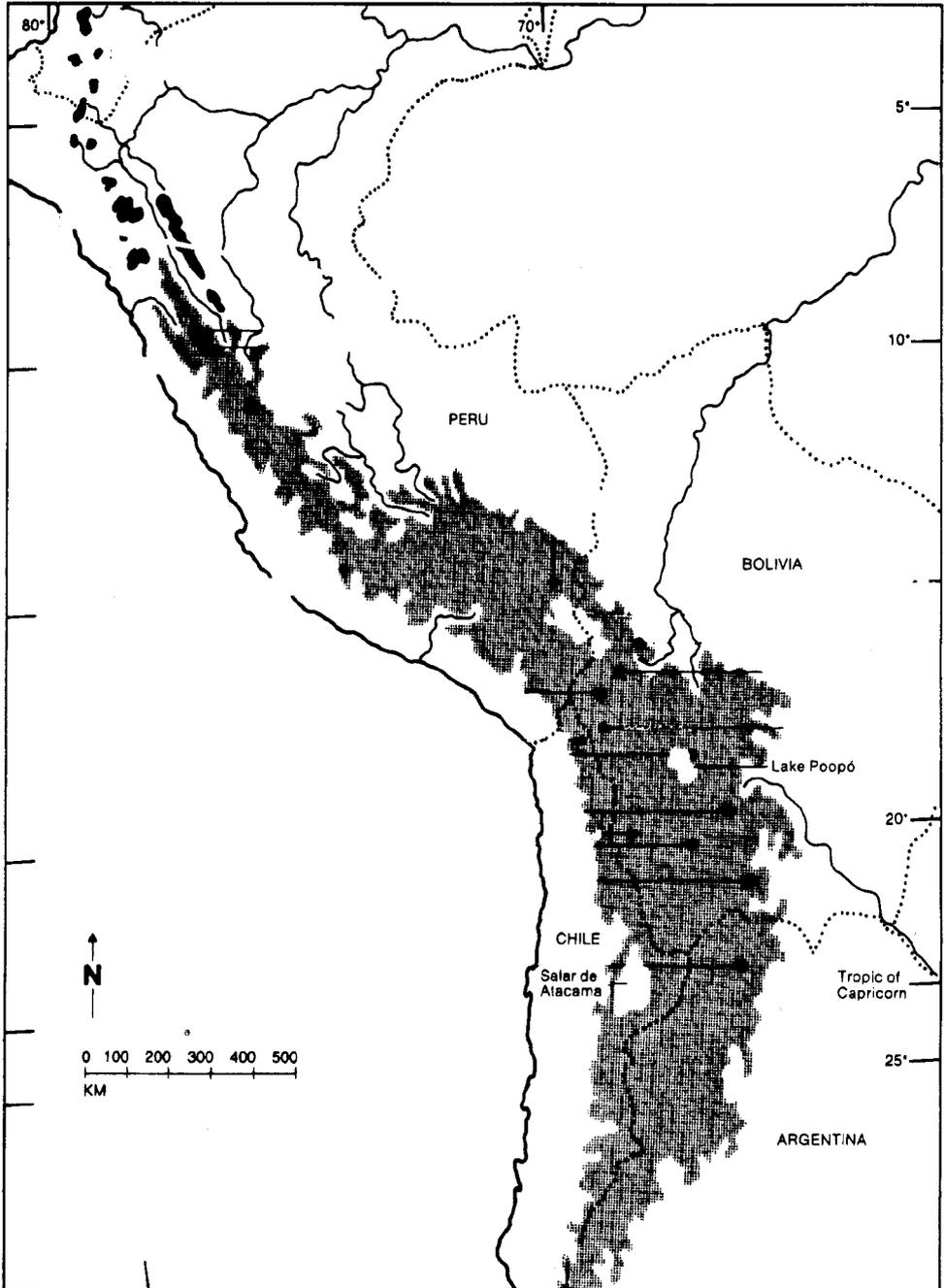


Fig. 1. Study area, located in the central Andes of South America. The shaded area represents the Puna; the lowland coastal area between about 5° and 27°S is the Chilean-Peruvian Pacific coastal desert (modified from Vuilleumier and Simberloff 1980).

desert, is the postulated existence of a centre of biotic diversification in the Andean area (Puna) adjacent to that desert (Mueller 1973; Reig 1984). This high diversity in the Puna highlands, characteristic of almost all vertebrate groups as well as of plants, is linked to the great opportunities for speciation provided by glacial advances, pluvial regimes, and lacustrine stages that dominated the Andean Pleistocene at these latitudes [see Ochsenius (1982) and Seltzer (1990) for reviews of the geological and climatic history].

In this paper, I will present preliminary data on diversity patterns of small mammals in the Atacama desert and the adjacent Andean area, with special emphasis on the effect of biogeographic and evolutionary processes upon local community patterns. I will focus on two major questions: (1) whether there is a pattern of altitudinal zonation in the assemblages of small mammals by latitude, and (2) whether there is a pattern of assemblage structure with regard to the number of locally coexisting species and species combinations across local sites within the area.

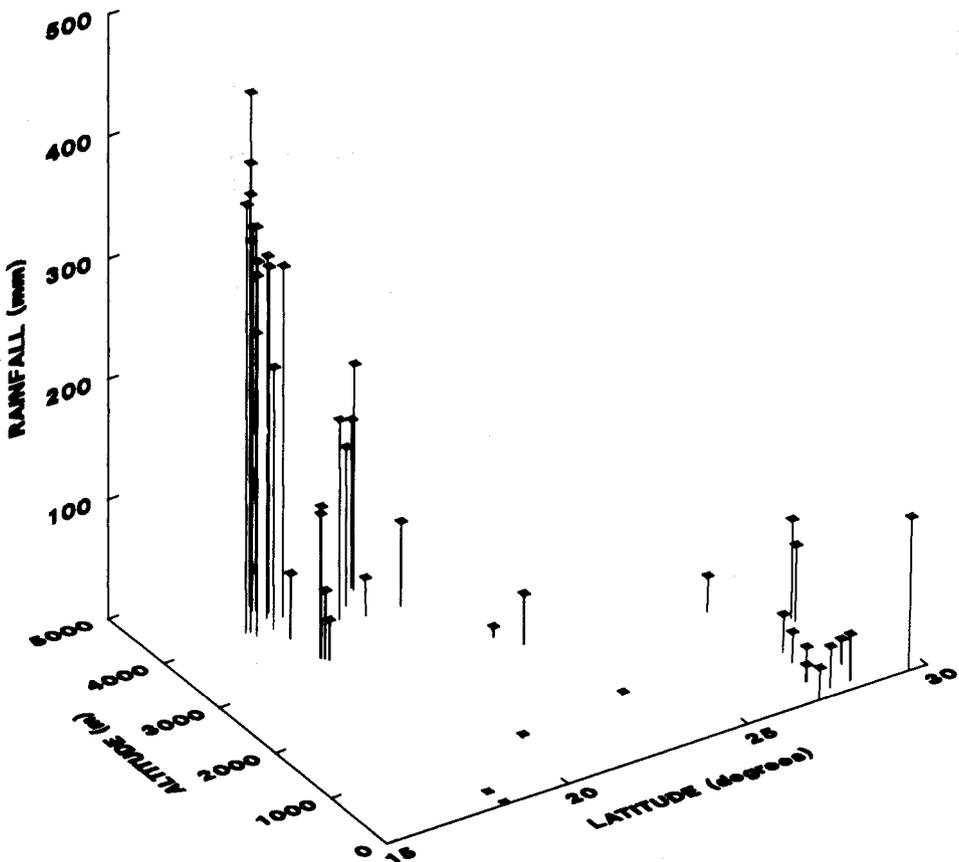


Fig. 2. Altitudinal and latitudinal variation in mean annual rainfall across the study area in northern Chile.

Material and Methods

Study Area

The Chilean-Peruvian Pacific coastal desert is located on the lowlands of the western slope of the Andes between latitudes 5° and 27°S, along the entire Peruvian coast and the northern

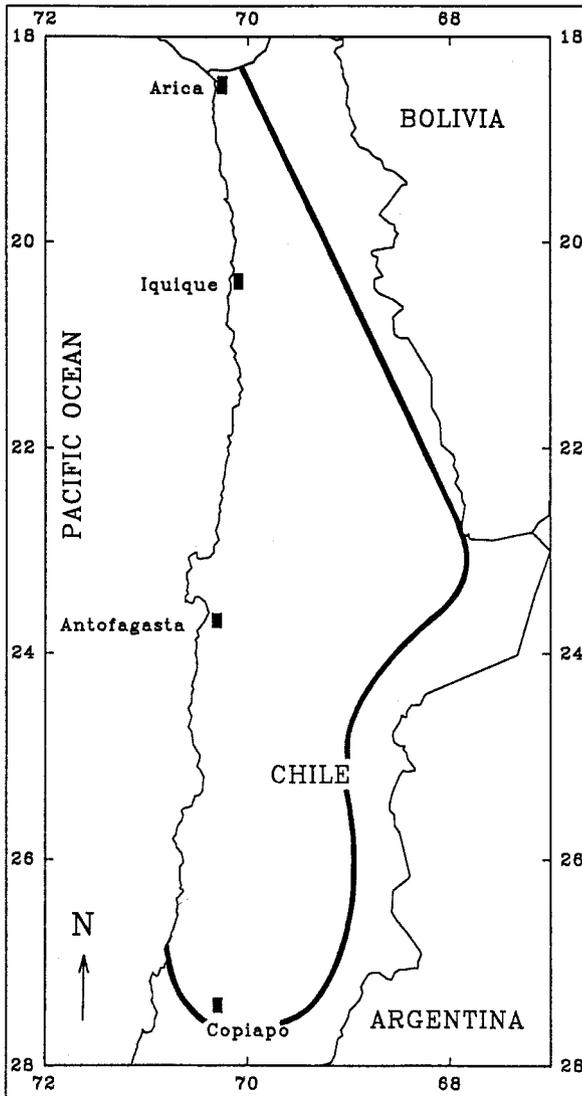


Fig. 3. The Atacama desert in northern Chile. The thick line represents the limit of the desert area. Note the latitudinal increase in the altitudinal limit of the Atacama desert (modified from Villagrán *et al.* 1983).

part of Chile [Fig. 1; see also Villagrán *et al.* (1983), Rauh (1985) and Arroyo *et al.* (1988) for a general description of its limits]. Most authors divide the Chilean–Peruvian Pacific coastal desert into Peruvian coastal desert and Atacama (Chilean) coastal desert. Physiographically, this region is composed of three major units from west to east; the Coastal mountain range, the Intermediate Depression, and the Andes mountain range. Vegetation along the Coastal range is restricted to the Lomas communities and the numerous dry valleys that dissect the landscape along the east–west axis (see Péfaur 1982; Rauh 1985; Rundel *et al.* 1991). The Intermediate Depression, between latitudes 18° and 20°S, is characterised by the existence of forest patches of *Prosopis tamarugo*. Rainfall steadily increases on the Pacific slope of the Andes from less than 1 mm in the lowlands up to 400 mm in the Puna area (above 3800 m; Fig. 2). Whereas the Pacific coastal desert is defined as a hot desert, the Puna area is a cold desert. The increase in rainfall with elevation is paralleled by changes in cover, physiognomy and dominant life forms characterising plant communities. According to Villagrán *et al.* (1983) and Arroyo *et al.* (1988),

it is possible to define four major vegetational belts along the western slope of the Andes in northern Chile: Prepuna, Puna, High-Andean and Subnival. The Puna area reaches its largest areal extent between latitudes 15° and 25°S, and narrows markedly towards northern and southern latitudes (Fig. 1). The Atacama desert, on the other hand, increases its altitudinal penetration towards the south, from 1500 m at latitude 17°S up to 3000 m at latitudes 24–25°S (Fig. 3).

Data and Analyses

The database used in this paper is made up of 15 altitudinal transects, between latitudes 5° and 37°S. The transects were latitudes 5, 9, 12, 13, 15, 17, 18, 19, 22, 24, 30, 33, 35, 36 and 37°S. I decided to include the latter five altitudinal transects, which lie well beyond the southern boundary of the Atacama desert, to obtain a better picture of latitudinal species turnover, and to improve resolution of the distinctiveness of the Pacific desert and Puna small mammal fauna. Each transect was one latitudinal degree in width, and encompassed the area between the coast and the Puna. The presence and absence of species were recorded in each transect at five altitudinal belts spaced 1000 m from each other, from 0 m up to 5000 m. The source data was retrieved from published studies (Mann 1945; Pearson 1951, 1982; Koford 1954; Greer 1965; Dorst 1971; Meserve and Glanz 1978; Pearson and Ralph 1978; Pine *et al.* 1979; Pizzimenti and DeSalle 1981; Reise and Venegas 1987) and the author's unpublished data. Both univariate and multivariate statistical methods were used to investigate patterns in this data set.

In order to reveal additional trends within the data, an ordination technique (Principal Components Analysis; PCA) based on the covariance matrix was employed. The nature of the data (i.e. presence/absence) is likely to cause a 'horseshoe effect' (Williamson 1978), rendering interpretation of the analysis difficult. In this study the considerable overlap in taxon composition among sample units has eliminated this anomaly (see also Duigan and Kovach 1991). Other examples of the use of PCA as applied to incidence data can be found in Jolliffe (1986) and Keller and Pitblado (1989). An additional analysis of clusters (not reported here) obtained with the UPGMA (Unpaired Group Mean Average) algorithm applied to a similarity matrix calculated with Jaccard's index, corroborated the pattern obtained by the PCA ordination technique.

Results and Discussion

Palaeobiogeography

A key element to understanding current patterns of diversity and distribution of sigmodontine rodents in the coastal desert and adjacent Puna area is the history of arrival and dispersal of these rodents in South America, as well as the palaeoclimatic history of the study area.

The time at which sigmodontine rodents entered South America and the pacing of their southward migration is a controversial issue. There are three major hypotheses; one advocates the arrival of the ancestral stock during the Late Pliocene, another suggests a time of arrival by Early Miocene, and yet another an Upper Miocene migration (see Webb 1985 for a review). Marshall (1979) proposed a palaeobiogeographic model suggesting that sigmodontine rodents arrived at South America by waif dispersal across the Bolivar Trough during a drop in sea level sometime between seven and five million years before present. After this initial dispersal event, in the Upper Miocene, these rodents underwent a major adaptive radiation in the northern Andean area. In a similar vein, Reig (1986) identified the Puna area as the major centre of diversification of both phyllotine and akodontine rodents, supported by palaeoclimatic evidence and current patterns of diversity and endemism. This is in agreement with evidence presented by Vuilleumier and Simberloff (1980) for Puna birds. As the issue stands, there is no doubt that sigmodontine rodents had potential access to the Puna area and to the Pacific coastal desert throughout most of the Pleistocene. Further, the palaeoclimatic evidence and the current patterns of diversity, as pointed out by Reig (1986) and Vuilleumier and Simberloff (1980), characterise the Puna area as a major centre of diversification for both birds and sigmodontine rodents.

In the following paragraphs I will briefly review the Pleistocene palaeoclimatic history of the Pacific coastal desert (of the Atacama desert in particular) and Puna, in order to better understand the origin of their biota.

The timing of origin and subsequent climatic dynamics of the Pacific coastal desert is a controversial issue. On one hand, it has been proposed that arid conditions have prevailed since at least the Middle Miocene (Mortimer 1973; Mortimer and Saric 1975; Rundel *et al.* 1991 and references therein). On the other hand, it is argued that hyperarid conditions are relatively recent in origin, dating back to the Late Quaternary (Axelrod 1979; Ochsenius 1982, 1985, 1986; Arroyo *et al.* 1988). Arroyo *et al.* (1988) provide an account of the historical development of aridity in the area on the basis of palaeobotanical and geological data. These authors suggest that, during the Miocene, in contrast to the present, the western side of the Andes was wetter than the eastern side, and propose the existence of a viney forest along the Pacific rim. Arroyo *et al.* (1988, p. 63) also propose that, during the Pliocene, there occurred '... a gradual transition from the closed Miocene forests into more open, savanna-like vegetation at low elevations, with small, evergreen treelets developing at mid elevation'. These authors further propose the existence, during the Pleistocene, of xeromorphic vegetation and marked alternating wet and dry periods. During this time there was an extensive development of forests of *Prosopis tamarugo* (Ochsenius 1982, 1986) supporting a rich assemblage of Pleistocene megafauna including genera such as *Mastodon*, *Macrauchenia*, *Equus*, *Megatherium* and *Scelidodon*. Most of these animals were present in the Pacific coastal desert area until the Late Pleistocene and the beginning of the Holocene (Casamiquela 1969; Ochsenius 1982, 1985, 1986; Marshall *et al.* 1984). One point on which most authors agree, although with different emphasis [see Arroyo *et al.* (1988) and Rundel *et al.* (1991), and references therein] is in the existence of more mesic conditions during the Pleistocene. These mesic conditions, in addition to the existence of deeply cut, vegetated valleys that have traversed the current arid coastal desert since the Miocene (Mortimer 1980) and the extensive development of lacustrine ecosystems during the Pleistocene stages Minchin (28 000 years before present) and Tauca (12 500–11 000 years before present) (Servant and Fontes 1978; Hanstenrath and Kutzbach 1985), provided the conditions for the colonisation of lowland areas by elements of Punaean flora and fauna (Ochsenius 1982, 1985, 1986; Arroyo *et al.* 1988; Marquet 1989; Meserve and Kelt 1990; Rundel *et al.* 1991; but see Caviades and Iriarte 1989). The increase in arid conditions during the Late Pleistocene not only caused the extinction of megafaunal elements (Ochsenius 1982, 1985, 1986) but also of some species of small mammals. The scenario that I propose entails three stages: (1) active diversification of phyllotine and akodontine rodents in the Puna area, (2) the subsequent dispersal and colonisation of some of those species into the coastal desert during Pleistocene times, and (3) the extinction of some forms during the increasingly arid Holocene. In the following sections I will focus on some contemporary biogeographic patterns affected by this sequence of diversification, colonisation and extinction processes.

Biogeography

Latitudinal patterns

Species diversity of small mammals reaches a maximum of 18 species at latitude 17°S and decreases towards southern and northern latitudes (Fig. 4). However, the decline in diversity is steeper towards the south, where it drops to three species at latitude 24°S, than towards the north (down to five species at latitude 5°S). This decrease on both sides of the diversity peak coincides with the concurrent decrease in areal extent of the Puna (see Fig. 1) and may be due to a peninsular effect. Towards the south of the diversity peak, there is the additional effect of the altitudinal penetration of the Atacama desert, almost causing the disappearance of the Prepuna vegetational belt, and the shrinking of the Puna, High-Andean and Subnival belts (Villagrán *et al.* 1983).

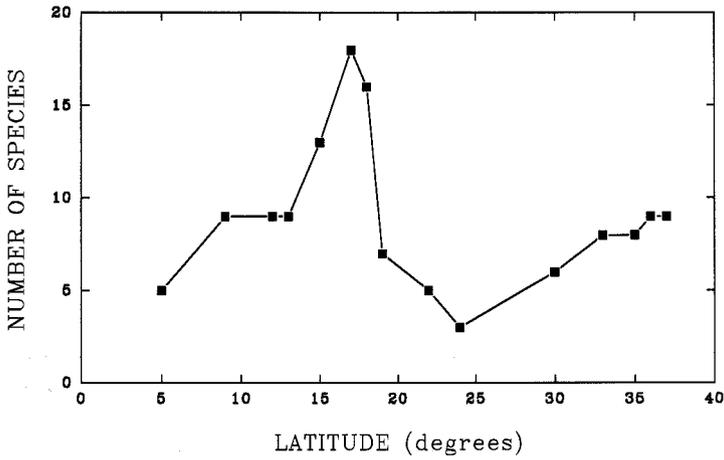


Fig. 4. Latitudinal variation in species richness along the Pacific slope of the Andes between latitudes 5° and 37°S.

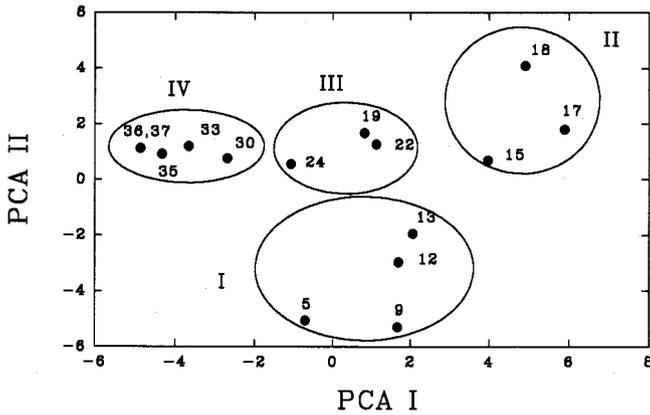


Fig. 5. Principal component analysis (PCA) of the 15 altitudinal transects along the Pacific coastal desert and Puna. The numbers inside the ellipses identify altitudinal transects by latitude.

The PCA (Fig. 5) shows the existence of at least four different groups, based on their similarity in species composition. Group I consists of species inhabiting the northern marginal Puna area. The northern limit of this group is set by the disappearance of the Puna area and by the appearance of the more mesic Paramo vegetation (Tosi 1960). The southern limit is set by the valley of the Acari river at latitude 14°S. As pointed out by Pearson (1982), this valley carves the landscape all the way from the coast to the Puna, acting as a barrier to dispersal. The latitudinal transect at 5°S occupies a more marginal position within Group I. This is apparently a reflection of the low number and uniqueness of the species found at this latitude. Species such as *Phyllotis gerbillus* and *Akodon mollis* do not occur in other transects along the Pacific slope of the Andes. The second group

of species is found in an area known as the arid Puna (Troll 1958). The northern limit of Group II is also determined by the Acari and Tambo rivers, which cause an areal bottleneck by cutting through the vegetational belts and stretching the Puna plateau. In addition, this limit coincides with a latitudinal change in the floristic composition of plant communities (Tosi 1960). The southern limit of Group II is associated with the peninsular effect produced by the narrowing of the Puna, and with the altitudinal penetration of the Atacama desert and consequent increase in aridity and shrinking of vegetational belts (Villagrán *et al.* 1983; Arroyo *et al.* 1988; Marquet 1989). The third group of species is found in an area called desert Puna (Troll 1958); Group III is characterised by the disappearance of species found in more northerly and southerly transects. This group of species is thus a depauperate subset of northern and southern faunal assemblages (only three species are present: *Akodon olivaceus*, *Akodon andinus* and *Phyllotis darwini*). The southern limit of Group III is associated with the maximum altitudinal penetration of the Atacama desert (Fig. 3). The northern limit is not clear. The fourth group of species is found in a semidesert and mediterranean area that abuts the Atacama desert to the north. Also included within Group IV are those transects found in the area of the temperate deciduous forests.

Table 1. Kendall's rank correlation coefficients between the number of species of small mammals and altitude, for 15 transects at different latitudes along the Pacific slope of the Andes

n.a., not applicable (see text); n.s., not significant; **, $P < 0.05$; ***, $P < 0.01$

Latitude	Total no. of species	r	P
5°S	5	0.0	n.s.
9°S	9	0.95	***
12°S	9	0.95	***
13°S	9	1.00	***
15°S	13	1.00	***
17°S	18	0.95	***
18°S	16	0.53	n.s.
19°S	7	0.53	n.s.
22°S	5	0.89	**
24°S	3	-0.41	n.s.
30°S	6	-0.81	**
33°S	8	-0.67	n.s.
35°S	8	n.a.	n.a.
36°S	9	n.a.	n.a.
37°S	9	n.a.	n.a.

Altitudinal patterns

The correlation analysis (Table 1) shows that, from latitude 9° to 22°S, correlation coefficients are positive (i.e. species richness increases with altitude). The transect at 5°S had a correlation coefficient of 0.0 because the same species were present in the three altitudes available for analysis. The low altitude reached by the Andes at this latitude precluded the inclusion of additional altitudinal belts. At latitudes 24°, 30° and 33°S, the sign of the correlation reversed. Transects 35°, 36° and 37°S were not included in the analysis because only two altitudinal belts were present, owing to the low altitude reached by the Andes at these latitudes. To further explore this pattern, I performed correlations between the total number of species of small mammals found at a given altitudinal transect and the number of species found present in each altitudinal belt. Only transects lying

within the desert area were included (i.e. 5–24°S). The results (Table 2) show that the number of species found in the altitudinal belts above 3000 m is positively correlated with the total number of species with access to a particular altitudinal transect. That is, an increase in the number of species in latitude only affect high-altitude environments; species tend to accumulate in the highlands. The factors affecting species diversity behave differently below 3000 m. Regional diversity probably affects local diversity (see Ricklefs 1987) only in those areas located above 3000 m, whereas below it the existence of the coastal desert imposes a serious barrier to the passive diffusion or spill-over of species from areas of high diversity in the highlands. In this scenario it is not surprising that desert lowland species may have evolved physiological adaptations, such as hydric independence and torpor (see Koford 1968; Bozinovic and Marquet 1991), to cope with one of the world's most arid deserts (Borgel 1973).

Table 2. Kendall's rank correlation coefficients between the total number of species present at each altitudinal transect and the number of species found at each altitudinal belt

n, number of observations; n.s., not significant; ***, $P < 0.01$

Altitudinal belt (m)	<i>n</i>	<i>r</i>	<i>P</i>
0–1000	9	–0.12	n.s.
1000–2000	9	–0.02	n.s.
2000–3000	9	0.36	n.s.
3000–4000	8	0.74	***
4000–5000	8	0.94	***

In general, these results are consistent with previous studies (Pearson 1951, 1982; Spotorno 1976; Pearson and Ralph 1978; Pizzimenti and DeSalle 1981) that point out the existence of a positive correlation between species richness and altitude in the area between the Pacific coastal desert and the Puna. At this point it is interesting to note that this finding contradicts the rule of decreasing number of species with increase in altitude (e.g. Stevens 1992 and references therein). A negative correlation between species richness and altitude is likely to arise if most speciation events have occurred in lowland habitats. Therefore, species' primary adaptations are suited to lowland environments, and highlands represent, to some extent, stressful habitats that are difficult to colonise and in which to persist. However, in the case of the Coastal desert–Puna axis, the opposite occurs. Here, most speciation events were associated with high-altitude environments, where a major centre of species diversification was located. The primary adaptations of these species were to cope with cold, high-altitude environments, and lowland habitats were of marginal value. Hence the positive correlation between altitude and species richness. As an alternative hypothesis, it could be argued that the positive correlation emerges because of the existence of a lowland hyperarid desert that limits diversity in lowland areas to such low levels as to produce a pattern of positive correlation that would otherwise be negative. Although I do not deny that the onset of arid conditions in the lowlands caused the extinction of some species (Marquet 1989), the historical effect of a high-altitude centre of diversification seems more pervasive. The key evidence in support of this hypothesis is the existence of a positive correlation between species richness and altitude along the eastern side of the Andes Cordillera (Patton 1986; Cadle and Patton 1988; J. Salazar, T. Yates and P. Marquet, unpublished data), where Puna vegetation gives way to Yungas forest and lowland tropical rainforest.

As emphasised earlier, the existence of a high-altitude centre of biotic diversification has affected both latitudinal and altitudinal patterns of species diversity, leaving strong signs behind, such as a latitudinal peak in species richness (Fig. 4) and an 'anomalous' positive correlation between species richness and altitude. The onset of hyperarid conditions during

the Late Pleistocene caused the extinction of some lowland species, further contributing to these altitudinal and latitudinal patterns of diversity, and also acted as a strong selective environment favouring the evolution of desert-adapted physiological traits in those species currently found within the confines of the coastal desert.

Community Structure

In light of the complex interactions among dispersal, diversification, adaptation and extinction processes that shaped patterns of species diversity in the coastal desert and adjacent Andean area, one is tempted to predict a highly individualistic pattern of community structure at a regional scale (see Graham 1986; Brown and Kurzius 1987). I have just started to address this question, following the lead of Brown and Kurzius' work on patterns in species distribution and coexistence at a regional scale. From the analysis of 120 sites distributed within the Atacama Desert and Puna areas of Peru, Argentina and Chile (Marquet, unpublished data), the following patterns arise. First, most sites (80%) are inhabited by 1–3 species (Fig. 6); this is significantly different from that expected from a random association of species with sites (i.e. under a Poisson distribution) ($G = 41.8$, d.f. = 12, $P < 0.001$). Second, when the number of different species combinations is analysed (Fig. 7), a distribution similar to that found in Fig. 6 emerges. However, because sites with few species are more likely to have redundant combinations of species, the frequency distribution of different combinations observed peaks at three, rather than two, species. A G -test shows that the observed distribution is significantly different from a Poisson distribution ($G = 76.44$, d.f. = 12, $P < 0.001$). Finally, with regard to the

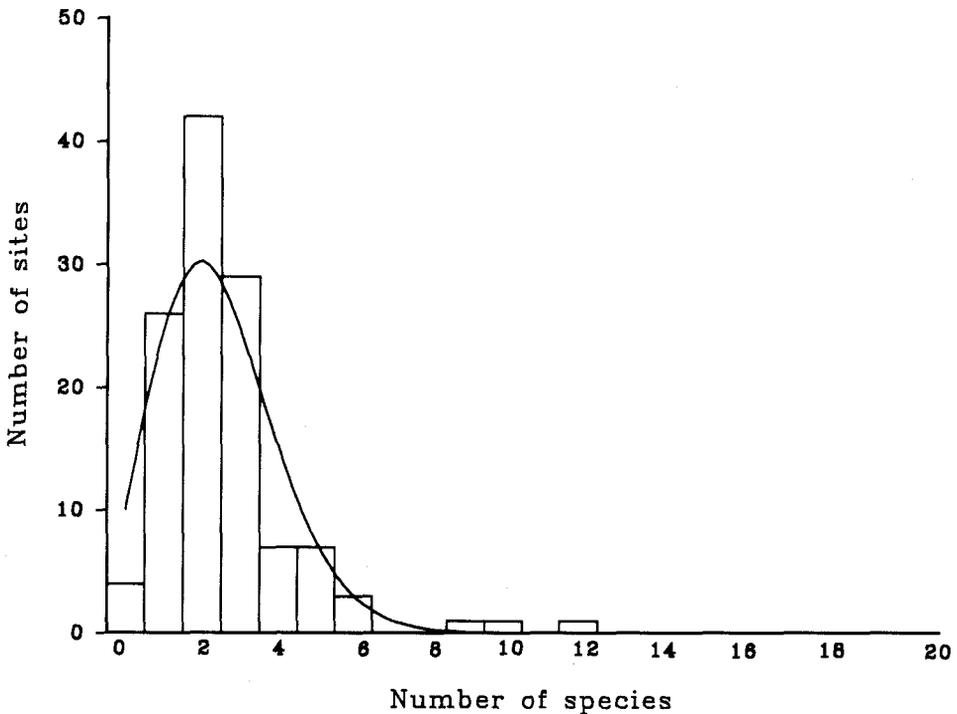


Fig. 6. Frequency distribution of the number of coexisting species among local sites. The curved line represents expectations under a Poisson distribution.

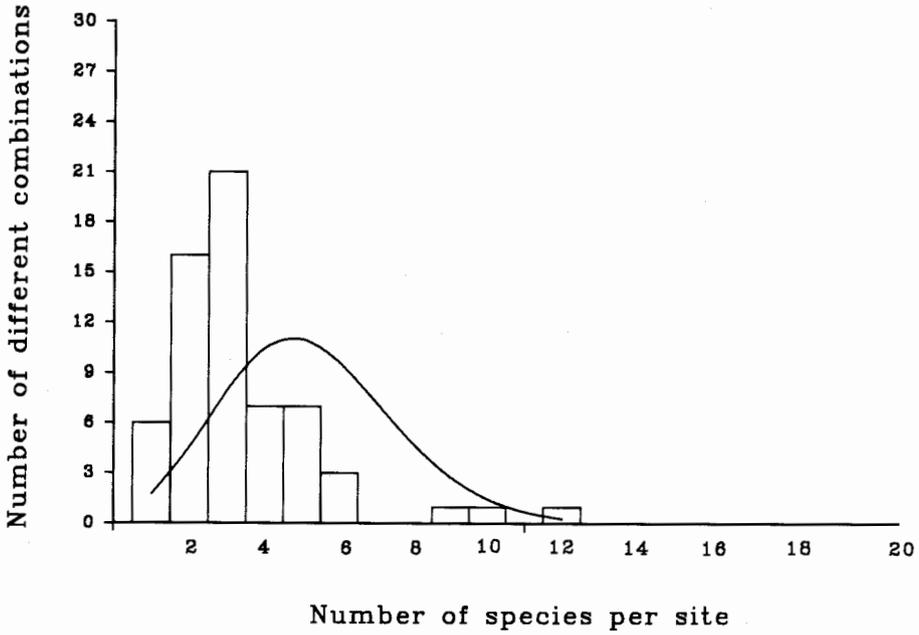


Fig. 7. The number of different combinations of different numbers of locally coexisting species. The curved line represents expectations under a Poisson distribution.

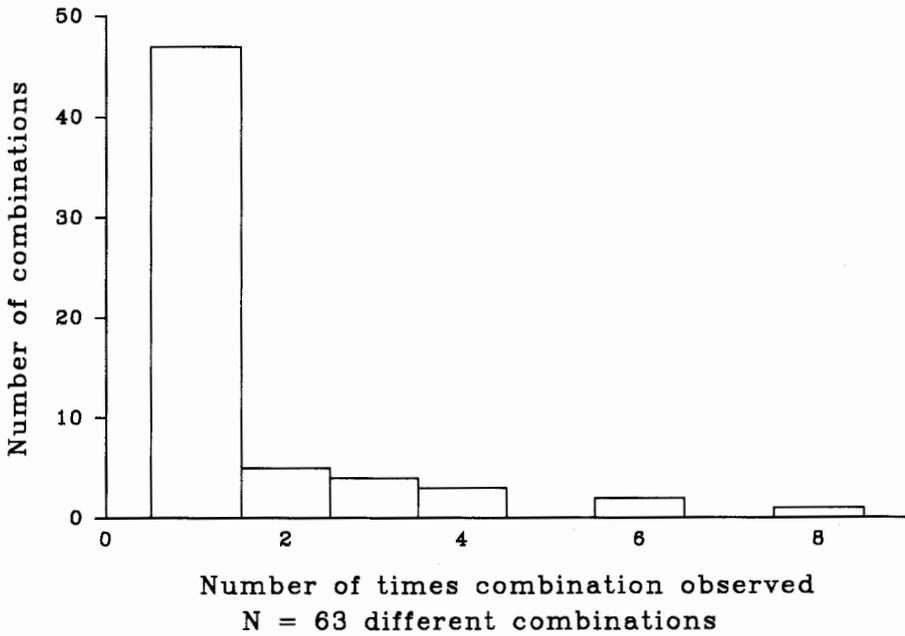


Fig. 8. The number of times that different combinations of locally coexisting species were observed.

frequency with which a particular combination of coexisting species occurred (Fig. 8), 63 different combinations of species were observed, 75% of which occurred only once. Most species occurred with many different combinations of other species. Six species occurred in more than 10 different combinations, and two occurred in more than 25 combinations.

When these patterns are compared with those described by Brown and Kurzius (1987) for North American deserts, some similarities can be detected. In both desert areas the frequency distribution of coexisting species is right-skewed. However, the modal number of coexisting species is two in the South American desert (Fig. 6) and three for that in North America. Similarly, most of the species coexist with a large array of different species, forming combinations that are generally unique. This individualistic pattern in the geographic structure of species assemblages may be characteristic not only of desert areas but a more widespread feature of regional faunas, indicating the complex interplay between large-scale biogeographic and evolutionary processes, as well as local species interaction and adaptation. These patterns do not conflict with the existence of deterministic processes affecting community organisation at regional scales. As has been shown by Bowers and Brown (1982), species of similar body size coexist locally less frequently than expected by chance. In addition, there is a nested hierarchy underlying patterns of species regional coexistence for North American desert rodents (Patterson and Brown 1991) as well as functional assembly rules underlying the build-up of local communities (Fox and Brown 1993). These types of analyses applied to the South American desert areas may contribute to a better understanding of the regularities underlying the geographic structure of species assemblages.

Concluding Remarks

Many of the relevant questions concerning the structure of natural communities can be fruitfully approached at the interface between ecology and biogeography (e.g. Brown 1984; Ricklefs 1987, 1989; Brown and Maurer 1989; Jackson and Harvey 1989; Lawton 1990; Tonn *et al.* 1990; Hinch *et al.* 1991; Cornell and Lawton 1992; Ricklefs and Schluter 1993). The traditional approach of working on small spatial scales (see Kareiva and Anderson 1988; Pimm 1992) has been preferred in the past because at this scale it is possible to perform experiments. These manipulations have proven to be a powerful way to test alternative hypotheses and to identify important processes and mechanisms that generate patterns of community structure (e.g. competition, predation). However, there is much more to the structure of natural systems than can be learned by studying their phenomenology at small spatial scales. An increase in the spatial scale of analysis beyond the local scale makes it possible to: (1) understand regional biogeographic patterns that emerge as the result of local dynamics and species' tolerance to biotic and abiotic conditions (e.g. Diamond 1975; Hanski 1982; Moulton and Pimm 1983; Brown 1984, 1987; Brown and Maurer 1989; Roughgarden 1989; Brown and Nicoletto 1991); and (2) address new questions about metapopulation dynamics and spatial variability in the structure of species assemblages (e.g. Hanski 1982; Brown 1984; Brown and Kurzius 1987, 1989; Gilpin and Hanski 1991).

As pointed out by Graham (1986), Brown and Kurzius (1987), and this study, most local communities are unique in terms of their species composition. This emphasises the need for caution in generalising about species interactions from the analysis of one or a few sites within a region.

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