Distributions of bats along an elevational gradient in the Andes of south-eastern Peru

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(With 7 figures in the text)

At least 193 species of mammals are known to occur within the Manu Biosphere Reserve in south-eastern Peru, contributing to its stature as one of the world's richest protected areas. Bats (Order Chiroptera) comprise more than 42% (82 species) of this diversity. Analyses of bat capture records over a transect extending more than 3 km in elevation show that most bat species at Manu are widely distributed in the Amazon Basin. Few are montane endemics or are localized in south-eastern Peru, although exceptions to this generalization include two species new to science. Highland bat faunas tend to be attenuated versions of those found below, and the elevational zonation of bat communities is weak. Species turnover with elevation is monotonic and more-or-less smooth, with Jaccard's similarity values falling to 0.5 for sites differing by 750 m in elevation. Subtle and orderly change in species composition with elevation is also reflected in the nested-subset structure of these communities; over 19 different levels, this pattern of hierarchical structure is both striking and highly significant. Elevational ranges of species generally increase with elevation, in accordance with Stevens' extension of 'Rapoport's rule' of range amplitude. However, support for 'Stevens' rule' may be trivial, given Amazonian richness and Andean impoverishment. Reduced richness and poorly developed endemism in Andean bat communities contrast with patterns shown by sympatric rodent faunas, which are diverse and strongly endemic on the Altiplano and markedly zoned along the Eastern Versant. Contrasts are less sharp with bird communities, which nevertheless exhibit stronger zonation and higher endemicity. Factors responsible for these distinctive distributional patterns are discussed.

Introduction

Highly diverse tropical communities have long intrigued biologists interested in species coexistence. The sheer numbers of taxa found in the tropics, the difficulties of sampling and studying them, and their multitudinous relationships *inter se* and with their biotic and abiotic environments, all have limited understanding. Imprecise systematic underpinnings for most major taxonomic groups also retard progress—use of confused or confounded nomenclature

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serves to obscure the very patterns we are trying to resolve. Consequently, scientists seeking to understand tropical communities usually rely heavily on studies of birds. Generally speaking, birds are easier to study and therefore have better-known species limits and better understood distributions and ecologies than other major taxa. However, for avian patterns to serve as general models (i.e. not be contingent on that group's unique biology and history), they must be corroborated in studies on other taxa (see also Rahbek, 1995).

Few, if any, tropical communities exceed the species diversity shown by those of the Eastern Versant of the Andes in Colombia, Ecuador, Peru, and northern Bolivia. Bathed by moist easterly trade winds, with an extensive elevational profile extending from bare rock and ice down to the world's largest lowland rainforest basin, the Amazon, this area of South America supports almost indescribable species richness. Even a single leguminous tree in the Tambopata Reserve of Peru may contain as many ant species as all of the British Isles combined (Wilson, 1987).

One of South America's largest national parks and protected areas, Manu National Park and Biosphere Reserve, is situated on the Eastern Versant in Peru's south-eastern departments of Madre de Dios and Cuzco. Covering 18,812 km² (approximately the size of Massachusetts or Wales), the Manu Reserve extends from 340 m elevation at the mouth of the Río Manu, to 3450 m at Puesto de Vigilancia Acjanaco. Recently, Pacheco et al. (1993) listed 190 species of mammals known from the reserve, and our subsequent work has added three more. To our knowledge—despite still being grossly incomplete (see below)—Manu's mammal list is the longest yet produced for any protected area in the world.

Bats (Order Chiroptera) comprise more than 42% of the mammalian species so far recorded at Manu (Pacheco et al., 1993). This predominance is striking because the reserve also harbours nine other mammalian orders, each moderately to highly diverse, as well as the world's richest known avifauna (Fitzpatrick, Willard & Stotz, pers. comm.). When surveys of Manu's entire mammalian fauna are complete, bats should comprise fully half the mammalian species, because on geographic and habitat grounds many additional bats should occur in the reserve.

If any other group of organisms should exhibit ecological patterns resembling those of birds, bats should. Bats and birds are the only living vertebrate groups capable of sustained flight; they have similar foraging and dispersal capabilities; they share the metabolic requirements of homeothermy; they overlap broadly in body-size distributions; they exploit many of the same ecological resources, albeit at different times of the circadian cycle; and the groups first appeared and diversified over the same (mostly Cenozoic) time scale. Distribution and abundance of avian communities in Peru has been documented by various studies, particularly those of Terborgh and his associates (Terborgh & Weske, 1975; Terborgh, 1977, 1985; see also Chapman, 1926).

A number of Eastern Versant bat faunas have been described, mostly from single lowland sites: in Colombia (Muñoz Arango, 1990, with 39 species), in Peru (Ascorra, Wilson & Romo, 1991, with 44; Woodman et al., 1991, with 42; Ascorra, Gorchov & Cornejo, 1993, with 62; Hutterer et al., 1995, with 52), and in Ecuador (Albuja, 1982) and Bolivia (Anderson, Koopman & Creighton, 1982; Anderson & Webster, 1983; regional treatments yielding tallies not directly comparable with the foregoing). However, no previous study of Eastern Versant bats matches this one in sampling effort, species richness, gradient length, or distributional detail. Although Graham (1983) also examined the distributions of bats on Andean slopes in Peru, and made cogent comparisons of distribution patterns shown by bats and birds (Graham, 1990), the bat data he used were necessarily assembled from regional distributional patterns: both his reports were based on records of 89 species drawn from localities spanning 9° in latitude (8–17 °S, from Huánuco to Puno) and a century of general zoological collecting. Here, we report distributional

data from the communities found over a 3200-m transect mostly lying within a single drainage system (Río Cosñipata–Alto Madre de Dios, 12–13°). Intensive work here and elsewhere on the Eastern Versant has enriched prior estimates of its regional diversity by almost 45% (see below) and nearly doubled the number of bat species known from Manu (cf. Ascorra, Wilson & Romo, 1991).

Methods

The surveys reported in this paper were undertaken by various field crews operating in Manu since 1980. Localities visited during these surveys and species taken in local sampling are enumerated and mapped by Pacheco *et al.* (1993). Early surveys of bats were a by-product of ornithological inventories undertaken by J. W. Fitzpatrick, D. E. Willard, and their Field Museum colleagues. The durations of these trips were 1 July–18 August 1980, 15 October–2 December 1981, 27 October–8 December 1983, 25 July–7 September 1985, and 1 November–4 December 1985. Later inventories, under the direction of V. Pacheco of Universidad de San Marcos, focused expressly on mammals; these included trips made 28 August–10 September 1990, 28 February–18 March 1991, 13 July–30 July 1991, and 7 September–29 September 1991. Lowland records were significantly enhanced by collections made at the nearby site of Pakitza, where the Smithsonian Institution and Universidad de San Marcos researchers have collaborated under the BIOLAT agreement. More than 1200 specimens and many more captures of bats have been recorded at Pakitza by researchers working with D. E. Wilson and C. Ascorra.

To identify voucher specimens, various identification keys were consulted, those by Vizzoto & Taddei (1973), Hall (1981), Linares (1986), Handley (1987), and by Pacheco & Solari (unpubl.) especially frequently. These primary data were treated in various ways to expand the scope of the analysis. Because each field season adds species to the Manu inventory, because our sampling methods are demonstrably biased ecologically (see below), and because finishing the inventory will take many more years, we have chosen to assess Manu's bat diversity hierarchically, i.e. with nested levels of assurance based on known distributions. These levels are: 1) sampled species, those documented by vouchers taken within the reserve; 2) recorded species, sampled species plus those recorded in adjacent Andean valleys in Cuzco, Madre de Dios, or Puno departments; 3) presumed species, recorded species plus those whose sparse geographical records define a range which likely includes the reserve; and 4) possible species, presumed species plus those found in central Peru or northern Bolivia in habitats resembling those within the reserve. Although the assignment of species to categories 2–4 is only approximate and subject to change with expanding reference materials, we believe these classes represent reasonable species pools contributing to the assembly of Manu's bat communities.

The elevational ranges of bat species at Manu were determined from published records in the Central Andes and western Amazon Basin (especially Tuttle, 1970; Gardner, 1976; Koopman, 1978; Graham, 1983, 1990; Graham & Barkley, 1984), as well as from recent accessions of The Field Museum and Museo de Historia Natural, Universidad de San Marcos. For sampled species, we also calculated the range spanned by capture records. In most cases (particularly for poorly sampled species), 'transect' ranges were smaller than the 'range' as documented in the literature, but new elevational limits were found for 19 species of bats (see below). Ranges tabulated as 'literature ranges' include these new distributional extremes, so in all cases are equal to, or greater than, transect ranges.

Because of sampling limitations, the composition of bat communities at different elevational levels was determined by interpolating between elevational extremes. We assumed a species occurred at a given elevation if it was recorded both above and below that level (evaluated in 100-m units). Interpolations were made from sampled ranges as well as against those from the literature, to insulate these analyses from sampling biases in range estimation. Species were assigned to trophic guilds on the basis of reports by Gardner (1977) and Willig (1983), as well as unpublished studies of the junior authors. Weights were taken either from voucher specimens (and are averages), the literature on each species, or from previously unreported specimens in museums.

TABLE I

Species of bats sampled in inventories of Manu Biosphere Reserve, Peru. The column marked by "#" cross-references entries with Fig. 4. Families are: E, Emballonuridae; F, Furipteridae; Ml, Molossidae; N, Noctilionidae; P, Phyllostomidae; T, Thyropteridae; V, Vespertilionidae. Guilds are: HFF, high-flying frugivore; HFI, high-flying insectivore; ICG, insecti-carnivore; IPI, insecti-piscivore; LFF, low-flying frugivore; LFI, low-flying insectivore; OMG, omnivorous nectarivore; OMP, omnivorous predator; SAN, sanguinivore. Weights given in g, ranges in m

#	Species	Family	Guild	Weight	Sample range	Literature range
5	*Nyctinomops laticaudatus*	Ml	HFI	9.7	340	200–340
6	*Dermanura cinerea*	P	HFF	12.8	340	200–340
7	*Glossophaga commissarisi*	P	OMG	9.3	340	200–340
10	*Lasiurus ega*	V	LFI	12.7	340	200–340
12	*Macrophyllum macrophyllum*	P	ICG	9	340	200–400
13	*Micronycteris brachyotis*	P	ICG	10.6	330	200–400
15	*Vampyressa nymphaea*	P	HFF	14	330	200–400
17	*Micronycteris hirsuta*	P	ICG	15	490	200–490
24	*Sphaeronycteris toxophyllum*	P	HFF	14.8	380	200–630
28	*Dermanura gnoma*	P	HFF	11.5	340–680	200–680
29	*Micronycteris cf. schmidtorum*	P	ICG	6.1	490–680	200–680
30	*Cormura brevirostris*	E	LFI	10.8	680	200–700
31	*Rhynchonycteris naso*	E	LFI	3.2	340–380	200–700
32	*Noctilio albiventris*	N	IPI	25.8	340–380	200–700
33	*Noctilio leporinus*	N	IPI	61.8	340	200–700
34	*Dermanura anderseni*	P	HFF	11	340–680	200–700
35	*Micronycteris minuta*	P	ICG	8.5	340–500	200–700
37	*Tonatia brasiliense*	P	ICG	12	340–490	200–700
38	*Myotis simus*	V	LFI	8.9	340	200–700
41	*Choeroniscus intermedius*	P	OMG	7.9	780	200–780
42	*Sturnira tildae*	P	LFF	28	340–780	200–780
44	*Choeroniscus minor*	P	OMG	10.5	340–825	200–825
45	*Rhinophylla pumilio*	P	LFF	11.3	340–825	200–825
47	*Saccopteryx bilineata*	E	LFI	8	340–550	200–900
48	*Saccopteryx leptura*	E	LFI	5.1	380	200–900
49	*Furipterus horrens*	F	LFI	3.2	340–900	200–900
50	*Platyrrhinus brachycephalus*	P	HFF	16.6	340–900	200–900
52	*Uroderma magnirostrum*	P	HFF	20.4	340–950	200–950
53	*Trachops cirrhosus*	P	ICG	36.5	330–980	200–980
55	*Chiroderma trinitatum*	P	HFF	17	340–950	200–1000
56	*Chiroderma villosum*	P	HFF	25.4	330–950	200–1000
58	*Tonatia sylvicola*	P	ICG	27.9	320–980	200–1000
59	*Vampyressa pusilla*	P	HFF	8.8	340–950	200–1000
60	*Vampyrum spectrum*	P	ICG	166	380–820	200–1000
62	*Thyroptera tricolor*	T	LFI	4.9	340–680	200–1000
63	*Tonatia bidens*	P	ICG	29.7	340–1030	200–1030
64	*Vampyressa bidens*	P	HFF	13	330–1050	200–1050
67	*Carollia castanea*	P	LFF	11.6	320–900	200–1100
68	*Artibeus lituratus*	P	HFF	74.8	340–950	200–1120

Most statistical analyses were performed using Statistica for Windows. Similarity among assemblages was assessed using NTSYS-pc (Rohlf, 1988) to generate matrices of Jaccard's coefficients. Jaccard's similarity, J, omits consideration of negative matches (i.e. mutual absences of a species from a pair of faunas; Sneath & Sokal, 1973), and so is particularly appropriate for use on large presence-absence matrices. To analyse whether these communities exhibit 'nested subset' structure, we employed a Visual Basic program designed to compute the 'system temperature' or biogeographic disorder, T, in a presence-absence matrix of species occurrences (Atmar & Patterson, 1995). This temperature metric is independent of matrix size and ranges from 0° (where distributions are perfectly nested) to 100° (where they are completely

TABLE I (cont.)

#	Species	Family	Guild	Weight	Sample range	Literature range
69	*Lionycteris spurrelli*	P	OMG	8.7	820–1100	200–1120
72	*Chiroderma salvini*	P	HFF	30.5	500–1200	200–1200
73	*Lonchophylla thomasi*	P	OMG	7.2	340–1200	200–1200
74	*Platyrrhinus helleri*	P	HFF	12.8	340–1200	200–1200
75	*Myotis riparius*	V	LFI	5.7	340–1200	200–1200
77	*Chrotopterus auritus*	P	ICG	84.4	380–520	200–1325
78	*Artibeus obscurus*	P	HFF	37	330–1030	200–1400
79	*Peropteryx kappleri*	E	LFI	8.1	600	200–1500
81	*Molossus molossus*	Ml	HFI	17.9	340–950	200–1500
82	*Phyllostomus elongatus*	P	OMP	¯37.3	330–1180	200–1500
83	*Platyrrhinus infuscus*	P	HFF	43	340–1300	200–1500
84	*Myotis albescens*	V	LFI	5.7	340–530	200–1500
85	*Vampyrodes caraccioli*	P	HFF	34.6	340–1200	200–1525
86	*Mesophylla macconnelli*	P	HFF	8.4	340–1200	200–1600
87	*Artibeus planirostris*	P	HFF	59.3	330–1050	200–1700
88	*Carollia perspicillata*	P	LFF	17.7	330–1300	200–1700
89	*Sturnira lilium*	P	LFF	21.7	340–1500	200–1700
90	*Uroderma bilobatum*	P	HFF	19.1	340–1050	200–1800
91	*Glossophaga soricina*	P	OMG	8.7	340–1060	200–1900
92	*Mimon crenulatum*	P	ICG	16.4	340–1200	200–1900
93	*Phyllostomus hastatus*	P	OMP	95	340–530	200–1900
98	*Eptesicus furinalis*	V	LFI	9.2	900–2250	200–2250
99	*Carollia brevicauda*	P	LFF	14.2	320–1700	200–2300
100	*Sturnira magna*	P	LFF	48.1	450–1550	200–2300
102	*Diphylla ecaudata*	P	SAN	34.8	340–980	200–2450
104	*Anoura cultrata*	P	OMG	16	980–1030	600–2300
105	*Phylloderma stenops*	P	OMP	50.6	340–1200	200–2700
106	*Platyrrhinus lineatus*	P	HFF	23.9	450–1700	200–2700
107	*Anoura caudifer*	P	OMG	10.5	340–1550	200–2800
108	*Sturnira oporaphilum*	P	LFF	22.1	500–1700	300–2750
109	*Dermanura glauca*	P	HFF	12.7	380–2600	360–2700
110	*Vampyressa melissa*	P	HFF	13.9	1180–1700	1000–2200
112	*Myotis nigricans*	V	LFI	5.9	340–3050	200–3300
113	*Micronycteris megalotis*	P	ICG	7.1	340–825	200–3400
115	*Desmodus rotundus*	P	SAN	26	340–3050	200–3500
116	*Enchisthenes hartii*	P	HFF	15.8	450–1700	200–3540
117	*Platyrrhinus dorsalis*	P	HFF	27	530–3450	200–3600
118	*Eptesicus brasiliensis*	V	LFI	11.6	2600	200–3600
120	*Carollia* sp. nov.	P	LFF	—	1700–2250	1700–2250
121	*Myotis keaysi*	V	LFI	6.7	500–3450	500–3540
125	*Anoura geoffroyi*	P	OMG	12.7	780–3450	700–3600
126	*Sturnira erythromos*	P	LFF	17.4	1050–3450	1000–3600
129	*Anoura* sp. nov.	P	OMG	10.3	3350–3450	3350–3450

random; Atmar & Patterson, 1993). The significance of T is assessed by Monte Carlo simulations, comparing the observed temperature to the distribution of T in a collection of simulated assemblages drawn at random. Each simulated assemblage has the same total number of 'presences' (i.e. '1's in a presence-absence matrix) as is actually observed, but their placement in the matrix is not constrained by row or column (see Discussion in Atmar & Patterson, 1993). Two matrices of bat distributions were analysed, both records of 82 sampled species at 19 elevational levels at Manu; the first was based on communities interpolated using sampled 'transect' ranges, whereas the second used literature ranges for these same species.

TABLE II

Hypothetical but likely additions to the bat species of Manu Biosphere Reserve. The list includes three sections of decreasing likelihood: species 'recorded nearby' (in adjacent Andean valleys in Cuzco, Madre de Dios, or Puno departments), those 'presumed present' (because of sparse geographical records elsewhere), and species 'possibly present' (i.e. found in central Peru or northern Bolivia in habitats represented in the reserve). Conventions as in Table I; family 'Mr', Mormoopidae

| #	Species	Family	Guild	Weight	Literature range
			Recorded Nearby		
1	Peropteryx leucoptera	E	LFI	6.2	200–340
2	Saccopteryx canescens	E	LFI	3.7	200–340
11	Pteronotus personatus	Mr	LFI	7.5	200–400
16	Diaemus youngi	P	SAN	37.5	200–480
18	Promops nasutus	Ml	HFI	19.9	220–525
19	Eumops glaucinus	Ml	HFI	33.2	200–600
20	Molossops abrasus	Ml	HFI	35.5	200–600
21	Molossops temmincki	Ml	HFI	6	200–600
22	Promops centralis	Ml	HFI	15.8	200–600
23	Nyctinomops aurispinosus	Ml	HFI	17.9	200–630
25	Nyctinomops macrotis	Ml	HFI	20.6	215–630
26	Eumops bonariensis	Ml	HFI	7.2	290–580
27	Molossops planirostris	Ml	HFI	12.6	200–670
36	Phyllostomus discolor	P	OMP	36.7	200–700
39	Lonchorhina aurita	P	OMP	14.5	200–750
40	Eumops perotis	Ml	HFI	65	200–760
46	Micronycteris sylvestris	P	ICG	8.8	200–890
57	Micronycteris behni	P	ICG	—	200–1000
61	Thyroptera discifera	T	LFI	4.7	200–1000
65	Eumops dabbenei	Ml	HFI	64.7	200–1100
66	Pteronotus parnellii	Mr	LFI	15	200–1100
76	Eumops auripendulus	Ml	HFI	32.5	200–1300
80	Molossus ater	Ml	HFI	29.5	200–1500
94	Pteronotus gymnonotus	Mr	LFI	13.3	200–2000
96	Peropteryx macrotis	E	LFI	5.6	570–1850
101	Lasiurus blossevillii	V	LFI	6.4	450–2150
103	Tadarida brasiliensis	Ml	HFI	11.7	680–2050
119	Histiotus montanus	V	LFI	15.5	700–3220
123	Platyrrhinus vittatus	P	HFF	52.4	1000–3200
124	Lasiurus cinereus	V	LFI	19.7	1000–3300
127	Histiotus macrotus	V	LFI	9.5	1000–3800
128	Sturnira bidens	P	LFF	16.8	1990–2835
			Presumed Present		
3	Molossops greenhalli	Ml	HFI	18.9	200–340
8	Lichonycteris cbscura	P	OMG	6.8	200–340
43	Artibeus concolor	P	HFF	19.1	200–820
51	Rhinophylla fischerae	P	LFF	6.9	200–900
71	Tonatia minuta	P	ICG	10.4	650–750
95	Lonchophylla handleyi	P	OMG	16.8	850–1525
97	Anoura latidens	P	OMG	12.7	200–2240
111	Sturnira nana	P	LFF	9.5	1600–1700
114	Mormopterus phrudus	Ml	HFI	12.5	1850
122	Myotis oxyotus	V	LFI	5.5	1050–3120
			Possibly Present		
4	Molossops neglectus	Ml	HFI	10	200–340
9	Tonatia carrikeri	P	ICG	22	200–340
14	Micronycteris daviesi	P	ICG	18	200–400
54	Eumops hansae	Ml	HFI	15.4	200–1000
70	Micronycteris nicefori	P	ICG	8.6	200–1125
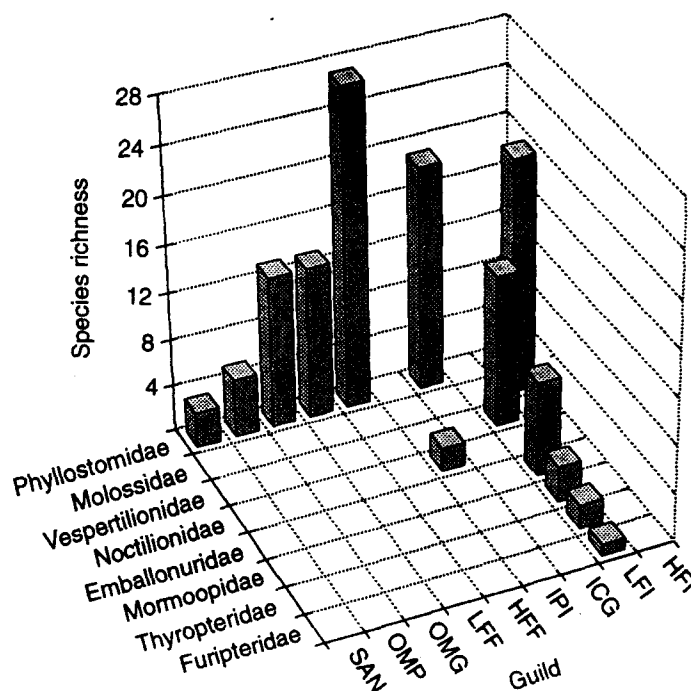
FIG. 1. Bat families, their trophic guilds, and species richness at Manu. Whereas most bat families exploit a single feeding niche (LFI, low-flying insectivore), the Neotropical endemic family Phyllostomidae exploits six of the nine guilds recognized, and is the only family there to exploit these guilds. Histograms include all 129 species which might occur within the reserve. Guild acronyms are decoded in Table I.

Results

Distributional records

During field surveys at Manu, 82 species of bats were documented by voucher specimens (Table I; in two cases, both discussed in Pacheco *et al.*, 1995, we admitted records based on identifiable photographs). Moreover, 32 additional species of bats have been recorded in adjacent Andean valleys in the departments of Cuzco, Madre de Dios or Puno ('Recorded Nearby'), 10 more are 'Presumed Present' on the basis of geographical records which may include the reserve, and still five others are regarded as 'Possibly Present' because they are found in central Peru or northern Bolivia in habitats resembling those within the reserve (Table II). Combining species lists in order of decreasing likelihood yields the following estimates of bat species richness in the reserve: 82 sampled, 114 recorded, 124 presumed, and 129 possible species.

The entire species pool includes eight families of bats, of which five—Noctilionidae, Furipter-idae,Thyropteridae, Mormoopidae, and Phyllostomidae—are endemic or nearly endemic to the Neotropics (the last two families also have limited Nearctic distributions). Another family (Emballonuridae) is pantropical, one (Molossidae) is found on all continents between 45 °N and S, and the last (Vespertilionidae) is practically cosmopolitan. This assemblage includes nine distinct trophic guilds. As is evident in Fig. 1, most families represent the same trophic
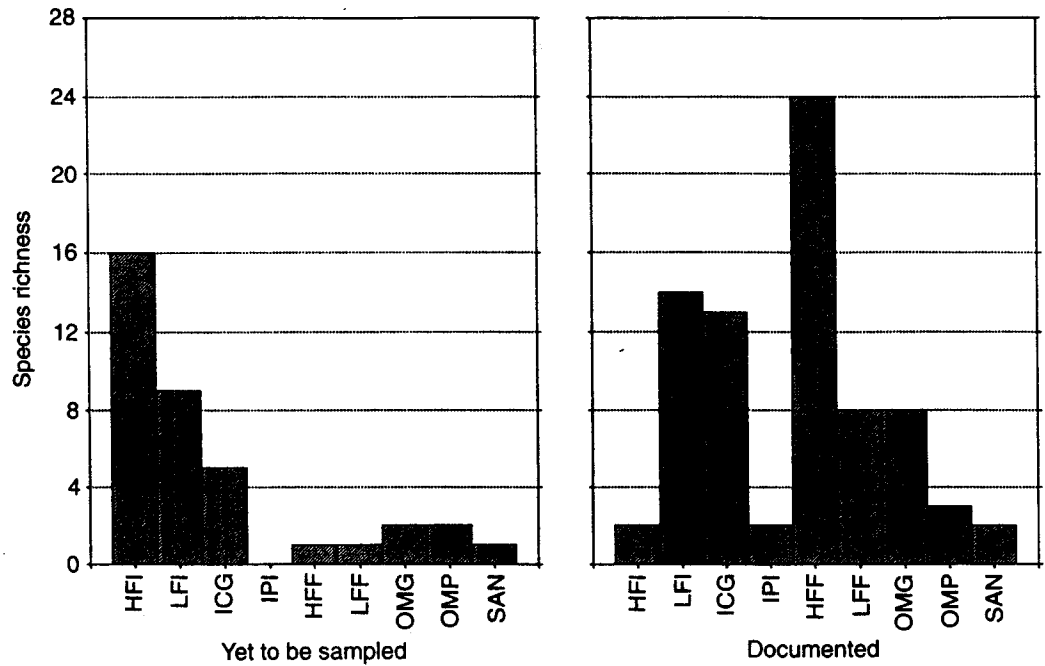
FIG. 2. Differential sampling of guilds in lowland bat communities. Histograms on the left depict the species richness of guilds not yet sampled in lowland forests (< 500 m), while those on the right detail guilds of sampled species. Guild acronyms are decoded in Table 1.

guild—low-flying insectivores—and within-family diversification has been modest, each representing only a single guild. However, the Phyllostomidae occupies six of the nine trophic guilds, and it is the only family present which exploits any of these life-modes.

Sampling at Manu has differentially unveiled the diversity of bat faunas there. The representation of guilds thus far sampled in the best-studied portion of our transect (lowland forest, between 300–500 m) contrasts strongly with the remaining species we expect to find there (Fig. 2). Sampling procedures are demonstrably effective in documenting the high-flying and low-flying frugivores (HFF and LFF) and, to a lesser degree, omnivorous nectarivores and insecti-carnivores (OMG and ICG). On the other hand, only two of 18 species of high-flying insectivores (HFI; all Molossidae) have been documented in these communities. The ecological bias of sampling is so strong that we feel it is essential to analyse the distributions of species inferred to be part of the reserve's fauna, as well as of those already documented there.

All nine of the guilds are represented in 'possible' lowland communities, but their proportions change with increasing elevation (Fig. 3). Only six of the nine are present in communities above 3000 m, high-flying insectivores, insecti-piscivores, and omnivorous predators all dropping out below this level. Low-flying insectivores comprise about 20% of the species in lowland communities, but nearly 50% of those at high elevations. Both guilds of frugivores remain important components of bat communities throughout the gradient.

For the species sampled, capture records were compared to elevational ranges documented in the literature or in museum collections. The following records (all in m) appear to represent new
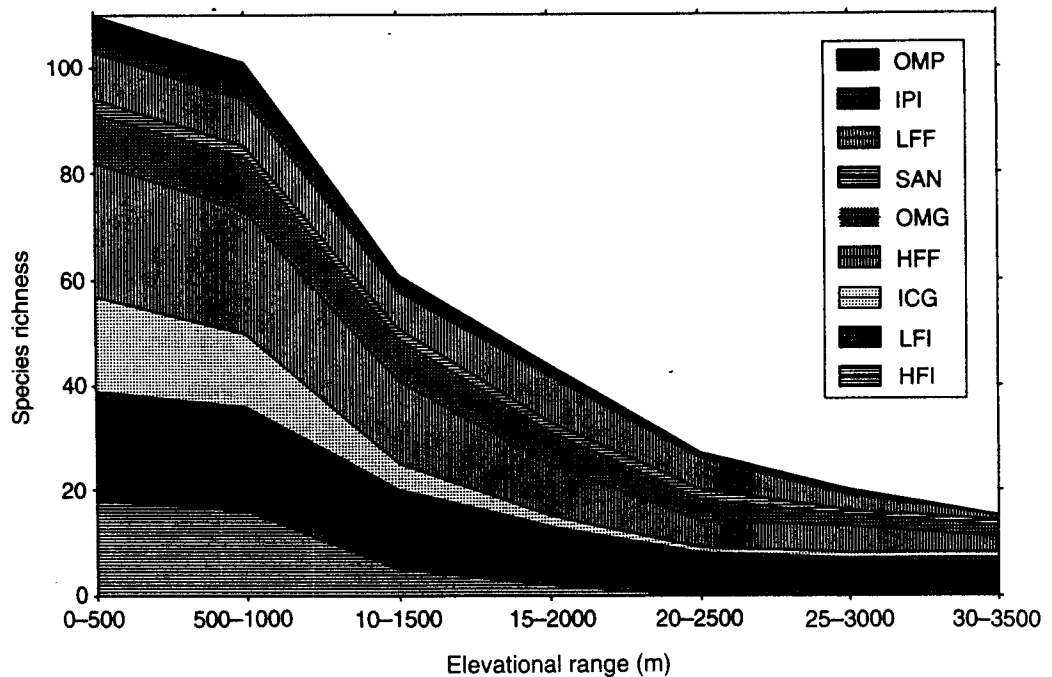
Fig. 3. Elevational variation in the richness of guilds at Manu. Guilds are: OMP, omnivorous predator; IPI, insecti-piscivore; LFF, low-flying frugivore; SAN, sanguinivore; OMG, omnivorous nectarivore; HFF, high-flying frugivore; ICG, insecti-carnivore; LFI, low-flying insectivore; and HFI, high-flying insectivore.

maximum elevations for species on the Eastern Versant in southern Peru: *Micronycteris hirsuta*, to 490; *M.* cf. *schmidtorum*, 680; *Tonatia bidens,* 1030; *Trachops cirrhosus*, 980; *Rhinophylla pumilio*, 825; *Lonchophylla thomasi*, 1200; *Choeroniscus intermedius*, 780; *C. minor*, 825; *Chir-oderma salvini*, 1200; *Dermanura gnoma,* 680; *Sturnira tildae*, 780; *Platyrrhinus brachycephalus*, 900; *Platyrrhinus helleri*, 1200; *Uroderma magnirostrum,* 950; *Vampyressa bidens*, 1050; *Furipterus horrens*, 900; *Myotis riparius*, 1200; and *Eptesicus furinalis*, 2250. The record of *Myotis keaysi* from 500 m appears to represent the lowest elevation at which this species has been recorded on the eastern slope. 'Literature range' in Table I incorporates these newly determined extremes.

Two sampled species of leaf-nosed bats (Phyllostomidae) appear to represent species new to science: a highland nectarivore, *Anoura* (Glossophaginae) and a mid-elevation frugivore, *Carollia* (Carolliinae). At this stage, we are unable to determine whether these species are actually endemic to the reserve or instead represent widespread, previously sampled taxa that have simply escaped prior notice and detection. Both forms represent polytypic genera with hard-to-delimit species boundaries and broad ranges in the Neotropics.

Maximum and minimum elevations of each of the 'possible' species at Manu is shown in Fig. 4, ordered by elevational midpoint. The ranges of sampled species are bisected by a closed square, indicating the average elevation of specimens sampled. Most species occur at low elevations, whereas only a minority range into the highlands. Furthermore, most of the highland species also extend into the lowlands (i.e. have larger ranges), whereas the reverse is not true. Regressing elevational range on to minimum elevation yields a non-significant regression that explains less
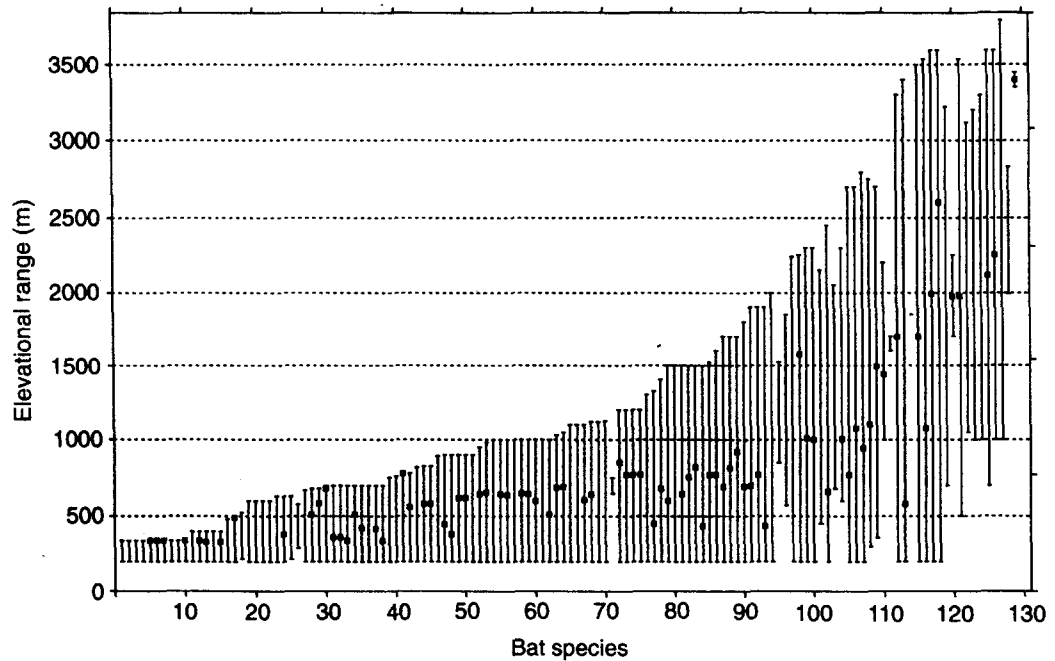
FIG. 4. Elevational ranges of 129 species of bats that possibly occur in the Manu Biosphere Reserve. Bat species numbers (abscissa) provide a cross-reference to Tables I and II. The elevational ranges of 82 sampled species are bisected by a small closed square, which indicates the mean elevation of samples collected. The tendency is clear for bats occupying higher elevations to exhibit broader elevational amplitudes (see text for discussion).

than 1% of variation in range amplitude. Regressing range on to elevational maximum, however, yields a relationship that is statistically significant and highly predictive ($R^2 = 0.808$).

Exceptions to the rule of increasing range amplitude with elevation do exist. These instances are indicated by the small bars (in one case of infinitesimal length) on the right side of Fig. 4. In most cases, these species are endemic to south-eastern Peru or the central Andes. By contrast, all of the lowland species with the smallest ranges are widespread in lowland forest throughout Amazonia.

Species richness

The species richness of bat assemblages across the elevational gradient at Manu is shown in Fig. 5. The richness of point samples fluctuates greatly, from 59 species taken between 300–400 m to a single species taken between 3200–3300 m. Part of this fluctuation can be attributed to uneven sampling efforts: across elevations, number of species is positively and significantly ($P < 0.05$) correlated with the number of individuals sampled ($r = 0.92$) and with the number of nights over which samples were recorded ($r = 0.76$), and the latter two variables are themselves correlated ($r = 0.72$); all of these variables are inversely correlated with elevation (-0.63, -0.61, and -0.83, respectively).

Sharp dips and peaks in the richness curve for point samples at neighbouring elevations are
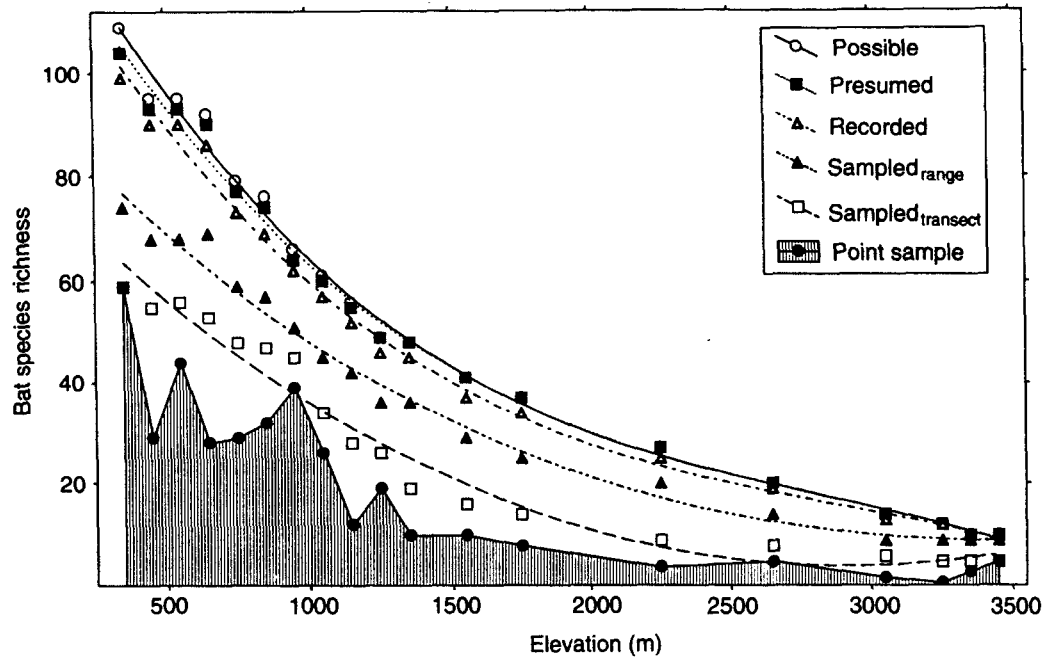
FIG. 5. Bat species richness in Manu Biosphere Reserve as a function of elevation. Symbols are: ● and pattern backdrop, point samples based on actual captures; □, sampled species interpolated to be present from transect ranges; ▲, sampled species inferred from literature ranges; △, recorded species inferred from literature ranges; ■, presumed species inferred from literature ranges; and ○, possible species inferred from literature ranges. Inferred richnesses fitted by least-squares cubic regressions (see text for discussion).

greatly dampened by interpolation. Interpolation generates diversity estimates which must equal or exceed those from point samples; in general, the degree to which interpolated values surpass point samples is inversely proportional to the sampling effort expended at that elevation. By definition, the highest and lowest points of the interpolated curve intersect the sampled points. Adding species from the three hypothetical pools to those sampled elevates species richness estimates, but does so in a non-linear manner. Fitting the six diversity estimates shown in Fig. 5 with a stepwise cubic polynomial regression, the lowest two estimates are best fitted by linear regressions, "sampled species inferred from range" by a quadratic regression, and the three highest estimates ('recorded', 'presumed', and 'possible') by cubic models (Table III). Each of the cubic regressions accounted for more than 99% of the variation in diversity among elevations. Models of this form indicate that diversity falls rapidly at higher elevations, with the rate of diversity change declining towards an asymptote at higher elevations (Fig. 5).

Species composition

Changes in species composition with elevation can be assessed by examining the similarity of adjacent bat assemblages. High similarity of adjacent assemblages indicates little turnover in species composition. On the other hand, dips in pairwise similarity signify greater community

TABLE III

Coefficients from stepwise polynomial regressions of bat species richness (as variously estimated; see Fig. 3) versus elevation; the cubic model had the form: Bat species richness = $\beta_0 + \beta_1$ (elevation) + β_2 (elevation)^2 + β_3 (elevation)^3. Only coefficients with significant contributions (*P < 0.05; **P < 0.01; ***P < 0.001) to the predictive equation are shown. R^2 values are those for the entire listed model

Estimator for bat species richness	β_0	β_1	β_2	β_3	R^2
Point sample	67.586***	−0.0603*			0.8514
Sampled species–transect	82.505***	−0.0533***			0.9705
Sampled species–literature	96.282***	−0.0605***	0.00001*		0.9884
Recorded species	132.742***	−0.1000***	0.00000***	−0.00000**	0.9943
Presumed species	137.013***	−0.1010***	0.00000***	−0.00000**	0.9942
Possible species	143.198***	−0.1089***	0.00000***	−0.00000**	0.9942

change—for example, discrete communities that are zoned by elevation should exhibit high similarities within each zone, with low similarities marking zone boundaries. Results for the Manu bat assemblages, as sampled and variously estimated, are shown in Fig. 6a. Pairwise similarity values rise and fall erratically, but most values are quite high, the majority exceeding 0.8. Lowest similarity, perhaps denoting zonal boundaries, is seen near the lowland forest-montane forest transition (c. 1000 m) and near the cloud forest-Altiplano transition (> 2600 m).

As might be expected, similarity among bat communities drops monotonically with increasing distance along the gradient (Fig. 6b). When the sites being compared are 750 m apart along the gradient, about half of their pooled species list is shared (i.e. J = 0.5).

Bat assemblages along the elevational gradient were significantly nested. That is, the faunas found at different elevations tended to contain nested subsets of the same species pool. This tendency holds whether the elevational ranges of bats at Manu are inferred using only records derived from this study's sampling (Fig. 7a), or using literature records of elevational occurrence in the central Andes (Fig. 7b). In the former case, the temperature of the presence-absence matrix is higher (15.87°), reflecting the greater disorder associated with our still incomplete sampling efforts. In the latter case, temperature is substantially lowered (to 10.5°) by eliminating the heterogeneity that is introduced by sampling biases. These two matrix temperatures lie 19.98 and 15.54 S.D., respectively, below the means of 1000 simulated distributions, and have vanishingly small probabilities of being randomly produced (10^{-45} and 10^{-63}, respectively).

The nestedness observed among bat assemblages is strongly associated with elevation. The thermodynamic measure of nestedness, T, is based on a re-ordering of matrix rows and columns that minimizes the disorder of non-nestedness. In doing this, however, the packing procedure very nearly reproduced the ordering of assemblages along the elevational gradient. Rank-correlations of elevation with row number in the packed matrices was 0.952 and 0.963 for sampled and inferred distributions, respectively (both $P \ll 0.001$).

System temperatures of 10° are not unusual (cf. Atmar & Patterson, 1993); they commonly result when numerous species each depart slightly from an overall nested pattern. In the present case, however, the majority of species are perfectly nested; a small handful of species contributes almost all of the 'heat' or disorder in this system. These 'idiosyncratic' species, identified in Fig. 7c alongside their respective individual contributions to system temperature, are plainly members of a highland biota whose distribution patterns contrast with those of the majority of species (see also Koopman, 1978).
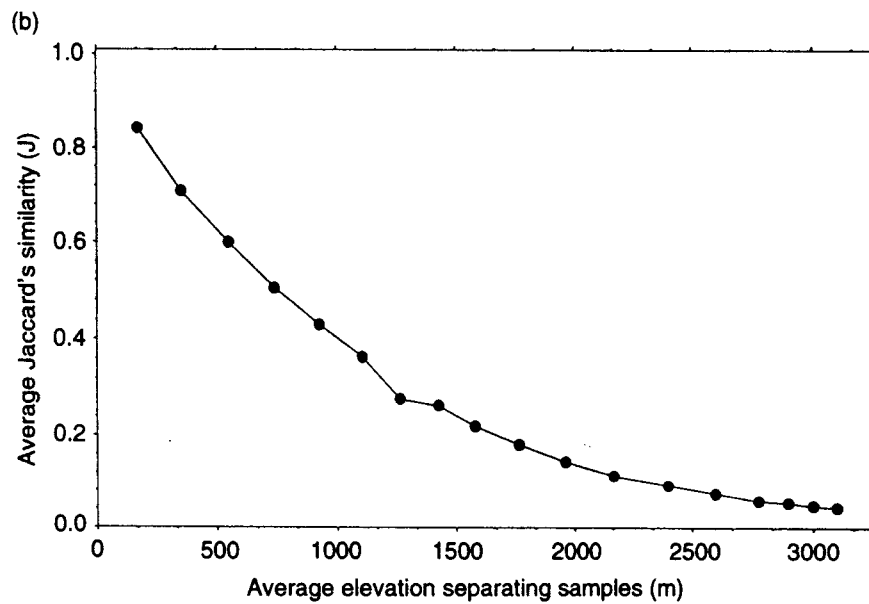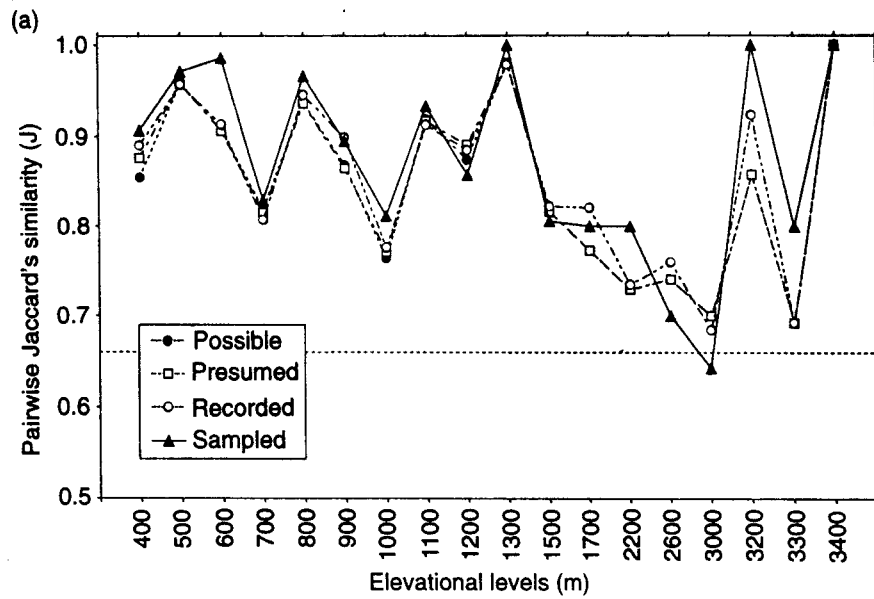
Fig. 6. Jaccard's similarity profiles for the Manu transect. (a) Pairwise similarities of adjacent assemblages, plotted for each of the documented and postulated species pools; the dotted line is for reference only and marks an arbitrary $J = 0.667$. (b) Average similarity values between sites separated by various vertical distances; as with all such plots, sample size for plotted points varies, from many at low distances to a single pair of points separated by 3100 m.

Discussion

After a decade of sampling by experienced field crews, fully one-third of the bat species that probably occur in Manu has eluded detection and documentation. Most of the species sampled were taken with mist-nets set at ground-level, an approach to sampling bat communities that is now practically universal (Findley, 1993). Yet the ecological biases evident in even our most intensively sampled stations (Fig. 2) demonstrate its limitations. Insectivores are under-represented, both in species and abundance, and canopy foragers are virtually absent from our samples. On the other hand, both canopy and understorey frugivores are well represented, so that foraging station is not the only variable involved in this bias. Because many insectivorous bats appear to be common and are routinely seen flying along trails (e.g. Ascorra *et al.*, 1991), they are probably infrequently captured because they rely on echolocation (and hence can elude the nets). Sampling many of the hard-to-document bat species at Manu will require a diverse complement of bat detectors, firearms, arboreal netting, and collecting at roost sites. This type of opportunistic sampling, while difficult to standardize, has proven effective in sampling many small insectivorous species elsewhere. Ironically, opportunistic sampling often leaves under-represented the very group of bats (Phyllostomidae: Stenodermatinae) that dominates mist-netted samples (cf. samples predating mist-nets in Patterson, 1992).

Two of the species in our list are new to science, and new elevational limits were established for 19 others (*c.* 25% of those sampled). Current knowledge of bat elevational ranges is too fragmentary to determine whether these range extensions typify bat distributions throughout the Central Andes or instead represent localized responses to the specific communities encountered within Manu. The former seems likely for two reasons. Most of these species are widespread, showing little turnover with geographic or elevational distance. Also, the elevational ranges of species within polytypic genera, such as *Sturnira, Platyrrhinus, Artibeus,* or *Anoura,* do not show the precise complementarity that is expected in cases of competitive replacement (Diamond, 1973; Terborgh & Weske, 1975). Koopman (1978: 27–28) identified several general instances of elevational replacement, involving species of *Sturnira, Platyrrhinus, Dermanura,* and *Vampyressa.* However, none resembles the paradigmatic species replacement established by Diamond (1973: fig. 6) for *Crateroscelis* warblers in New Guinea.

Poor understanding of bat distributions precludes our using micro-geographic comparisons to understand the importance of competitive interactions (Terborgh & Weske, 1975) or ecotones (Terborgh, 1985). We can, however, draw some general conclusions concerning species richness, species composition, and endemism patterns.

Species richness

Findley (1993) recently tallied global diversity patterns in bats, using the 500 × 500 km quadrat method. According to his figure 6.3, no quadrat in Africa holds more than 80 species, and none in the Eastern Hemisphere supports more than 120 species; the putative centre of Neotropical diversity lies in the Guianan Shield, with more than 120 species comprising the regional fauna. Yet our records establish that a 120-species isophene should also encircle the Eastern Versant fauna. Given diversity patterns established for other groups and several distinctive habitats found along the Eastern Versant, but not in the heart of the Amazon Basin, it seems likely that the bat fauna present at Manu and other undisturbed Eastern Versant sites in South America represents the richest pool of mammalian species belonging to a single order ever assembled at a local geographic scale.
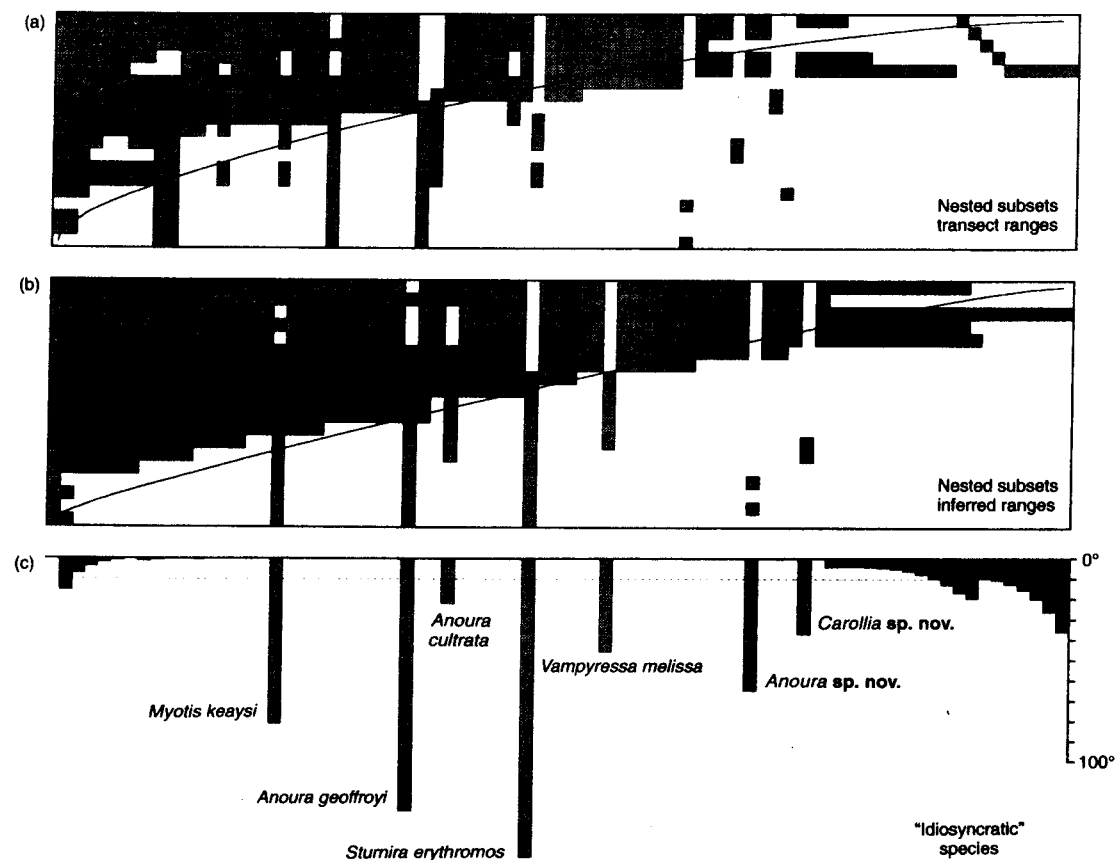
Fig. 7. Nested patterns of species composition for Manu bats over 19 elevational levels. (a) Presence-absence matrix for the transect ranges of 82 sampled species, packed so as to maximize nestedness. 'Presence' is indicated by the shaded squares, and the black curved line denotes the presence-absence boundary in a perfectly and maximally nested matrix (see Atmar & Patterson, 1993). The temperature of this matrix, T, is $15.82°$ $(P = 10^{-45})$. (b) Matrix for the ranges of these same species as inferred from literature records, which dampens the noise of sampling bias by filling apparent holes in the distributions $(T = 10.5°, P = 10^{-63})$. (c) Plot of 'idiosyncratic' species scores for (b), indicating the contributions of individual species to matrix temperature. Note that a handful of species is responsible for most of the noise in the system, that most of these species are found only at middle and high elevations, and that this list includes most of Manu's endemic species (see text for discussion).

Because the grain of our sampling is relatively coarse (particularly so for guilds difficult to sample using mist-nets), our estimates of bat diversities remain regional ones rather than being strictly local. Scale differences probably explain the fact that, over transects of similar length, the species richness of bats declines by almost an order of magnitude, while that for birds declines only three-fold (Terborgh, 1977). Use of regional versus syntopic diversities for bats differentially enhances estimates of their lowland diversity, invalidating statistical comparisons of richness-elevation regressions for bats and birds.

Richness patterns can undoubtedly be traced to the diversity of regional species pools in areas adjoining the transect: the Amazon Basin, the Andean Slopes, and the Altiplano. Highly unequal diversity of bats in these different regions, which in turn may be related to their grossly unequal areas, exerts a major influence over the overall diversity pattern.

The Manu preserve presents one of the world's longest continuously forested transects, extending 3 km in elevation. Despite numerous species reaching their range boundaries along this transect, species richness peaks in the lowlands and declines monotonically above (Fig. 5). Monotonic decline of bat species richness, as variously measured, follows the 'general' gradient pattern, which was established for birds (Rahbek, 1995). However, it contrasts with richness patterns for many other groups, which often show a hump at intermediate elevations (e.g. Patterson, Meserve & Lang, 1989; Rosenzweig, 1992; Olson, 1994; Rahbek, 1995). The deviation of bat diversity from the 'revised general pattern' is especially noteworthy, because the interpolations used to generate species richness estimates would tend to inflate mid-slope values, creating a hump-shaped distribution, even if point diversities were uniform across the gradient.

Unfortunately, we lack the data to discuss the productivity-diversity pattern as it relates to bats. Terborgh (1977) showed that temperature varies nearly linearly with elevation in the nearby Cordillera Vilcabamba, but there is little reason to think that precipitation or evaporation should do so (cf. Nullet & Juvik, 1994). Besides lacking either direct or indirect data on productivity along the gradient, sampling intensity at different elevations can only be crudely quantified, given the different field crews with different overall objectives that assembled them over different field seasons. Monotonic declines in species richness of bats may be underlain by a hump-shaped curve of diversity per unit sampling effort when plotted against elevation, as is true for Andean bird communities (cf. Terborgh, 1977; Rahbek, 1995). Despite the importance of diversity-per-unit-sampling-effort to community ecology and the assembly of local communities, it is practically irrelevant to the largely historical factors that define the species pool. Whereas species-packing and evenness might be higher at mid-elevations, species diversity is incontrovertibly highest below, in parallel with the greater area (both locally and geographically) and diversity of lowland habitats. Regenerating oxbow lakes (cochas), swamp (igapó) forests, seasonally flooded (várzea) forests, sand bars, and the like each support species not typical of terra firme forests. All contribute to the heterogeneous mosaic of the Manu lowlands and thereby to the diversity of its lowland communities (cf. Foster, 1980).

Range amplitude

In a highly original monograph on biogeography, Rapoport (1982) documented a pattern of range-size variation subsequently christened 'Rapoport's Rule': the tendency for high-latitude species to range over a broader latitudinal belt than equatorial species. More recently, this argument has been extended to elevational ranges along elevational gradients, a relationship that might be suitably termed 'Stevens' Rule' (cf. Stevens, 1992). The ranges of Manu bats (Fig. 4)

appear to offer strong support for Stevens' Rule. Many low-elevation species have the narrow ranges expected of stenotypic forms closely adapted to stable and predictable tropical climates. On the other hand, many highland species extend over most of the transect; in physiology and habits. These species are demonstrably adapted to cope with the climatic variation that high-elevational habitats typically present. It seems more than coincidental that species ranging above 2000m elevation at Manu represent the same three families that range north into the conterminous United States: Phyllostomidae, Vespertilionidae, and Molossidae. By trophic specialization, hibernation, or migration, these groups all exhibit specializations to inclement climates and resource scarcity.

Several problems beset interpreting these patterns as supportive of Stevens' Rule. First, as detailed by Lyons & Willig (In prep.), there is a methodological problem inherent in such correlations—wide-ranging species must range up the transect (i.e. it is impossible to range widely below the foot of the transect). Second, the differential richness of lowland and highland bat faunas (i.e. many lowland species but only a few highland ones) means that rarefaction analysis is needed to provide comparable estimates of the range amplitude of lowland faunas. Just as regional biogeographic patterns may produce patterns which conflict with those predicted using ecogeographic rules (Roy, Jablonski & Valentine, 1994), so are they capable of generating coincidental agreement. A third difficulty—that history may fully account for observed distributions—looms larger for studies of Rapoport's Rule than Stevens' Rule: elevational gradients bring most species into geographic proximity, strengthening inferences that observed distributions are ecologically mediated. This is especially true for Manu bats, as the Andes are geologically young (Simpson, 1979). Still, for the time being, agreement with Stevens' Rule seems an unremarkable by-product of regional diversity patterns.

Species composition

Declining diversity and weak endemism of higher-elevation bat faunas along the Eastern Versant contrast sharply with patterns shown by syntopic rodents. At Hacienda Pairumani, 35 km SW Ilave, Depto. Puno at 3950 m, Pearson (1951) recorded 12 species of native sigmodontine Muridae, all belonging to the tribes Akodontini or Phyllotini: *Akodon boliviensis, Akodon albiventer, Bolomys amoenus, Chroeomys jelskii, Calomys lepidus, Phyllotis xanthopygus, Phyllotis osilae, Auliscomys boliviensis, Auliscomys pictus, Auliscomys sublimis, Chinchillula sahamae,* and *Neotomys ebriosus.* Twelve species of murids are also known to occur at the foot of the transect (below 400 m, pooling records for Cocha Cashu, Manu, and Pakitza listed in Pacheco *et al.,* 1993): *Neacomys spinosus, Nectomys squamipes, Oecomys bicolor, Oecomys superans, Oligoryzomys microtis, Oryzomys capito, Oryzomys macconnelli, Oryzomys nitidus, Rhipidomys couesi, Oxymycterus* sp., *Holochilus brasiliensis,* and *Neusticomys peruviensis.* None of the species or genera in these lists is shared (although *Oligoryzomys* and *Oxymycterus* range elsewhere up to the Altiplano, near Cerro Macho Cruz in the upper reaches of Manu Biosphere Reserve; Pacheco *et al.,* 1993), and only one of the lowland species (*Oxymycterus* sp.) belongs to a tribe (Akodontini) that dominates the highland faunas.

Although the distributions and systematics of rodents along the gradient are very poorly known, studies by Patton, Myers & Smith (1990) and Leo & Romo (1992) suggest that: (1) rodent faunas at intermediate elevations are no richer and are probably more impoverished than those either above or below (i.e. that there may even be an 'inverse hump'); and (2) there is turnover in species composition within the Eastern Versant fauna itself, with species

replacements among elfin forest, upper montane, and lower montane forest assemblages. Furthermore, (3) the Altiplano, Eastern Versant, and Amazon Basin each represent centres of non-volant mammalian diversity and endemism (Patterson, In prep.; see also Cracraft, 1985, for birds). Neotropical bat faunas are divisible only into Amazonian and Eastern Versant regions, and even these are only weakly differentiated, with 8 and 4% endemic species, respectively (Koopman, 1982).

Rodents and bats differ so greatly in dispersal rates, generation time, evolutionary rate, 'grain' of environmental exploitation, and geographic range size, that no simple explanation for these differences presents itself. However, these groups are not equally diversified ecologically or phylogenetically. Manu bats undoubtedly play more varied ecological roles than this collection of murids. In addition, the common ancestor of the eight bat families lived in Eocene or earlier times, not the Pliocene or Miocene as for the murids. Many biogeographic patterns that contrast with expected or 'general' ones are based on groups with circumscribed taxonomic limits, idiosyncratic ecologies, or both (e.g. the temperate-zone peak of species richness among voles and lemmings [Mammalia: Arvicolinae]). In their great ecological diversity and remote kinship, bats more strongly resemble Manu's birds than Manu's murid rodents.

Nested subsets

That bat communities at different elevations at Manu exhibit nested subsets is at once both striking and unsurprising. It is remarkable that an elevational gradient spanning three vertical kilometres and extensive habitat diversity does not produce stronger turnover in bat species. The progressive diminution of bat species richness at higher elevations is only rarely accompanied by compensatory replacement. As species drop out with increasing elevation, they are seldom replaced by higher-elevation specialists. 'Idiosyncratic species' represent exceptions to this trend, because their distributions lie mainly outside the theoretical 'boundary curve' that separates expected presences and absences (cf. Atmar & Patterson, 1993).

On the other hand, 'nested subsets' appear to be one of the most frequent and trenchant patterns of species composition. Generally, nested subsets can be attributed to two prevalent ecological patterns: (1) high variance in the abundance of species within local assemblages (e.g. Preston, 1962); and (2) correlation between local abundance and regional incidence patterns (Hanski, 1982; Bock & Ricklefs, 1983; Brown, 1984). Some species are far more abundant than others in local communities, and such species tend to have higher incidence in neighbouring communities. In a general sense, 'nested subset' structure reflects a natural gradation of species incidence which spans the conceptually useful but operationally forced designations of species as either 'core' or 'satellite' (Hanski, 1982).

Declining species richness along the gradient sets the stage for elevational assemblages to exhibit nested subsets of species. Even so, the strength of this correlation is surprising. All estimates of species richness (Fig. 3) are better fitted by an exponential (rather than linear) relationship; although species richness drops dramatically with elevation at the foot of the gradient, the diversity of highland communities changes much more slowly. That a maximally ordered ('packed') presence-absence matrix so nearly reconstructs the elevational order of these communities strongly ties this ecological structure to elevation.

The significance of 'nested subsets' structure for conservation is debatable (Cutler, 1994; Lomolino, 1994). By definition, nested subsets imply that the species present in smaller biotas also tend to be found in richer ones (Patterson & Atmar, 1986); accordingly, to conserve

the maximum number of species, one needs to focus attentions on the richest biotas. In fragmented systems, like landbridge islands and habitats made insular by climatic or anthropogenic change, nestedness is strong (Wright & Reeves, 1992) and widespread (Patterson, 1990), with the richest communities commonly occupying the largest parcels. With reference to the Manu reserve, nested subset structure of the bat communities could be used to argue for concentrating protection on the highly diverse communities at lower elevations. Yet this action would be unwarranted for three important reasons, all of which are extrinsic to patterns of species composition. First, development threats are distributed unequally along the gradient, with far higher pressures focused on montane communities adjoining areas of dense human settlement (Young et al., 1994). Second, the total geographic extent of communities at different elevations varies greatly, with lowland communities extending in a vast patchy mosaic from the Andes to the Atlantic, while montane communities are confined to narrow ribbon-like bands along the Andean slopes (Graves, 1988). Finally, endemicity is distributed non-randomly across the gradient, with endemic species disproportionately common in the more impoverished highland communities. More than 63% of Peru's endemic mammals are restricted to the Eastern Versant (Pacheco, In press). Thus, for Manu and for many other areas worldwide, species richness per se provides a highly inadequate guide to the global conservation importance of different elevational levels. Peterson et al. (1993) discussed conservation priorities for Mexico's biodiversity, which exhibits similar patterns of diversity and endemism.

On the other hand, the fact that Manu's bat faunas are nested offers some interesting theoretical predictions for the mostly unknown ecological interactions that contribute to the structure of these assemblages. It is characteristic of nested distributions that species co-occurrence patterns are asymmetric (Patterson & Brown, 1991). Consider four communities containing nested species assemblages as represented by letters—ABCD, ABC, AB, and A; species 'A' is present in every community that is occupied by 'B', but 'C' is not. Therefore, 'A' represents a predictable and repeated part of the biotic environment in which 'B' must fashion ecological strategies for feeding, roosting, reproducing, etc., whereas 'C' does not. The more that two otherwise comparable species differ in incidence ('A' and 'Z', vs. 'A' and 'C'), the more asymmetric their competitive relations should be.

REFERENCES

Albuja, V. L. (1982). *Murciélagos del Ecuador*. Escuela Politécnica Nacional, Departamento de Ciencias Biológicas, Quito.

Anderson, S., Koopman, K. F. & Creighton, G. K. (1982). Bats of Bolivia: an annotated checklist. *Am. Mus. Novit.* No. 2750: 1–24.

Anderson, S. & Webster, W. D. (1983). Notes on Bolivian mammals. 1. Additional records of bats. *Am. Mus. Novit.* No. 2766: 1–3.

Ascorra, C. F., Gorchov, D. L. & Cornejo, F. (1993). The bats from Jenaro Herrera, Peru. *Mammalia* 57: 533–552.

Ascorra, C. F., Wilson, D. E. & Romo, M. (1991). Lista anotada de los quiropteros del Parque Nacional Manu, Peru. *Publ. Mus. Hist. Nat. Univ. Nac. May. San Marcos, Ser. A, Zool.* 42: 1–14.

Atmar, W. & Patterson, B. D. (1993). The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia* 96: 373–382.

Atmar, J. W. & Patterson, B. D. (1995). *The nestedness temperature calculator: a Visual Basic program, including 294 presence-absence matrices*. University Park, NM: AICS Research, Inc. and Chicago: The Field Museum.

Bock, C. E. & Ricklefs, R. E. (1983). Range size and local abundance of some North American songbirds: a positive correlation. *Am. Nat.* 122: 295–299.

Brown, J. H. (1984). On the relationship between abundance and distribution of species. *Am. Nat.* 124: 255–279.

Chapman, F. M. (1926). The distribution of bird-life in Ecuador: a contribution to a study of the origin of Andean bird-life. *Bull. Am. Mus. Nat. Hist.* 55: 1–784.

Cracraft, J. (1985). Historical biogeography and patterns of differentiation within the South American avifauna: areas of endemism. In *Neotropical ornithology*: 49–84. Buckley, P. A., Foster, M. S., Morton, E. S., Ridgely, R. S. & Buckley, F. G. (Eds). Washington DC: American Ornithologists Union. *Ornithol. Monogr.* No. 36.

Cutler, A. H. (1994). Nested biotas and biological conservation: metrics, mechanisms, and meaning of nestedness. *Landscape Urban Plann.* 28: 73–82.

Diamond, J. M. (1973). Distributional ecology of New Guinea birds. *Science Washington DC* 179: 759–769.

Findley, J. S. (1993). *Bats: a community perspective*. Cambridge: Cambridge University Press.

Foster, R. B. (1980). Heterogeneity and disturbance in tropical vegetation. In *Conservation biology: an evolutionary-ecological approach*: 75–92. Soulé, M. E. & Wilcox, B. A. (Eds). Sunderland, MA: Sinauer Associates.

Gardner, A. L. (1976). The distributional status of some Peruvian mammals. *Occas. Pap. Mus. Zool. LA State Univ.* 48: 1–18.

Gardner, A. L. (1977). Feeding habits. In *Biology of bats of the New World family Phyllostomatidae. Part II*: 293–350. Lubbock, TX: Special Publ., The Museum, Texas Tech. University.

Graham, G. L. (1983). Changes in bat species diversity along an elevational gradient up the Peruvian Andes. *J. Mammal.* 64: 559–571.

Graham, G. L. (1990). Bats versus birds: comparisons among Peruvian vertebrate faunas along an elevational gradient. *J. Biogeogr.* 17: 657–668.

Graham, G. L. & Barkley, L. J. (1984). Noteworthy records of bats from Peru. *J. Mammal.* 65: 709–711.

Graves, G. R. (1988). Linearity of geographic range and its possible effect on the population structure of Andean birds. *Auk* 105: 47–52.

Hall, E. R. (1981). *The mammals of North America* 1 & 2. New York: Wiley-Interscience.

Handley, C. O., Jr (1987). New species of mammals from northern South America: fruit-eating bats, Genus *Artibeus* Leach. In *Studies in Neotropical mammalogy: essays in honor of Philip Hershkovitz*: 163–172. Patterson, B. D. & Timm, R. M. (Eds). Chicago. *Fieldiana Zool.* NS No. 39.

Hanski, I. (1982). Communities of bumblebees: testing the core-satellite species hypothesis. *Ann. Zool. Fenn.* 19: 65–73.

Hutterer, R., Verhaagh, M., Diller, J. & Podloucky, R. (1995). An inventory of mammals observed at Panguana Biological Station, Amazonian Peru. *Ecotropica* 1: 3–20.

Koopman, K. F. (1978). Zoogeography of Peruvian bats with special emphasis on the role of the Andes. *Am. Mus. Novit.* No. 2651: 1–33.

Koopman, K. F. (1982). Biogeography of the bats of South America. In *Mammalian biology in South America*: 273–302. Mares, M. A. & Genoways, H. H. (Eds). Linesville, PA: Special Publication, Pymatuning Laboratory of Ecology No. 6.

Leo, M. & Romo, M. (1992). Distribución altitudinal de roedores sigmodóntinos (Cricetidae) en el Parque Nacional Río Abiseo, San Martín, Peru. In *Biogeografía, ecología y conservación del bosque montaño en el Perú*: 105–118. Young, K. R. & Valencia, N. (Eds). *Mem. Mus. Hist. Nat. Univ. Nac. May. San Marcos, Lima* No. 21.

Linares, O. J. (1986). *Murciélagos de Venezuela*. Caracas: Cuadernos Lagoven.

Lomolino, M. V. (1994). An evaluation of alternative strategies for building networks of nature reserves. *Biol. Conserv.* **69:** 243–249.

Muñoz Arango, J. (1990). Diversidad y hábitos alimenticios de murciélagos en transectos altitudinales a través de la Cordillera Central de los Andes en Colombia. *Stud. Neotrop. Fauna Environ.* **25:** 1–17.

Nullet, D. & Juvik, J. O. (1994). Generalised mountain evaporation profiles for tropical and subtropical latitudes. *Singapore J. Trop. Geogr.* **15:** 17–24.

Olson, D. M. (1994). The distribution of leaf litter invertebrates along a Neotropical altitudinal gradient. *J. Trop. Ecol.* **10:** 129–150.

Pacheco, V. (In press). Diversidad y conservación de los mamíferos peruanos. In *Ecología y conservación de los mamíferos de Latinoamerica.* Ceballos, G. Y. & Simonetti, J. (Eds). Fondo de Cultura Economica, Mexico, D.F.

Pacheco, V., de Macedo, H., Vivar, E., Ascorra, C., Arana-Cardó, R. & Solari, S. (1995). Lista anotada de los mamíferos peruanos. *Occas. Pap. Conserv. Biol.* **2:** 1–35.

Pacheco, V., Patterson, B. D., Patton, J. L., Emmons, L. H., Solari, S. & Ascorra, C. F. (1993). List of mammal species known to occur in Manu Biosphere Reserve, Peru. *Publ. Mus. Hist. Nat. Univ. Nac. May. San Marcos, Ser. A, Zool.* **44:** 1–12.

Patterson, B. D. (1990). On the temporal development of nested subset patterns of species composition. *Oikos* **59:** 330–342.

Patterson, B. D. (1992). Mammals in the Royal Natural History Museum, Stockholm, collected in Brazil and Bolivia by A. M. Olalla during 1934–1938. *Fieldiana Zool.* NS No. 66: 1–48.

Patterson, B. D. & Atmar, W. (1986). Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biol. J. Linn. Soc.* **28:** 65–82.

Patterson, B. D. & Brown, J. H. (1991). Regionally nested patterns of species composition in granivorous rodent assemblages. *J. Biogeogr.* **18:** 395–402.

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. *J. Mammal.* **70:** 67–78.

Patton, J. L., Myers, P. & Smith, M. F. (1990). Vicariant versus gradient models of diversification: the small mammal fauna of eastern Andean slopes of Peru. In *Biogeography and systematics in the tropics, Bonn, June 5–8 1989:* 355–371. Peters, G. & Hutterer, R. (Eds). Bonn: Alexander Koenig Zoological Research Institute and Zoological Museum.

Pearson, O. P. (1951). Mammals in the highlands of southern Peru. *Bull. Mus. Comp. Zool.* **106**(3): 115–174.

Peterson, A. T., Flores-Villela, O. A., León-Paniagua, L. S., Llorente-Bousquets, J. E., Luis-Martinez, M. A., Navarro-Sigüenza, A. G., Torres-Chavéz, M. G. & Vargas-Fernández, I. (1993). Conservation priorities in Mexico: moving up in the world. *Biodivers. Let.* **1:** 33–38.

Preston, F. W. (1962). The canonical distribution of commonness and rarity: Part I. *Ecology* **43:** 185–215.

Rahbek, C. (1995). The elevational gradient of species richness: a uniform pattern? *Ecography* **18:** 200–205.

Rapoport, E. H. (1982). *Areography: geographic strategies of species.* Oxford: Pergamon Press.

Rohlf, F. J. (1988). *NTSYS-pc: Numerical taxonomy and multivariate analysis system.* Ver. 1.40. Setauket, NY: Exeter Publ.

Rosenzweig, M. L. (1992). Species diversity gradients: we know more and less than we thought. *J. Mammal.* **73:** 715–730.

Roy, K., Jablonski, D. & Valentine, J. W. (1994). Eastern Pacific molluscan provinces and latitudinal diversity gradient: No evidence for 'Rapoport's Rule'. *Proc. Natl. Acad. Sci. USA* **91:** 8871–8874.

Simpson, B. B. (1979). Quaternary biogeography of the high montane regions of South America. In *The South American herpetofauna: its origin, evolution, and dispersal:* 157–188. Duellman, W. E. (Ed.). Lawrence, KS. *Monogr. Mus. Nat. Hist. Univ. Kans.* No. 7.

Sneath, P. H. & Sokal, R. R. (1973). *Numerical taxonomy: the principles and practice of numerical classification.* San Francisco: W. H. Freeman.

Stevens, G. C. (1992). The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. *Am. Nat.* **140:** 893–911.

Terborgh, J. (1977). Bird species diversity on an Andean elevational gradient. *Ecology* **58:** 1007–1019.

Terborgh, J. (1985). The role of ecotones in the distributions of Andean birds. *Ecology* **66:** 1237–1246.

Terborgh, J. & Weske, J. S. (1975). The role of competition in the distribution of Andean birds. *Ecology* **56:** 562–576.

Tuttle, M. D. (1970). Distribution and zoogeography of Peruvian bats, with comments on natural history. *Univ. Kans. Sci. Bull.* **49:** 45–86.

Vizzoto, L. D. & Taddei, V. (1973). *Chave para determinação de quirópteros brasileiros.* São José do Rio Preto (São Paulo): Grafica Francal.

Willig, M. R. (1983). Composition, microgeographic variation, and sexual dimorphism in caatingas and cerrado bat communities from northeastern Brazil. *Bull. Carnegie Mus. Nat. Hist.* **23**: 1–131.

Wilson, E. O. (1987). The arboreal ant fauna of Peruvian Amazon forests: a first assessment. *Biotropica* **2**: 245–251.

Woodman, N., Timm, R. M., Arana-C., R., Pacheco, V., Schmidt, C. A., Hooper, E. D. & Pacheco, A. C. (1991). Annotated checklist of the mammals of Cuzco Amazónico, Peru. *Occas. Pap. Mus. Nat. Hist. Univ. Kans.* **145**: 1–12.

Wright, D. H. & Reeves, J. H. (1992). On the meaning and measurement of nestedness of species assemblages. *Oecologia* **92**: 416–428.

Young, K. R., Church, W. B., Leo, M. & Moore, P. F. (1994). Threats to Río Abiseo National Park, northern Peru. *Ambio* **23**: 312–314.