

Faunal nestedness and species–area relationship for small non-volant mammals in “sky islands” of northern Venezuela

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We study the biogeography of small non-volant mammals in mesic montane sky islands of northern Venezuela. Fieldwork, examination of museum specimens, and critical use of literature yielded species lists for the Cordillera de Mérida, Cordillera de la Costa, Serranía de San Luis, and Cerro Santa Ana. Fieldwork confirmed the species known from Cerro Santa Ana and added 12 species for the Serranía de San Luis. Richness decreases with smaller area. Furthermore, the faunas are highly nested, with taxa dropping out at successive depressions. Species deviating from nestedness provide a signal indicative of *in situ* speciation in rodents but not in marsupials.

Keywords: biogeography; cloud forest; Didelphimorphia; endemism; Rodentia; Venezuela

Introduction

Islands provide key insights into ecology and evolution (Lomolino & Heaney 2004). Furthermore, many similarities exist between real islands and disjunct patches of particular habitat types in terrestrial systems. Often, such naturally fragmented habitats correspond to what have been termed sky islands – montane forests that transition abruptly into drastically different, typically drier, vegetation in the surrounding lowlands (e.g. Brown 1971; Patterson 1982). Studies of these naturally fragmented systems can lend insight into important current environmental issues (Knowles 2001; Peterson 2003).

A fascinating system of montane sky islands exists in north-central South America, where successive depressions separate various ranges of the Andes and several associated mountain chains (Figure 1). The first of these breaks occurs in northwestern Venezuela, where the Depresión del Táchira divides the Cordillera Oriental from the Cordillera de Mérida. The Depresión de Barquisimeto lies to the north of the Cordillera de Mérida and separates it from various sections of the Cordillera de la Costa and other smaller ranges that run roughly parallel to the Caribbean. Each of these disjunct ranges harbors montane evergreen forest, including cloud forest at higher elevations; in contrast, most of the vegetation in

the surrounding lowlands originally corresponded to drier vegetation types (deciduous forests, thorn forests, natural savannas, and deserts; Huber 1997; Ataroff-S 2003; IGVSB 2003).

Two especially isolated elements – the Serranía de San Luis and Cerro Santa Ana – hold particular biogeographic interest (Matteucci 1987). To the north of the Cordillera de Mérida and northwest of the Cordillera de la Costa, the Serranía de San Luis (=San Luis) runs ca. 50 km and rises to an elevation of 1501 m (Steyermark 1975). Cerro Santa Ana (=Santa Ana) lies on the Península de Paraguaná approximately 70 km north of the Serranía. Only ca. 4 km long, the Cerro rises abruptly from the lowlands and reaches an elevation of 830 m (supplementary Figure S2; Tamayo 1941, 1971). Although broad connections existed in earlier periods of lower sea level (e.g. the Last Glacial Maximum), the Península de Paraguaná was an island during marine introgressions such as at the Last Interglacial and is linked to the rest of the mainland today only by the narrow and sparsely vegetated Istmo de los Médanos (Lara & González 2007).

Here, we study the biogeography of small non-volant mammals in this system, giving special emphasis to the Serranía de San Luis and Cerro Santa Ana. Small non-volant mammals (in the Neotropics:

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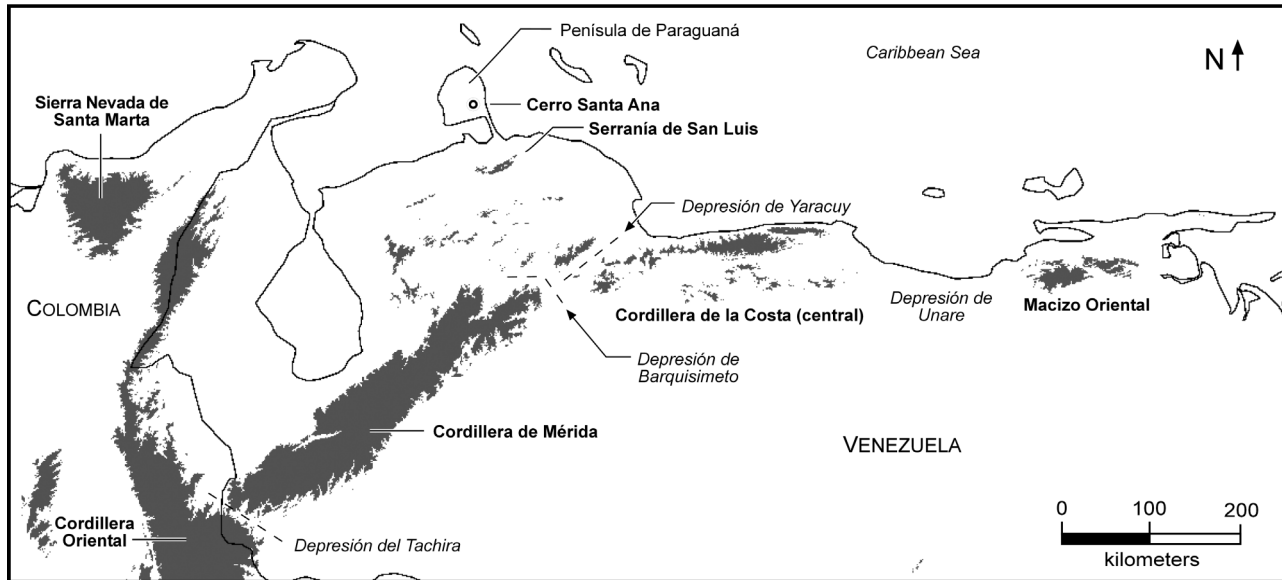


Figure 1. Map of north-central South America, showing the major mountain ranges (“sky islands”) and intervening lowland depressions. Mesic vegetation clothes the slopes of each range, with cloud forests occurring at higher elevations; in contrast, most of the vegetation in the surrounding lowlands originally corresponded to deciduous forests, thorn forests, natural savannas, and deserts (Huber 1997; Ataroff-S 2003). Areas ≥ 1000 m in elevation appear in gray shading. Cerro Santa Ana, which reaches an elevation of 830 m on the Península de Paraguaná, is indicated by a hollow dot.

rodents, marsupials, and shrews) often show high habitat fidelity, small home ranges, and low dispersal abilities, making them propitious for biogeographic studies (Kelt & Van Vuren 1999; McCain 2004; Jezkova et al. 2009). Whereas parts of the extensive Cordillera de Mérida and Cordillera de la Costa have received substantial attention by mammalogists (Handley 1976; Soriano et al. 1999; Rivas & Salcedo 2006), we build upon preliminary work in the smaller Serranía de San Luis and Cerro Santa Ana to allow the present biogeographic analyses. Several species of small non-volant mammals have been reported for San Luis, but only four are known from Santa Ana (Handley 1976; Bisbal-E 1990; MARN 2003). In addition, the species of spiny pocket mouse present on Santa Ana (*Heteromyidae: Heteromys oasicus*) shows substantial morphological differentiation in comparison with its mainland relative (*H. anomalus*; Anderson 2003b), bringing attention to the biogeographic and evolutionary importance of the Cerro.

In this study, we focus on the Cordillera de Mérida, the central portion of the Cordillera de la Costa, the Serranía de San Luis, and Cerro Santa Ana. To characterize the major biogeographic patterns in these ranges, we conducted fieldwork, examined museum specimens, critically evaluated information from the literature, and carried out quantitative analyses of sampling completeness, the species–area relationship, and faunal nestedness. In this system, area correlates highly (and negatively) with distance from the

main body of the northern Andes (the Cordillera Oriental in eastern Colombia and extreme northwestern Venezuela). The configuration of the sky islands and the successive nature of the depressions dividing them hinder separation of the effects of area from those of distance.

Hence, we aim to characterize the biogeographic patterns of species richness and distributions among the four ranges, deferring tests of driving processes for future studies. The regression-based species–area analyses conducted here examine the relationship between those variables for the four ranges. Furthermore, we use a regression to predict the species richness of Santa Ana based on the area and richness of the other three ranges, allowing comparison of its predicted versus observed richness. Complementarily, the analyses of nestedness characterize patterns of species richness and composition, quantifying the degree to which the species present in the ranges with lower richness constitute proper subsets of those found on successively richer ranges (Wright & Reeves 1992; Atmar & Patterson 1993). For example, in a perfectly nested system of three elements, all species present in the element with the lowest richness also would exist in the element with the next-highest richness, and all species present in that second element also would inhabit the element with the highest richness. Any pattern of nestedness detected in the system could be due to differential immigration and/or extinction. Examination of the particular species whose distributions deviate from

an overall pattern of nestedness (termed idiosyncratic species) can allow additional biogeographic insights, for example the detection of possible immigration from other areas or of *in situ* speciation.

Materials and methods

Fieldwork

To allow for faunal comparisons, we conducted fieldwork in the Serranía de San Luis and Cerro Santa Ana (Appendix 1) and examined previously collected specimens from both areas (supplementary Appendix S1 online only). At the Monumento Natural Cerro Santa Ana, we surveyed seven different elevational bands in mesic habitats, with additional limited sampling at one lower, xeric area (supplementary Figure S2; Appendix 1). For San Luis, we sampled several sites in and near the Parque Nacional Juan Crisóstomo Falcón (Figure 2; Appendix 1). The three principal sites corresponded to high elevations in mesic habitats: El Haitón, Cerro Galicia, and Uria. In addition, we conducted limited sampling at two sites on the lower slopes of the Serranía (one mesic, Cabure; one xeric, La Chapa) and two in the foothills to the south (both xeric, Santa Juana and La Encrucijada). Consistent with recommendations for wild taxa (Sikes et al. 2012), our fieldwork followed taxon-specific guidelines produced by the American Society of Mammalogists (Sikes et al. 2011).

Sampling completeness

Based primarily on the results of our fieldwork, we estimated species richness and inferred levels of inventory completeness. We conducted analyses using specimens from our fieldwork unless otherwise noted. All data related to previous fieldwork in San Luis derived from our identification of museum specimens (supplementary Appendix S1). Given the sampling techniques employed, we determined which species we consider to be incidentally captured (those unlikely to be sampled consistently with the given techniques, despite their continual presence at a site); we then excluded such species from the analyses. Among small non-volant mammals, we interpret that our methods are likely to capture individuals up to ca. 100–120 g. Hence, we flag as incidental all species for which the smallest adult body size is 120 g or greater (Linares 1998; supplemented with Nowak 1999 when necessary). We used EstimateS 8.0.0 to calculate the Chao2 (Chao 1984, 1987) estimator of species richness using default settings except as noted below. Chao2 was calculated as modified by Colwell & Coddington (1994) excluding situations when the coefficient of variation was >0.5 , in which cases we report the result of the classic option.

We conducted these analyses in two ways that differed in the sampling unit employed. First, we analyzed data by day of sampling within a site, estimating the number of species that would have been

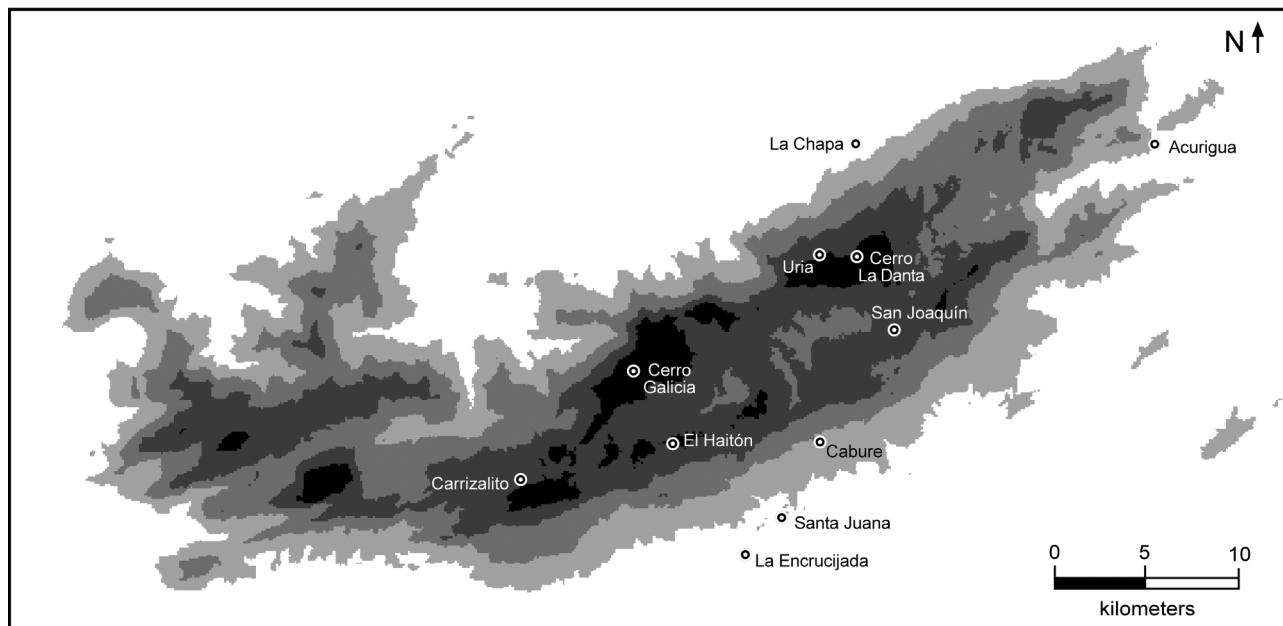


Figure 2. Map of the Serranía de San Luis in the Estado Falcón of northwestern Venezuela, showing the sites of our and previous fieldwork. See Figure 1 for the placement of the Serranía within northern Venezuela. Appendix 1 provides descriptions of the sites where we conducted fieldwork as well as geographic coordinates for all sites, and the specimens examined appear in supplementary Appendix S1. Progressively darker shading indicates the following elevations: pale gray ≥ 500 m, medium gray ≥ 750 m, dark gray ≥ 1000 m, and black ≥ 1250 m.

recorded eventually if sampling had continued. Then, we conducted analyses by site (or trapline), estimating the richness if additional sites/traplines (within either Santa Ana or San Luis) had been added indefinitely. For Santa Ana, we first estimated richness by day of sampling with data for all traplines in mesic habitats pooled. Then, we analyzed the data with trapline as the sampling unit. At San Luis, we estimated richness with day as the sampling unit for each of our sites in mesic habitats as well as for the mesic site Acurigua, which was sampled by previous workers (MARN 2003). Then, we estimated richness with site as the sampling unit, including information from previous fieldwork by other researchers at the same (or nearby) mesic sites (Appendix 1, supplementary Appendix S1).

These analyses rest on the assumption that the units of sampling (day or site/trapline) constitute equivalent independent samples. Although climatic variability exists throughout the year in this region, natural history information for other small non-volant mammals suggests that they do not move great distances and that detectability likely remains similar across time periods. Generally, the techniques that we employed were comparable, but effort

did vary somewhat among samples. Therefore, the resulting estimates should be considered approximate. However, the assumption regarding sampling was violated further because we selected sites (and traplines) to span our understanding of the diversity of macrohabitats. This bias should inflate variation among sites artificially and, hence, lead to overly wide confidence intervals (CI) and artifactually high estimates of richness in analyses with site or trapline as the sampling unit.

Biogeographic analyses

We compiled data for the biogeographic analyses from several sources, to produce lists of the species inhabiting mesic montane habitats. Records from Cerro Santa Ana and the Serranía de San Luis correspond to museum specimens that we examined and identified (from either our or previous fieldwork). In contrast, data for the better-studied Cordillera de Mérida and central portion of the Cordillera de la Costa (hereafter Cordillera de la Costa) derive from the literature (primarily Linares 1998; Soriano et al. 1999; Rivas & Salcedo 2006; Table 1). As defined here, the central portion of the Cordillera de la Costa includes both

Table 1. Species of small non-volant mammals known from four mesic sky islands in northern Venezuela. Records for the Serranía de San Luis and Cerro Santa Ana correspond to museum specimens that we examined and identified; documentation for the Cordillera de Mérida derives from Linares (1998) and Soriano et al. (1999), and that for the Cordillera de la Costa comes from Linares (1998) and Rivas & Salcedo (2006), as well as other sources¹ as necessary. ²Indicates species that constitute noteworthy records for the Serranía de San Luis; see supplementary Appendix S1 for specimens examined of these species and of two noteworthy records for xeric areas of the Serranía. ³Indicates species considered incidentally captured by the field techniques that we employed (see text).

	Cordillera de Mérida	Cordillera de la Costa (Central)	Serranía de San Luis	Cerro Santa Ana
Didelphidae				
<i>Caluromys lanatus</i> ³	x			
<i>C. trinitatis</i> ³	x	x		
<i>Chironectes minimus</i> ³	x	x		
<i>Didelphis marsupialis</i> ³	x	x	x ²	
<i>D. pernigra</i> ³	x			
<i>Gracilinanus dryas</i>	x			
<i>G. marica</i>	x	x	x ²	
<i>Gracilinanus</i> sp.	x	x		
<i>Marmosa demerarae</i>	x	x	x	
<i>M. murina</i>	x			
<i>M. robinsoni</i>	x	x	x	x
<i>Marmosops fuscatus</i>	x	x	x	
<i>Metachirus nudicaudatus</i> ³	x			
<i>Monodelphis adusta</i>	x			
<i>M. palliolata</i>	x	x	x ²	
<i>Philander mondolfii</i> ³	x			
Soricidae				
<i>Cryptotis meridensis</i>	x			
Sciuridae				
<i>Sciurus granatensis</i> ³	x	x	x	
Echimyidae				
<i>Olallamys edax</i> ³	x			
<i>Proechimys guairae</i>	x	x	x	x

(Continued)

Table 1. (Continued).

	Cordillera de Mérida	Cordillera de la Costa (Central)	Serranía de San Luis	Cerro Santa Ana
Heteromyidae				
<i>Heteromys anomalus</i>	x	x	x	
<i>H. australis</i>	x			
<i>H. catopterius</i>		x		
<i>H. oasicus</i>				x
Cricetidae				
<i>Aepeomys lugens</i>	x			
<i>A. reigi</i>	x			
<i>Akodon bogotensis</i>	x			
<i>Chilomys instans</i>	x			
<i>Ichthyomys hydrobates</i>	x			
<i>I. pittieri</i>		x		
<i>Melanomys caliginosus</i>	x			
<i>Microryzomys minutus</i>	x	x		
<i>Neacomys tenuipes</i>	x	x	x	
<i>Necomys urichi</i>	x	x		
<i>Nectomys rattus</i> ³	x			
<i>Nephelomys caracolus</i>		x	x ²	
<i>N. meridensis</i>	x			
<i>Nephelomys</i> sp.	x			
<i>Neusticomys mussoi</i>	x			
<i>Oecomys bicolor</i>	x	x	x ²	
<i>O. flavicans</i>	x	x	x ²	
<i>O. trinitatis</i>	x	x		
<i>Oligoryzomys fulvescens</i>	x	x	x	
<i>Rhipidomys couesi</i>	x	x		
<i>R. venezuelae</i>	x	x	x	x
<i>R. venustus</i>	x	x	x ²	
<i>Sigmodon alstoni</i>		x		
<i>S. hirsutus</i>	x	x	x ²	
<i>Sigmodontomys alfari</i>	x			
<i>Thomasomys laniger</i>	x			
<i>T. vestitus</i>	x			
<i>Transandinomys talamancae</i>	x	x	x ²	
<i>Zygodontomys breviceauda</i>	x	x	x ²	
Richness	48	29	19	4
Richness (without incidentals)	39	25	17	4
Area (mesic; km ²)	18,712.9	9654.0	632.8	4.3

¹Taxonomic notes: *Caluromys trinitatis*: *C. philander* of Soriano et al. (1999) and Rivas & Salcedo (2006); included within *C. philander* of Linares (1998); see López-Fuster et al. (2008) and Sánchez-H & Lew (2012); *Didelphis pernigra*: *D. albiventris* of Linares (1998) and Soriano et al. (1999); see Lemos & Cerqueira (2002) and Gardner (2005); *Gracilinanus* sp.: reported as *G. agilis* by Linares (1998), but that species does not occur north of Peru (Gardner 2005); *Marmosa demerarae*: *Micoureus demerarae* of Linares (1998), Soriano et al. (1999), and Rivas & Salcedo (2006); see Voss & Jansa (2009); *Marmosa murina*: see also Rossi (2005); *Monodelphis palliolata*: included within *M. breviceaudata* of Linares (1998), Soriano et al. (1999), and Rivas & Salcedo (2006); see Voss et al. (2001) and Gardner (2005); *Philander mondolfii*: included within *P. opossum* of Linares (1998); see Lew et al. (2006); *Cryptotis meridensis*: but note one possible record from the Cordillera de la Costa (Linares 1998; Woodman 2002); *Proechimys guairae*: included within *P. trinitatis* of Linares (1998); see Aguilera & Corti (1994) and Aguilera, Reig, et al. (1995); *Heteromys australis*: from Anderson & Soriano (1999); *Heteromys catopterius*: from Anderson & Gutiérrez (2009); *Aepeomys reigi*: from Ochoa-G. et al. (2001); *Akodon bogotensis*: *Microxus bogotensis* of Linares (1998); see Musser & Carleton (2005); *Necomys urichi*: *Akodon urichi* of Linares (1998) and Soriano et al. (1999); see Musser & Carleton (2005); *Nectomys rattus*: included within *Nectomys squamipes* of Linares (1998) and Soriano et al. (1999); see Voss et al. (2001) and Musser & Carleton (2005); *Nephelomys caracolus*: included within *Oryzomys albigularis* of Linares (1998) and considered *O. caracolus* by Rivas & Salcedo (2006); see Aguilera, Pérez-Zapata, et al. (1995), Márquez et al. (2000), Percequillo (2003), and Weksler et al. (2006); *Nephelomys meridensis*: included within *Oryzomys albigularis* of Linares (1998) and Soriano et al. (1999); see Aguilera, Pérez-Zapata, et al. (1995), Márquez et al. (2000), Percequillo (2003), and Weksler et al. (2006); *Nephelomys* sp.: now included in *Nephelomys* (Weksler et al. 2006); apparently a species distinct from other *Nephelomys* formerly considered part of the *Oryzomys albigularis* complex, based on karyology and morphometric data (Aguilera, Pérez-Zapata, et al. 1995; Márquez et al. 2000); *Sigmodon hirsutus*: *Sigmodon hispidus* of Linares (1998) and Soriano et al. (1999); see Peppers & Bradley (2000); *Transandinomys talamancae*: considered *Oryzomys talamancae* by Linares (1998) and Rivas & Salcedo (2006) and also included within *Oryzomys capito* of Linares (1998); see Musser et al. (1998) and Weksler et al. (2006); *Zygodontomys breviceauda*: from Voss (1991). Note: after this publication went to review, *Marmosa waterhousi* was reported for the Cordillera de Mérida (Gutiérrez et al. 2011).

the Serranía del Litoral and Serranía del Interior, to the exclusion of the Macizo Oriental, which lies to the east of the low and wide Depresión de Unare; furthermore, we exclude the Sierra de Aroa to the west of the Depresión de Yaracuy (Anderson & Gutiérrez 2009). Because we have less confidence in the species lists that include incidentally captured species (see above), we excluded such species from the quantitative biogeographic analyses. However, we provide these additional data to allow a more comprehensive taxonomic and ecological sample and as a baseline for future work.

To examine the relationships between species richness and area in this system, we conducted regressions based on the species–area relationship (Lomolino 2000). First, we regressed log richness on log area for the four ranges, providing a characterization of the relationship for the overall system. Then, we predicted the richness of Cerro Santa Ana based on its area and compared that prediction with its observed richness. To do so, we regressed log richness on log area for the Cordillera de Mérida, Cordillera de la Costa, and Serranía de San Luis and used the results to predict the expected richness of Cerro Santa Ana. Base-10 logarithms were used here (Rosenzweig 1995). Although regressions using information from a larger number of mountain ranges within this system would be desirable, data for other ranges remain lacking. Hence, we interpret the results of the current analyses with caution, especially given the low statistical power afforded by the available data.

Because our analyses concerned species from mesic montane habitats, we estimated the area of such vegetation types for each range. The lower elevational limits of mesic vegetation differ according to range, slope, and exposure (e.g. Massenerhebung Effect; Richards 1952, p. 346–374; Grubb 1977). We approximated the relevant area for each range largely following Ataroff-S (2003). For the three largest ranges, we calculated the area above the elevation representing the average between the estimates for relevant vegetation types (Cordillera de Mérida, 800 m wet slopes, 1600 m dry exposures; Cordillera de la Costa, 400 m northern versant, 900 m southern slope; Serranía de San Luis, 400–700 m). For Cerro Santa Ana, we used the area above 350 m (based on our fieldwork, Appendix 1; Tamayo 1941, 1971). For all calculations, we used the Albers equal-area conic projection of a digital elevation model from WorldClim (Hijmans et al. 2005) in ArcView 3.2.

Complementarily, we performed a series of analyses to assess the level of nestedness of the species in the four ranges. We calculated nestedness for three groupings: all taxonomic groups, rodents alone, and marsupials alone. For each dataset, we used the program

NESTEDNESS to calculate the NODF measure (Nestedness Metric Based on Overlap and Decreasing Fill; Almeida-Neto et al. 2008) using the fixed–fixed sequential-swap option (Ulrich & Gotelli 2007; Ulrich 2008; Ulrich et al. 2009). We then inspected the results to identify the species whose distributions deviate from the observed pattern of nestedness. In cases where the results highlighted cases of closely related species that occupy different mountain ranges (indicative of possible *in situ* speciation), we repeated the analyses considering each pair as a single entity. This determined the degree to which the faunas would be nested when removing the (here assumed) role of *in situ* speciation (Heaney 2000), more directly considering the possible roles of differential immigration and/or extinction in driving distributional patterns in the system.

Results

Fieldwork and sampling completeness

Our fieldwork confirmed the species of small non-volant mammals known previously for Cerro Santa Ana and yielded greatly improved knowledge of the fauna of the Serranía de San Luis (supplementary Appendix S1). Ten species constitute new reports for mesic areas of the Serranía or even larger regions (including identifications of previously reported specimens for three species), as do two from xeric areas, leading to 12 total noteworthy records. Of the small non-volant mammals likely to be captured with our sampling techniques, six species of marsupials (five in mesic habitats, plus one only in xeric areas) and 13 species of rodents (12 in mesic habitats, plus one xeric only) are now documented from the Serranía de San Luis. All species known from Santa Ana inhabit a wide range of elevations in mesic habitat (up to the ridgeline), but marked elevational structuring of species exists in San Luis.

The analyses of sampling completeness indicated that the inventory of Santa Ana is complete but that a few more species likely exist in San Luis (Table 2). In the analysis by day with data for the various traplines on Santa Ana merged, the estimator predicted no additional species. Likewise, the analysis with trapline as the sampling unit did not suggest the capture of any additional species with sampling of other traplines/habitats. In contrast, most analyses of sampling completeness for San Luis predicted the existence of a few undocumented species. For the analyses of individual sites with day as the sampling unit, the mesic highland sites (Cerro Galicia, Haitón, and Uria) were estimated to lack one to three species. For these sites, the 95% CIs were wide and asymmetrical with respect to the mean. This asymmetry indicates a substantially less dense upper tail to the probability

Table 2. Results of analyses of sampling completeness for Cerro Santa Ana and the Serranía de San Luis (either by day of sampling or by site/trapline), indicating predicted and observed species richness. At Santa Ana, estimates matched observed richness closely. At San Luis, analyses generally indicated the possible presence of up to a few additional species for highland sites (Cerro Galicia, Haitón, and Uria) but not for middle-elevation sites (Cabure and Acurigua). See Appendix 1 for descriptions of sampling effort and the habitats at each site. The sample size given (n) indicates the number of days of sampling, or the number of sites/traplines sampled, as relevant for each analysis.

Mountain range	Type of analysis	Trapline or site	Observed richness	Chao2 mean	Chao2 95% CI	n
Cerro Santa Ana	By day	Traplines merged	4	4.0	4.0–4.1	10
	By trapline	n/a	4	4.0	4.0–4.4	6
Serranía de San Luis	By day	Cerro Galicia	5	7.5	5.3–25.6	6
	By day	Haitón	3	3.9	3.1–14.3	7
	By day	Uria	9	10.7	9.2–22.7	6
	By day	Cabure	4	4.0	4.0–5.0	8
	By day (previous fieldwork)	Acurigua	4	4.0	4.0–5.8	8
	By site (including previous fieldwork)	n/a	17	21.8	18.0–39.3	5

distribution, making the likelihood of the true richness occurring near the upper limit of the CI relatively low. Conversely, the two middle-elevation mesic sites (Cabure and Acurigua) had estimates of richness the same as the observed totals. The analysis with sites as the sampling unit implied the existence of a few more species (five); again, the 95% CI for Chao2 was wide and asymmetrical.

Biogeographic analyses

Species richness declines with decreasing area in these sky islands. The regression for all four ranges explained an overwhelming proportion of the variance in richness and was statistically significant ($R^2 = 98.1\%$; $p = 0.010$ for slope; $p = 0.031$ for intercept; $\log \text{ species} = 0.459 + 0.254 [\log \text{ area}]$). The regression for the Cordillera de Mérida, Cordillera de la Costa, and Serranía de San Luis also showed lower species richness with decreasing area but did not reach statistical significance. Nevertheless, it had values for slope and intercept similar to those for the first regression and indicated that area explained a high proportion of the variance in richness among the three ranges ($R^2 = 87.5\%$; $p = 0.230$ for slope; $p = 0.280$ for intercept; $\log \text{ species} = 0.630 + 0.210 [\log \text{ area}]$). It predicted a richness of 5.8 species for Cerro Santa Ana based on its area (higher than the observed richness of four species).

The species in these four sky islands follow strongly nested distributional patterns (Figure 3). For the analysis of all taxonomic groups, the faunas were significantly nested (NODF = 62.27; 95% CI for random null hypothesis, 63.23–65.12; standardized Z score = -3.70). The corresponding analysis for rodents was nearly significant (NODF = 60.43;

95% null CI, 60.16–63.80; $Z = -2.85$), and that for marsupials showed perfect nestedness (NODF = 78.57). Analyses for the perfectly nested marsupials lack meaningful 95% null CIs because of the lack of a “checkerboard” nature to the matrix with the fixed–fixed model (W. Ulrich, personal communication).

Most of the particular species that deviate from the overall pattern of nestedness (idiosyncratic species) are morphologically similar to congeners from the Cordillera de Mérida (and likely closely related to them; Table 1). First, two species of spiny pocket mice (*Heteromys catopterus* and *H. oasicus*) occur on more species-poor ranges (the Cordillera de la Costa and Cerro Santa Ana, respectively). Both are morphologically similar to the widespread *H. anomalus* (especially *H. oasicus*). Next, each of the highland species *Nephelomys caracolus* and *Ichthyomys pittieri* found in the Cordillera de la Costa (and also the Serranía de San Luis, for *N. caracolus*) has a morphologically similar congener in the Cordillera de Mérida. *Sigmodon alstoni* represents the final idiosyncratic species; it principally inhabits lowland and piedmont areas. After considering each of these morphologically similar congeneric pairs (*Heteromys anomalus* and *H. oasicus*; *Nephelomys caracolus* and *N. meridensis*; and *Ichthyomys hydrobates* and *I. pittieri*) as a single entity, the results indicated even higher levels of nestedness, all significant (all taxonomic groups, NODF = 70.09; rodents, NODF = 71.18; marsupials unchanged). Although not perfectly nested, these altered matrices for all taxonomic groups and for rodents alone were so close to that ideal that they displayed the same property with regard to the 95% null CI as the perfectly nested analyses of marsupials above.

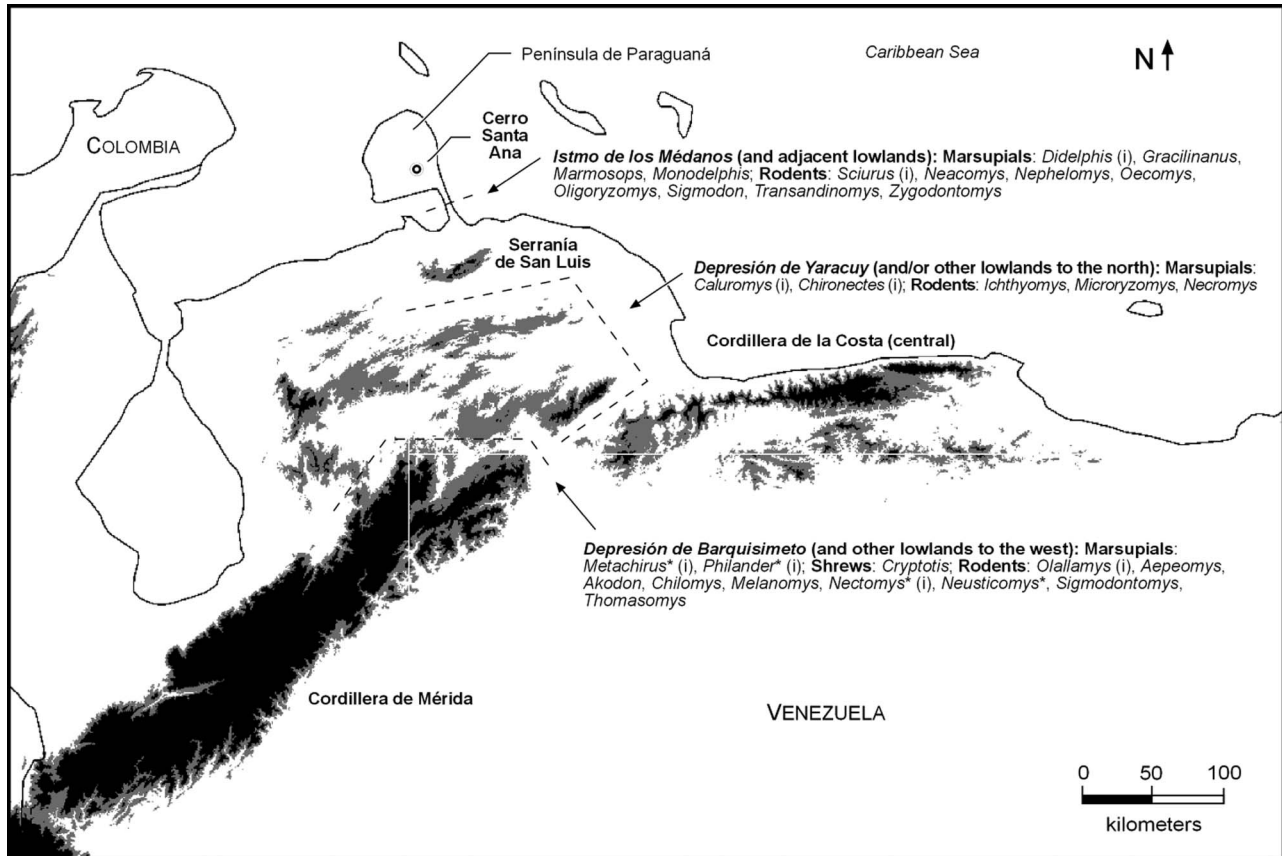


Figure 3. Results of analyses of faunal nestedness of small non-volant mammals in the sky islands of northwestern and north-central Venezuela. Species richness drops with decreasing area and with increased distance from the main body of the Andes along the Colombia–Venezuela border in the southwest. The faunas are highly nested; at each successive lowland depression separating major mountain ranges studied here (Cordillera de Mérida, Cordillera de la Costa, Serranía de San Luis, and Cerro Santa Ana), the genera are listed whose distribution does not extend to the north and/or east. Genera marked with an asterisk also contain species present in northeastern Venezuela, but their placement here corresponds to the distributions of the particular species present in mesic areas of the presently defined sky islands. Genera marked with “(i)” contain species only incidentally captured by our field techniques. Areas ≥ 700 m are shown in gray shading, and regions ≥ 1200 m appear in black.

Discussion

Inventory completeness

Excluding incidentally captured species, the analyses of data from our and prior fieldwork indicate that the list of small non-volant mammals for mesic portions of Cerro Santa Ana is now complete, and that for the Serranía de San Luis is likely nearly so. Considering results for Santa Ana by day of sampling with all traplines merged, it is unlikely that more species exist in addition to the four presently documented there. Similarly, the analysis by trapline suggests that adding more traplines (in macrohabitats as different as those that we sampled) would not lead to the collection of more species. Additionally, our traplines spanned the variety of macrohabitats present on the Cerro (Tamayo 1941), further lessening the possibility of more species. We note, however, that additional species likely are present in xerophytic

thorn forests and other dry habitats found on the lower slopes of the Cerro. Likely candidates consist of *Marmosa xerophila*, *Calomys hummelincki*, and perhaps even *Oecomys speciosus* or the larger (and incidental) *Pattonomys carrikeri* (see Emmons 2005; Sánchez-H & Lew 2012; L. H. Emmons and J. L. Patton, personal communication).

For San Luis, results and interpretations differ between the analyses by day for individual sites and the one by site. Regarding the former, the three highland mesic sites appear to be missing up to a few species, but the middle-elevation mesic sites show inventories that are complete or nearly so. In all cases, previous researchers documented species that we lacked at the highland sites. Additionally, our own fieldwork at other highland sites hints at likely candidates for most or all of the missing species. Complementarily, the analysis by site (including information from previous

collectors) suggests that adding more sites in different habitats and elevations would lead to the collection of a few more species in addition to the 17 presently documented for the Serranía. At least two related reasons make the estimate for the by-site analysis unreasonably high. First, we chose sites to encompass the widest variety of mesic macrohabitats and elevations present in the Serranía. Hence, it is unlikely that more macrohabitats that are as diverse (different) as those that we sampled exist on the Serranía. Second, our non-randomly (overly) diverse sites should tend to lead to overestimates of richness (see Materials and Methods). In conclusion, although a few undetected species are likely to be present on San Luis, the list is sufficiently complete to warrant making biogeographic comparisons, with concomitant caveats to the interpretations.

Biogeography

The small non-volant mammals of this system show a highly nested pattern of distributions, with species richness falling with decreasing area and various taxa dropping out after successive lowland depressions. The regression characterizing the species–area relationship for all four ranges explains an exceptionally high proportion of the variation in species richness among the ranges. Furthermore, the second regression predicts a potential richness for Cerro Santa Ana that is two species higher than the four that actually inhabit it. Nevertheless, these results should be interpreted with caution, due first to the small number of ranges in the regressions, affording low statistical power and reduced precision in the estimates; in addition, if a few additional species inhabit the Serranía de San Luis (as suggested by the analyses of inventory completeness), that would alter the regressions, leading to a higher estimate of potential richness for Santa Ana in the second regression. The phenomenon of even lower empirical richness than that predicted by area for extremely small islands has been characterized in the literature (Lomolino 2000; Lomolino & Weiser 2001) but debated on statistical terms recently (Dengler 2010); often, such patterns have been attributed to the increased importance of stochastic factors, especially extinction.

The analyses of nestedness show that a strong faunal attenuation occurs from the larger to smaller ranges, a gradient that also corresponds to a greater distance from the main body of the Andes. First, several genera reach their easternmost distributions in the Cordillera de Mérida. The most striking examples include characteristically montane groups: three genera of thomomyine rodents (*Aepeomys*, *Chilomys*, and *Thomasomys*; Ochoa-G et al. 2001;

Musser & Carleton 2005) and shrews of the genus *Cryptotis*; but see Woodman (2002). Given intensive sampling in several areas of the Cordillera de la Costa (e.g. Handley 1976; Linares 1998), it seems unlikely that the absences identified here represent artifacts of inadequate sampling, with the possible exceptions of *Cryptotis* (see Woodman 2002) and the rare and incidentally captured *Olallamys* (Nowak 1999). A second, weaker break occurs between the Cordillera de la Costa and the Serranía de San Luis. Conspicuous absences in the Serranía include the montane rodent genera *Microryzomys* and *Ichthyomys*. Nevertheless, additional fieldwork as well as analyses of either inventory completeness or sampling effort (Anderson 2003a) remain necessary to reach firm conclusions regarding the absence of these and other taxa in San Luis. Finally, a remarkable faunal break occurs between the Serranía de San Luis and Cerro Santa Ana on the Península de Paraguaná. Of the taxa likely to be captured with our field techniques, those found on the Serranía but not on the Cerro include three marsupial genera and seven genera of rodents (including five of the tribe Oryzomyini). Notably, two genera of incidentally captured species also drop out here: the large marsupial *Didelphis* and the tree squirrel *Sciurus*. When present, species of these genera are conspicuous to local inhabitants and trained mammalogists alike, making it unlikely that they exist undetected on Santa Ana.

Finer comparisons at the species level indicate that although the overall system is strongly nested, this pattern is driven most strongly by marsupials, whereas a few pairs of congeneric rodents reduce nestedness substantially. Notably, marsupials show a perfect pattern of proper subsets among the four ranges, but that for rodents alone does not quite reach statistical significance. Interestingly, most of the particular species that diverge from the pattern of nestedness (the idiosyncratic species, all rodents) are morphologically similar to a congeneric species present on the Cordillera de Mérida, indicative of putative *in situ* speciation. When considering each of these three pairs as a single entity, rodents (as well as the overall system) demonstrate a highly nested pattern, with only two idiosyncratic species remaining (*Heteromys catopterus* and *Sigmodon alstoni*). We detect no corresponding insinuation of *in situ* speciation in marsupials. However, this may be due to a lack of taxonomic studies of these marsupials. Interestingly, two of the three cases of putative *in situ* speciation in rodents come to light only because of detailed alpha-level taxonomic revisions and karyological investigations (Aguilera, Pérez-Zapata et al. 1995; Márquez et al. 2000; Anderson 2003a; Percequillo 2003). Based on their elevational and habitat requirements, the

marsupials *Marmosops fuscatus*, and to a lesser degree *Gracilinanus marica* and *Marmosa demerarae* (at least for the subspecies present in northern Venezuela), seem especially ripe for renewed taxonomic attention.

Future directions

Our results point to several areas for productive future research in this system. First of all, the low richness, small area, and extreme isolation of Cerro Santa Ana beg for continued analyses assessing the taxonomic status of populations there and examining the factors that may have contributed to such low richness. Second, the distributional patterns on Santa Ana also hint at interesting ecological processes. *Marmosa robinsoni* and *Proechimys guairae* inhabit cloud-forest habitats on the Cerro that they do not occupy in the Serranía de San Luis. This may derive from lowered and compressed vegetational bands (Richards 1952, p. 346–374; Ataroff-S 2003), competitive release, and/or the paucity of predators. Interestingly, we encountered extremely high trap success for *M. robinsoni*, possibly related to the absence of other species in this depauperate community.

Finally, increasing the number of sky islands considered, as well as adding ecological niche modeling and statistical phylogeography, holds great promise in this system. Inclusion of a greater number of sky islands will enhance the detail attainable for the faunal comparisons and should increase confidence in the regressions. More generally, the combination of ecological niche modeling (Peterson et al. 2011) and phylogeographic studies holds great promise for separating ecological and historical drivers of distributional patterns, especially when models are applied to reconstructions of past climates (Martínez-Meyer et al. 2004; Kozak et al. 2008; Carnaval et al. 2009). The sky islands of northern Venezuela seem especially propitious for such research, as a terrestrial exemplar from a near-equatorial region of rugged relief and stark climatic contrasts.

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Appendix 1

Description of field techniques and sites of sampling

We sampled small non-volant mammals at Cerro Santa Ana and the Serranía de San Luis with a variety of baits and traps (mainly Sherman live traps and Victor snap traps, supplemented with National live traps at some sites). At the principal sites, traplines sampled all available macrohabitats (including streams when present) and were composed of traps separated by approximately 10 m. We set traps in all suitable microhabitats; generally, Sherman and National traps were placed on the ground, and most Victor traps were secured to branches and vines 1–2 m above the ground. We employed various baits, including ripe plantains, manioc (cassava), mixed seeds, crabs, sardines, and a mixture made of peanut butter, oatmeal, raisins, vanilla, vegetable oil, and bacon. Sampling at the other sites was less intensive and included subsets of these traps and baits. Principal sites are listed below by ascending elevation within Santa Ana and San Luis, respectively, with the additional sites for each region listed at the end. Total sampling effort included 1118 trap nights at Santa Ana and 2139 trap nights at San Luis (grand total of 3257 trap nights). We took geographic coordinates using a Garmin GPS 12. For each entry, boldface type indicates the place name to which geographic coordinates correspond.

We collected voucher specimens and tissue samples. Additional individuals of common species for which field identification was feasible were noted and released. Voucher specimens are deposited at the Museo de la Estación Biológica de Rancho Grande (EBRG), Maracay, Venezuela and American Museum of Natural History, New York, USA (AMNH; supplementary Appendix S1). Duplicate tissue samples are deposited at the Universidad Simón Bolívar, Caracas, Venezuela and the Ambrose Monell Collection for Molecular and Microbial Research at the AMNH.

Cerro Santa Ana

Falcón: Península de Paraguaná; **Cerro Santa Ana; ca. 4 km N Santa Ana: ca. 270–330 m** (11°48.730' N, 69°56.839' W at middle of trapline). Deciduous forest on southern slope of Cerro. Dense low-canopy forest lacking well-differentiated strata; large terrestrial bromeliads common in some areas; cacti scarce. Goats occasionally present, but other anthropogenic influence limited. 16–20 October 2005; 65 Sherman, 65 Victor; Grand total 130 trap nights.

Falcón: Península de Paraguaná; **Cerro Santa Ana; ca. 4 km N Santa Ana: ca. 350–400 m** (no GPS reading available; ca. 11°49' N, 69°57' W). Mature evergreen forest just above deciduous forest. Much taller trees, often buttressed; sparse understory; humus soil dark and moderately moist, in contrast to lower areas. Human influence low for many decades. 17–20 October 2005; 3–6 August 2006; 76 Victor, 116 National; Grand total 192 trap nights.

Falcón: Península de Paraguaná; **Cerro Santa Ana; ca. 4 km N Santa Ana: ca. 450–500 m** (11°49.183' N, 69°56.669' W at upper end of trapline). Higher area of evergreen forest. Trees shorter and smaller in diameter than lower evergreen forest, but understory denser; some epiphytes present, including bromeliads. Part of area cultivated many decades ago. 15–20 October 2005; 3–6 August 2006; 186 Sherman, 138 Victor; Grand total 324 trap nights.

Falcón: Península de Paraguaná; **Cerro Santa Ana; ca. 4 km N Santa Ana: ca. 520–620 m** (no GPS reading available; ca. 11°49' N, 69°57' W). Dwarf forest along eastern side of Cerro. Short trees (ca. 3–4 m tall); much wetter than lower areas of Cerro; moss and ferns common, with abundant epiphytes, especially bromeliads; lowest area of Cerro showing many characteristics typical of cloud forest, but much shorter than in most cloud forests of northern Venezuela. Mature and nearly pristine. 16–20 October 2005; 3–6 August 2006; 146 Sherman, 40 Victor; Grand total 186 trap nights.

Falcón: Península de Paraguaná; **Cerro Santa Ana; ca. 4 km N Santa Ana: ca. 620–680 m** (11°49.282' N, 69°56.778' W at lower end of trapline). Patch of sedges (Cyperaceae; Tamayo 1971) and shrubs along eastern side of eastern peak (Picacho Buena Vista). Diminutive vegetation, with shrubs not exceeding 2 m, dwarfed by strong, nearly continuous eastern winds. No human intervention apparent. 16–20 October 2005; 3–6 August 2006; 102 Sherman; Grand total 102 trap nights.

Falcón: Península de Paraguaná; **Cerro Santa Ana; ca. 4 km N Santa Ana: ca. 680–700 m** (11°49.250' N, 69°56.803' W at Picacho Buena Vista to 11°49.229' N, 69°57.083' W at western end of trapline). Shrubs along ridge running from easternmost peak (Picacho Buena Vista) towards central peak (Picacho Santa Ana). Shrubs reaching only 1–3 m in height; extremely wet with abundant mosses and palms; ferns and melastomes common; epiphytic bromeliads not as abundant as in dwarf forest. 3–6 August 2006; 164 Sherman; Grand total 164 trap nights.

Falcón: Península de Paraguaná; **Cerro Santa Ana; ca. 3 km N Santa Ana: ca. 200 m** (11°48.352' N, 69°56.667' W). Limited sampling in xerophytic thorn forest on lowest southern slopes of Cerro. Diverse herbs and few cacti in low understory below short trees (primarily legumes of genus *Prosopis*) forming open-canopy thorn forest. Goats common. 16–20 October 2005; 20 Victor; Grand total 20 trap nights.

Serranía de San Luis

El Haitón. Falcón: Serranía de San Luis; Parque Nacional J. C. Falcón; **ca. 8 km W + 1 km N Cabure; Sector El Haitón: ca. 1200 m** (11°08.989' N, 69°41.390' W at El Haitón del Guarataro to 11°08.994' N, 69°41.189' W near end of trapline). Evergreen forest at El Haitón (=El Haitón del Guarataro) near crest of southern ridge of Serranía. Abundant palms, melastomes, and epiphytes. Some secondary forest, but more mature closer to ridgeline. 19–25 April 2006; 310 Sherman, 330 Victor, 4 National; Grand total 644 trap nights.

Cerro Galicia. Falcón: Serranía de San Luis; Parque Nacional J. C. Falcón; **ca. 10 km W + 4 km N Cabure; Sector Cerro Galicia: ca. 1300 m** (11°10.981' N, 69°42.267' W at beginning of trapline to 11°11.154' N, 69°42.064' W at end of trapline). Evergreen forest at Cerro Galicia on northern ridge of Serranía. Abundant mosses and epiphytes, especially bromeliads. Mosaic of secondary cloud forests, shrubby regrowth, and small plots of bananas and coffee. 21–26 April 2006; 160 Sherman, 230 Victor; Grand total 390 trap nights.

Uria: Cumbres de Uria/El Chorro. Falcón: Serranía de San Luis; Parque Nacional J. C. Falcón; **Sector Cumbres de Uria; ca. 9 km N Cabure: 1320–1370 m** (11°13.581' N, 69°36.932' W at western end of trapline to 11°13.541' N, 69°36.840' W toward eastern end of trapline); and Falcón: Serranía de San Luis; Parque Nacional J. C. Falcón; **Sector El Chorro; ca. 9 km N Cabure: ca. 1280–1340 m** (11°13.735' N, 69°37.111' W near stream at beginning of trapline to 11°13.619' N, 69°37.143' W at end of trapline). Evergreen forests at two nearby areas along crest of northern ridge of Serranía (collectively, referred to as Uria). Cumbres de Uria (above hamlets

named *Uria* and *Cumbre de Uria*): dense understory with many ferns, palms, melastomes, and aeroids. Secondary forest (with abundant palms and *Heliconia*) and mature cloud forest with abundant epiphytic bromeliads and orchids. El Chorro (just to northwest): mature cloud forest with abundant palms and epiphytic bromeliads but fewer ferns and orchids and less moss than at Cumbres de Uria. 9–14 August 2006; 264 Sherman, 264 Victor, 15 National; grand total 543 trap nights for Cumbres de Uria; 9–12 August 2006; 108 Sherman, 56 Victor, 9 National; Grand total 173 trap nights for El Chorro.

Limited sampling at four additional sites at lower elevations. Falcón: Serranía de San Luis; **Cabure: 650 m** (11°08.788' N, 69°36.897' W). Southern slope of Serranía on outskirts of town of *Cabure*. Mesic habitats in remnant evergreen forest along permanent stream and in adjacent highly disturbed areas of shrubs and grasses. 19–26 April 2006; 88 Sherman, 53 Victor, 18 National; Grand total 159 trap nights. Falcón: Serranía de San Luis; **ca. La Chapa; ca. 15 km N Cabure: ca. 350–380 m** (11°16.911' N, 69°36.370' W at beginning of trapline). North of hamlet *La Chapa* on northern slope of Serranía. Xerophytic thorn forest; legume *Prosopis*, as well as *Agave* and *Opuntia*, common, with some columnar cacti and spiny terrestrial bromeliads present. 11–15 August 2006; 29 Sherman, 100 Victor; Grand total 129 trap nights. Falcón: Serranía de San Luis; **ca. 4 km S + 3 km W Cabure: ca. 425 m** (11°06.672' N, 69°38.263' W at end of trapline). Foothills south of Serranía near small hamlet *Santa Juana*. Xerophytic thorn forest along dry streambed dominated by short (ca. 2–4 m) legumes and with few *Opuntia* and columnar cacti. 23–25 April 2006; 57 Victor; Grand total 57 trap nights. Falcón: Serranía de San Luis; **ca. 5 km S + 3 km W Cabure: ca. 400 m** (11°06.025' N, 69°38.914' W). Foothills south of Serranía near hamlet *La Encrucijada*. Xerophytic thorn forest in extremely dense mixture of short legumes dotted by occasional cacti, with ground covered by thick, thorny bed of spiny terrestrial bromeliads. 25–26 April 2006; 30 Sherman, 14 Victor; Grand total 44 trap nights.

Gazetteer of sites sampled by previous workers

Sites sampled by previous workers at Cerro Santa Ana and the Serranía de San Luis. Secondary information deriving from sources other than the collector is included in brackets (followed by the source when applicable). Localities in San Luis are arranged by ascending elevation (see Figure 2, where they are plotted). For each entry, boldface type indicates the place name to which geographic coordinates correspond. We estimate that most coordinates are accurate to within at most 5 km (ca. 2 minutes); the placement of “ca.” immediately before the coordinates indicates those accurate to an estimated 6–10 km. See supplementary Appendix S1 for specimens examined.

Cerro Santa Ana

Cerro Santa Ana. Falcón: 49 km N, 32 km W of Coro [=15 km SSW Pueblo Nuevo], **Cerro Santa Ana: 500 m, 520 m, 530 m, 545 m, 550 m, 555 m, 560 m, 565 m, 570 m, 575 m, 580 m, 585 m, 590 m, 593 m, 595 m, 600 m, 605 m, 610 m, 615 m** [11°49' N, 69°57' W; rounded from GPS readings; based on map and description of sampling sites on western slope of Cerro just below Picacho Moruy; N. E. Peterson field notes, 1968; J. O. Matson, pers. comm.]; Falcón: Península de Paraguaná, 15 km SSW Pueblo Nuevo, **Cerro Santa Ana: 575 m, 580 m, 615 m** [same coordinates]; Falcón: **Cerro Santa Ana**, Península de Paraguaná: 300 m, 400 m, 420 m, 450 m, 550 m [11°49' N, 69°57' W; rounded from GPS readings; specimens collected on southern slopes of Cerro, F. J. Bisbal-E., pers. comm.]; Falcón: **Cerro Santa Ana**, Península de Paraguaná: 120 m [precise location on lower slopes of Cerro not available].

Serranía de San Luis

Acurigua. Falcón: **Parque Nacional Juan Crisóstomo Falcón, Sector Acurigua**: 650 m [11°17' N, 69°28' W; MARN (2003); F. Espinoza, in litt.].

Cabure. Falcón: **Cabure**, Sierra San Luis [ca. 11°09' N, 69°37' W; precise area of sampling not available; rounded from GPS reading; DCN (1969)]; Falcón: **Cabure**: 800 m [same coordinates; precise area of sampling not available].

El Haitón. Falcón: Parque Nacional J.C. Falcón, **El Haitón**: 1100 m [11°09' N, 69°41' W; rounded from GPS readings; MARN (2003); DOH [date unknown]; F. Espinoza and A. Lander pers. comm.]; Falcón: Parque Nacional J.C. Falcón, **El Haitón**, Municipio Petit: 1100 m [same coordinates].

San Joaquín. Falcón: **1.3 km SE San Joaquín**, Parque Nacional Sierra de Falcón [= Parque Nacional J.C. Falcón]: 1200 m [11°12' N, 69°35' W; Anderson (2003b); DOH [date unknown]; Falcón: Parque Nacional Sierra de San Luis [= Parque Nacional J.C. Falcón], **1.3 km SE San Joaquín**: 1000–1200 m [same coordinates].

Carrizalito. Falcón: Piedra Preñada, **Carrizalito**, Sierra de San Luis [ca. 1200 m; 11°08' N, 69°45' W; DCN (1969); Aguilera, Reig, et al. (1995)].

Uria: El Chorro/Las Filipinas. Falcón: Parque Nacional Sierra de San Luis [= Parque Nacional J.C. Falcón], **Sector El Chorro, Las Filipinas**: 1300 m [11°14' N, 69°37' W; rounded from GPS readings, adjacent to our fieldwork at Cumbres de Uria and El Chorro].

Cerro La Danta. Falcón: Parque Nacional J.C. Falcón, **Cerro La Danta, N de La Soledad de Uria**, Sierra de San Luis, Distrito Miranda: 1300–1400 m [11°14' N, 69°36' W; Anderson (2003b); DOH [date unknown]].

Cerro Galicia. Falcón: Parque Nacional J.C. Falcón, **Cerro Galicia**, Municipio Petit: 1500 m [11°11' N, 69°42' W; rounded from GPS readings; DCN (1984); MARN (2003); F. Espinoza and A. Lander pers. comm.].

Not located. Falcón: Sierra de San Luis [precise location within Sierra not available].