

ECOGRAPHY

PATTERN AND DIVERSITY IN ECOLOGY



37

AUGUST 2014, no. 8
ISSN 0906-7590



Can biotic interactions cause allopatry? Niche models, competition, and distributions of South American mouse opossums

Eliécer E. Gutiérrez, Robert A. Boria and Robert P. Anderson

E. E. Gutiérrez (*GutierrezE@si.edu*), R. A. Boria and R. P. Anderson, Dept of Biology, City College of the City Univ. of New York, New York, 526 Marshak Science Building, 160 Convent Avenue, NY 10031, USA. EEG and RPA also at: Graduate Center of the City Univ. of New York, 365 Fifth Avenue, New York, NY 10016, USA. EEG also at: Division of Mammals, MRC 108, National Museum of Natural History Smithsonian Inst., PO Box 37012 Washington, DC 20013-7012, USA, and Center for Conservation and Evolutionary Genetics, National Zoological Park, PO Box 37012 MRC 5503 Washington, DC 20013-7012, USA. RPA also at: Division of Vertebrate Zoology (Mammalogy), American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA.

Based on our own empirical data and a literature review, we explore the possibility that biotic interactions, specifically competition, might be responsible for creating, and/or maintaining, geographic isolation. Ecological niche modeling was first used to test whether the distributions of 2 species of Neotropical marsupials (*Marmosa robinsoni* and *M. xerophila*) fit the predicted geographic pattern of competitive exclusion: one species predominates in areas environmentally suitable for both species along real contact zones. Secondly, we examined the connectivity among populations of each species, interpreted in the light of the niche models. The results show predominance of *M. xerophila* along its contact zone with *M. robinsoni* in the Península de Paraguaná in northwestern Venezuela. There, *M. robinsoni* has an extremely restricted distribution despite climatic conditions suitable for both species across the peninsula and its isthmus. The latter two results suggest that *M. xerophila* may be responsible for the geographic isolation of the peninsular populations of *M. robinsoni* with respect to other populations of the latter species in northwestern Venezuela. These results may represent an example of allopatry caused, or at least maintained, by competition. Our results and a review of numerous studies in which biotic interactions restrict species distributions (including at the continental scale) support a previously overlooked phenomenon: biotic interactions can isolate populations of a species. We propose 2 general mechanisms, intrusion and contraction, to classify allopatric conditions caused by various classes of biotic interactions. We present a necessary modification of the concept of ecological vicariance to include biotic interactions as possible vicariant agents regardless of whether genetic differentiation occurs or not.

Despite ongoing debate about species concepts, most researchers agree that the origin of independent lineages under geographic isolation (= allopatry) constitutes the prevalent mode of animal speciation (Salomon 2001, Gavrillets 2003, Coyne and Orr 2004, de Queiroz 2007, Sobel et al. 2009, but see Berlocher and Feder 2002, Fitzpatrick and Turelli 2006). Whether or not speciation occurs, allopatry has implications for population-level divergences by promoting the origin of lineages, or 'evolutionary significant units' (e.g. Holycross and Douglas 2007). As perceived by most authors either explicitly or implicitly, the kinds of barriers that promote vicariance (hence lead to allopatry) are physical or climatic in nature (e.g. see definitions of 'vicariance' and/or 'vicariant agents' in Futuyma 1998, Coyne and Orr 2004, Lomolino et al. 2006). Typical examples include mountain ranges, rivers, and marine transgressions for terrestrial organisms, or the emergence of land bridges bisecting bodies of water for aquatic species. The disappearance of suitable habitat as

a consequence of climatic change can also act as a vicariant agent (Wiens 2004, Kozak and Wiens 2006).

These traditional notions of vicariance do not consider the possibility that geographic isolation – and therefore allopatric speciation – could also be promoted by the emergence and persistence of biotic interactions that act as barriers to dispersal and gene flow. For example, such biotic interactions might include the presence of particularly effective predators or strong competitors, or the absence of important prey or essential mutualistic species. Indeed, biotic interactions commonly affect species ranges, for example causing parapatric ranges (contiguous but non-overlapping; see Lomolino et al. 2006, Peterson et al. 2011, Wisz et al. 2012 and references therein). In contrast, although the possibility that biotic interactions could create and/or maintain allopatry (rather than just parapatry) has been contemplated (Wiens 2004, Waters 2011; see Polechová and Barton 2005 regarding sympatric and parapatric speciation), little empirical evidence exists to support the

idea (but see Jaeger 1971, Pellissier et al. 2012). We address this possibility with regard to interspecific competition, specifically the principle of competitive exclusion – i.e. species that are ecologically very similar will be unable to coexist due to exclusion of the inferior competitor (Gause 1934; see also Hutchinson 1959, Hardin 1960). Furthermore, we address whether competitive exclusion between two species (A and B) could cause the geographic separation of species A into two disjunct allopatric (not parapatric) populations of species A (A1 and A2), with species B present between the subpopulations, A1 and A2.

A battery of technological, methodological, and conceptual advances has empowered researchers to document the role of competition as an important evolutionary force. Empirical evidence demonstrates that interspecific competition is capable of driving phenotypic diversification (Hone and Benton 2005, Moen and Wiens 2009), causing extinctions (Mooney and Cleland 2001, Banks et al. 2008), and shaping both species' distributional ranges (Bullock et al. 2000, Leathwick and Austin 2001, Leathwick 2002, Arif et al. 2007, Wisz et al. 2008; but see Gifford and Kozak 2012) and the composition of communities (Cooper et al. 2008, Kamilar and Ledogar 2011). Additionally, GIS-based ecological niche modeling (ENM; often termed species distribution modeling) allows for testing the geographic predictions of competitive exclusion and release (Anderson et al. 2002; see also Brito and Crespo 2002, Martínez-Freiría et al. 2008, Brito et al. 2011).

Niche theory and the principle of competitive exclusion lead to the following predictions regarding the distributional patterns of a pair of species experiencing competitive exclusion (from Anderson et al. 2002; see Material and methods for assumptions). The first predictions concern areas of potential sympatry – i.e. those with environmental conditions suitable for both species. Specifically, they address the presence of the species along real contact zones, areas where the distributions of both species come into contact. If consistent competitive exclusion of 1 species over the other does not occur, then localities of the 2 species should be present in approximately equal proportions in areas of potential sympatry along real contact zones. Alternatively, if consistent competitive exclusion does occur, then the superior competitor will predominate (in terms of the number of occupied localities) in areas of potential sympatry along real contact zones. Complementarily, if competitive release occurs, the inferior competitor will inhabit broader ecological conditions (more like those characteristic of the superior competitor) in the absence of the other species, whereas the superior competitor would inhabit similar environmental conditions regardless of the presence or absence of the inferior competitor. In addition to considering these hypotheses, we compared prediction strengths (values of predicted suitability) between the models of each species to test if the particular species present is affected by relative environmental suitability, within areas suitable for both species.

To test these hypotheses, the focal species pair must meet certain requirements (Anderson et al. 2002). First, either prior studies or examination of localities should indicate that the species do not co-occur broadly in sympatry, but rather show parapatric distributions with narrow contact zones. This requirement implies that competition may exist and

yield geographic manifestations in their occupied distributional areas. Second, one or more areas of potential sympatry along real contact zones must exist, providing some regions where competitive exclusion could occur. Third, localities for the putative inferior competitor should be known from geographic regions where the putative superior competitor is not present, providing some regions where competitive release could occur. In addition, it is desirable (but not required) that the focal species possess 2 characteristics commonly presented by species involved in strong competition: morphological similarity (Gause 1934, MacArthur and Levins 1967, Abrams 1983 for a review, Juliano and Lawton 1990) and a close phylogenetic relationship (Burns and Strauss 2011, Violle et al. 2011).

We assess whether the distributions of a pair of sister species of small Neotropical mouse opossums (*Marmosa xerophila* and *M. robinsoni*) fit the predicted geographic patterns expected under competitive exclusion. As is the case with other studies based on correlational approaches (Pellissier et al. 2010), our methods cannot conclusively demonstrate competitive exclusion; however, they can generate specific directional hypotheses to be tested in experimental field and laboratory studies (Brown 1971, Murie 1971, Thompson and Fox 1993, LeBrun et al. 2007). If corroborated, such a phenomenon would represent a rare example where a biotic interaction can be demonstrated to contribute to create and/or maintain geographic isolation. This possibility has implications for research regarding population-level divergence, and even speciation itself, as competition might represent a cryptic yet currently overlooked factor driving genetic differentiation. Nevertheless, we do not aim to demonstrate genetic differentiation in any population of our focal species. Rather, this study tests whether the species' distributional patterns relative to environmental suitability are congruent with the expectations under competitive exclusion and whether any such patterns are consistent with isolation of populations of either species. In addition to the implications of this possibility to population divergence and speciation, it also holds relevance in landscape ecology, macroecology, conservation biology, and the effects of climatic changes on species distributions.

Material and methods

Focal species and requirements for tests

Marmosa robinsoni and *M. xerophila* fulfill the requirements for testing the geographic predictions of competitive exclusion: parapatric ranges, overlapping environmental tolerances, and at least 1 known contact zone. As currently understood (Rossi et al. 2010), *M. robinsoni* is found in Panama, Colombia, Venezuela, Trinidad and Tobago, and Grenada. The majority of known records of *M. robinsoni* correspond to xeric shrublands, savannas, and deciduous forests, at elevations from sea level to ca 1200 m; however, the species has also been collected at a few localities with more mesic conditions, and up to 2000 m (Fig. 1; Supplementary material Appendix 1). Furthermore, it inhabits mesic habitat in the tiny, isolated Cerro Santa Ana, on the Península de Paraguaná in northern Venezuela, where

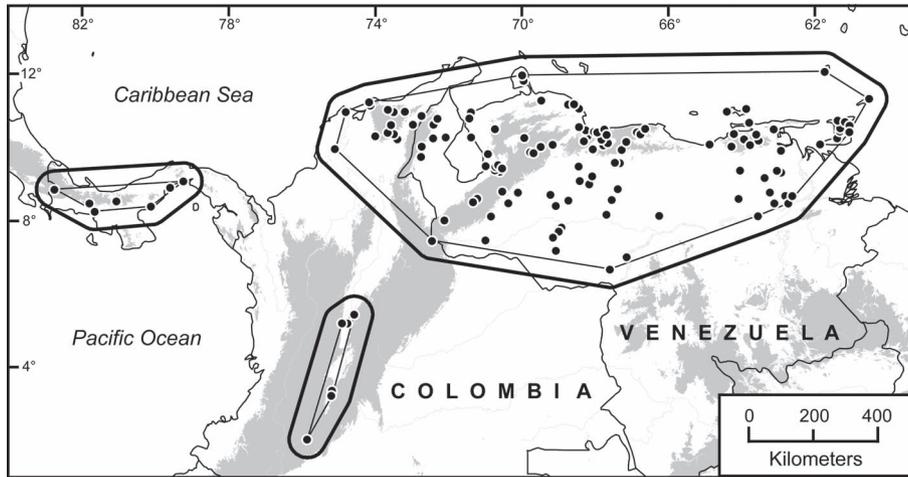


Figure 1. Spatially filtered localities of *Marmosa robinsoni* and study region used to calibrate models of its abiotically suitable areas. For each section of the study region, minimum convex polygons (thin lines) and their corresponding buffer (thick lines) are indicated (Material and methods). Shaded areas represent elevations ≥ 500 m.

a gradient of thorn, deciduous, evergreen, and cloud forests occurs at low elevations (120–700 m; Anderson et al. 2012). The distribution of *M. xerophila* is restricted to xeric shrublands in the lowlands of northeastern Colombia and northwestern Venezuela, at elevations from sea level to ca 350 m (Fig. 2; Anderson et al. 2012). The distributional ranges of these species do not broadly overlap, with only 1 narrow contact zone documented to date: on the Península de Paraganá at the base of Cerro Santa Ana and its immediately surrounding lowlands (ca 80–120 m; Anderson et al. 2012; see also Bisbal-E. 1990; Supplementary material Appendix 1). There, *M. xerophila* is the only species present in the lowlands surrounding Cerro Santa Ana, where *M. robinsoni* exists. In addition, the 2 species are morphologically similar (Rossi et al. 2010), and phylogenetic analyses have yielded evidence of a sister-taxon relationship between them (Gutiérrez et al. 2010). Moreover, *M. robinsoni* and *M. xerophila* appear to overlap broadly

with regard to feeding habits, climatic tolerances, and habitat use (Thielen et al. 1997, 2009, Alvizu and Aguilera 1998, Zambrano 2001). These characteristics make our focal species excellent candidates to test the geographic prediction of competitive exclusion.

Complementarily, this study system allows the test for competitive release for 1 species but not the other. To test the geographic prediction of competitive release, it is necessary to identify biogeographic regions where the other species (putative competitor) is not present. Therefore, conducting such a test for *Marmosa xerophila* is not possible. This is because the entire extent of the distributional range of *M. xerophila* is surrounded by and in close proximity to localities of *M. robinsoni*. Conversely, *M. robinsoni* is indeed known from several regions in which *M. xerophila* is not present – likely due to historical factors – and, therefore, the predicted geographic pattern for competitive release of *M. robinsoni* can be tested.

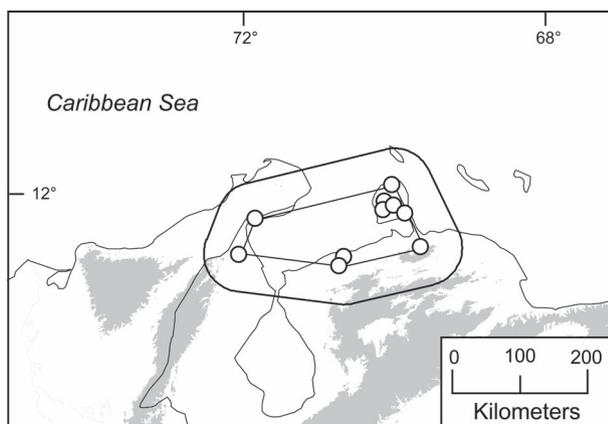


Figure 2. Spatially filtered localities of *Marmosa xerophila* and study region used to calibrate models of its abiotically suitable areas. The minimum convex polygon (thin line) and its corresponding buffer (thick line) are indicated (Material and methods). Shaded areas represent elevations ≥ 500 m.

Data sources

To model the species' abiotically suitable areas (based on climatic data; see Peterson et al. 2011 for terminology regarding ecological niche modeling [ENM]), we used high-quality occurrence localities and climatic data interpolated from weather stations. We gathered localities by using only information from voucher specimens with taxonomic identifications that derive either from our examination (specimens from our fieldwork and in museums in Venezuela) or from a recent revisionary work (Rossi et al. 2010, Gutiérrez et al. 2011; Supplementary material Appendix 1). Several qualitative morphological traits permitted unambiguous taxonomic identifications of these species (Rossi et al. 2010). We georeferenced all localities using information from collectors' field notes, specimen tags, and publications, and then consulting topographic maps, gazetteers, and other sources (see Supplementary material Appendix 1 for sources used for georeferencing each individual record). In addition to georeferencing localities corresponding to specimens that

we identified, we also refined georeferences provided by Rossi et al. (2010). Because georeferencing errors can misinform the algorithms used to create niche models, we discarded localities whose estimated spatial errors exceeded 5 km in mountainous areas with high topographic relief (elevation > 500 m) and 10 km in much more climatically homogeneous lowland areas (elevation < 500 m). Because a maximum possible error of 5 km could potentially include a diversity of habitats in mountain areas, we used topographic and vegetation maps for the specific regions of interest and verified that records with such possible errors were located in montane forest (a well-known habitat type for the species), and that none fell in unreported habitat types for the species (e.g. subpáramo or páramo). The estimated errors of these few records (6 of 175 for *M. robinsoni*; none for *M. xerophila*) were more a linear distance through areas with similar elevations rather than a radius; therefore, we do not expect that these records provide a signal that would mislead model calibration despite the fact that the environmental variables had a finer resolution [although with unquantified error (Hijmans et al. 2005, Anderson and Raza 2010, p. 1382)]. All other records had either smaller georeferencing errors or were located in lowlands with homogenous climatic conditions (e.g. the Venezuelan Llanos). Overall, our georeferencing yielded a dataset with smaller estimated errors than those typically used in ENM analyses (unpubl., Yesson et al. 2007, see also Costello et al. 2013, pp. 2–3).

Because clusters of localities – typically resulting from more sampling in areas easily accessible to researchers (Reddy and Dávalos 2003, Hortal et al. 2008) – might create bias in environmental space, we spatially filtered localities of each species to obtain the maximum number that were at least 10 km apart (following Anderson and Raza 2010, Boria et al. 2014). When multiple equally optimal solutions were possible for a given cluster of localities, we retained the combination of localities with the lowest possible total georeferencing error. Final (filtered) datasets contained 133 unique localities for *M. robinsoni* and 10 unique localities for the geographically restricted *M. xerophila* (Supplementary material Appendix 1). Despite the latter having a low number of unique localities, these records cover the entire known distribution of *M. xerophila* (see Pearson et al. 2007 for building and evaluating models with few localities; see also Shcheglovitova and Anderson 2013; Supplementary material Appendix 2).

For the environmental data, we used 19 bioclimatic variables from WorldClim 1.4 (Hijmans et al. 2005; <<http://biogeoberkeley.edu/worldclim/worldclim.htm>>, at 30'' resolution; $0.93 \times 0.93 \text{ km} = 0.86 \text{ km}^2$ at the equator). The bioclimatic variables employed are based on mean monthly climatic data and reflect various aspects of temperature, precipitation, and seasonality. They likely are important in determining species distributions and have been used for small non-volant mammals in the region (Anderson and Raza 2010, Anderson and Gonzalez 2011).

Study region

We selected study regions based on the principles from the literature (Anderson and Raza 2010, Barve et al. 2011,

Peterson et al. 2011, Anderson 2012) and using a set of simple operational rules. For each species, we created minimum convex polygons surrounding major groups of localities, and then delimited regions for background selection by setting buffers of 0.5° around each polygon. Extensive fieldwork in numerous areas and biomes of southern Central America and northern South America over the last century (see Rossi et al. 2010 and references therein) show that localities of *Marmosa robinsoni* are geographically distributed in 3 major groups. Consequently, the study region for this species was comprised of 3 sections: one enclosing localities from northeastern Colombia, northern Venezuela, and the islands of Trinidad, Tobago, and Grenada; another for localities from the upper valley of the Río Magdalena in Colombia; and a third containing localities from Panama (Fig. 1). Only 1 polygon (and its corresponding buffer) was needed to create the study region of *M. xerophila* (Fig. 2).

Model calibration and evaluation

To model the species' abiotically suitable areas, we employed Maxent ver. 3.3.3h, which implements the maximum entropy method (Phillips et al. 2006, Phillips and Dudík 2008). This presence-background modeling technique has performed well in comparisons with other such techniques (Elith et al. 2006, Hernandez et al. 2006, Wisz et al. 2008; see also Phillips 2008). When calibrating models for each species, Maxent sampled background data of environmental variables only from the respective study region (i.e. within the minimum convex polygons and their respective buffers) by use of a mask as a dummy variable. To produce the best possible models – i.e. those with optimal complexity, which implies the best approximation to reality with the least degree of overfitting – we tuned model settings (Elith et al. 2010, Anderson and Gonzalez 2011, Warren and Seifert 2011) using preliminary models of each species, and then making final models using all localities (and the settings selected as optimal during the tuning process). Specifically, we varied feature classes and regularization multipliers and selected the combination with the highest performance (Supplementary material Appendix 2).

We employed threshold-independent and threshold-dependent measures to evaluate preliminary-model performance according to 2 criteria: 1) the degree to which they avoided overfitting and 2) their discriminatory power (Radosavljevic and Anderson 2013, Shcheglovitova and Anderson 2013; Supplementary material Appendix 2). Additionally, we assessed the statistical significance of a subset of the preliminary models. Specifically, we did so for replicates that corresponded to the feature class and regularization multiplier combination that yielded optimal performance in the tuning experiments. Additionally, we visually inspected geographic projections of preliminary models made with those settings. Then, to calibrate final models, we used the settings identified as optimal in the tuning exercises, now employing all of the filtered localities available for each species. Lastly, we examined the multivariate environmental similarity surfaces produced by Maxent to determine whether in any areas the environmental variables were outside the range present in the calibration study regions

(Elith et al. 2010). If so, we examined the map (produced by Maxent) showing the degree of ‘clamping’ – i.e. constraining feature values to remain within the range in the calibration data; see Anderson and Raza 2010, Elith et al. 2011, Anderson 2013 – to determine if this situation had a strong effect on the model predictions.

Tests of competitive exclusion and release

We projected the final model for each species onto geographic space to identify their respective abiotically suitable areas as well as areas of potential sympatry. These projections were made onto the rectangular region (extent 10–13°N and 60–76°W) that included the northcentral and northeastern portion of the known range of *Marmosa robinsoni* and the entire range of *M. xerophila*. To identify areas of potential sympatry within this region, we then superimposed the binary predictions of both models, using the same thresholding rule as in the model evaluations.

We analyzed the proportions of species localities in areas of potential sympatry along their known contact zone, directly testing the geographic patterns predicted under competitive exclusion (Anderson et al. 2002). To do so, we used localities in the Península de Paraguaná and the isthmus connecting it to the ‘mainland’, areas that surround the known contact zone. We tested for the patterns expected for competitive exclusion under 2 approaches: first, 1 species consistently predominates (using binary maps of suitable vs unsuitable environmental conditions) in terms of the number of unique localities; second, each species predominates wherever environments are more suitable for it than for its putative competitor (considering maps of suitability for each species). In the first approach, if neither species consistently excludes the other, localities of the 2 should be present in approximately equal proportions in areas of potential sympatry along their real contact zone. This approach rests on 2 assumptions: a) the 2 species have identical requirements and preferences with regard to resources in the study region; b) both species are equally likely to be captured, if present, by the sampling methods used. Given their close phylogenetic relationship and similar morphologies, our focal species are likely to have highly similar requirements and preferences regarding resources in the study region (see Introduction). Also, based on known natural history information (Handley 1976, Thielen et al. 1997, Alvizu and Aguilera 1998, Zambrano 2001, Rossi et al. 2010, Anderson et al. 2012), the latter assumption seems reasonable for our focal species. Deviations from expected values generated from overall proportions of filtered localities were determined using 2-tailed tests (exact binomial probability). However, we made an improvement to the method proposed by Anderson et al. (2002) that allowed us to avoid bias towards the most broadly distributed species. To do so, rather than using all records in all areas of potential sympatry (some of which are not accessible for *M. xerophila*), we calculated the expected values of locality records based only on the number of records of each species in the greater Maracaibo Basin (Fig. 3c). This region is accessible for both of the two species – i.e. no prominent geographic barriers there prevent dispersal of

either species. In other words, we were conservative (and much more realistic) by calculating expected values based only on the numbers of known localities in the greater Maracaibo Basin (27 for *M. robinsoni* and 10 for *M. xerophila*). For the second approach, we examined localities in areas of potential sympatry surrounding the known contact zone in more detail, determining for each pixel which species had higher values of predicted suitability. Here, we expect that the species present is the one with the higher predicted value of suitability, regardless of whether the difference in prediction strengths is large or small (following Anderson and Martínez-Meyer 2004). This expectation rests on 2 assumptions: the first assumes that a putative superior competitor will exclude the other species from areas even minimally more suitable for the former; the second assumption implies that the models accurately characterize the abiotic abiotically suitable areas of each species.

We also tested for the geographic prediction of competitive release for *Marmosa robinsoni* (test not possible for *M. xerophila*; see above). To do so, we inspected areas of potential sympatry far from the known contact zone between the species. Specifically, we searched such areas for the localities of *M. robinsoni* in areas more strongly predicted for *M. xerophila*.

Results

Models and regions of potential sympatry

Given the known (documented) distributions of the species and available natural history information, the final models provided reasonable predictions of abiotically suitable areas. The final model of *Marmosa robinsoni* predicted extensive areas as suitable for the species (Fig. 3a). Strong predictions largely corresponded to regions harboring dry habitats, including xeric shrublands, savannas, and deciduous forests; however, a few areas with more mesic conditions were also predicted as suitable (e.g. lowland rainforest on the islands of Trinidad and Tobago). The final model of *M. xerophila* predicted as suitable various regions harboring dry habitats, essentially xeric shrublands, with stronger predictions close to the coastline (Fig. 3b).

Once overlapped, the models indicated potential sympatry in several regions (Fig. 3c). These regions are the northern extreme of the Península de La Guajira in northeastern Colombia; extensive areas of the Estado Falcón in northwestern Venezuela, including most of the Península de Paraguaná; the Península de Araya in northeastern Venezuela; and the islands of Aruba, Curaçao, Bonaire, Margarita, Tobago, St Lucia, Barbados, and some smaller islands nearby. For *Marmosa robinsoni*, examination of the multivariate environmental similarity surface and the map showing the degree of clamping indicated the lack of areas where environmental variables were outside the range present in the calibration region (not shown). For *M. xerophila*, the multivariate environmental similarity surface showed a few variables with values outside the range present in the calibration data, but the degree of clamping was minimal (not shown).

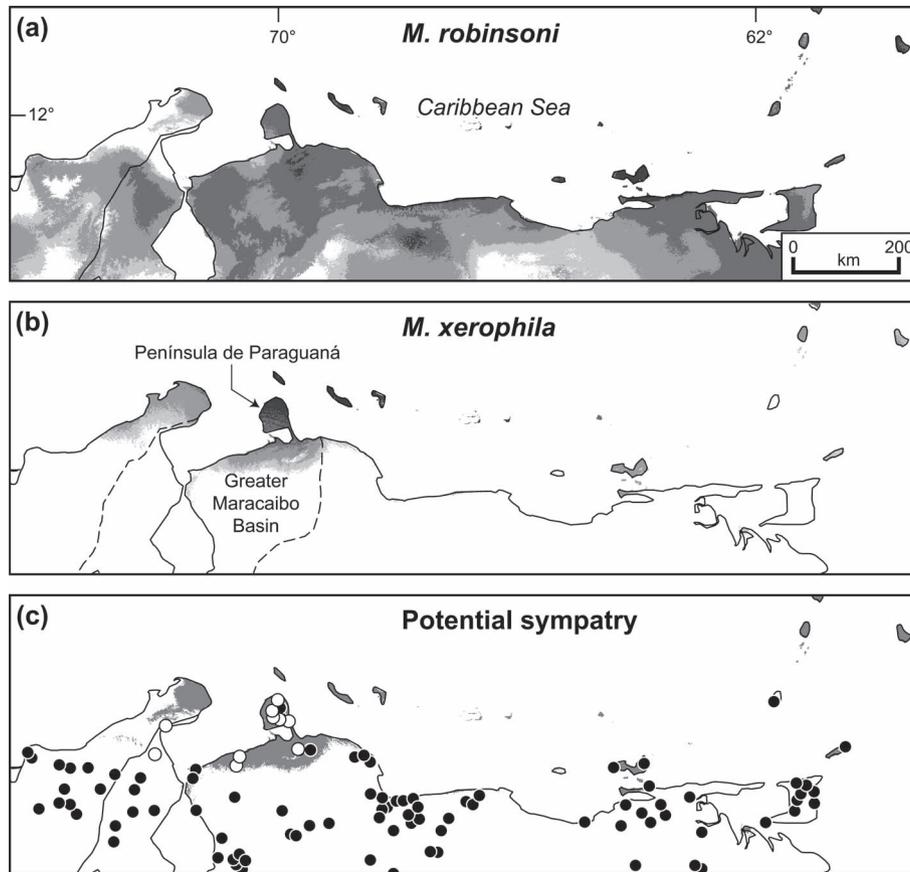


Figure 3. Results of ecological niche models, shown in northcentral South America and adjacent Caribbean islands: (a) final Maxent model of abiotically suitable areas for *Marmosa robinsoni*; (b) final Maxent model of abiotically suitable areas for *M. xerophila*, and (c) areas of potential sympatry for both species. Abiotically suitable areas (given the 10th percentile threshold; Supplementary material Appendix 2) are indicated with shades of gray; increasingly stronger predictions are indicated with progressively darker shades. Areas of potential sympatry are those where suitable environmental conditions exist for both species. The dashed line in (b) indicates the approximate limits of the greater Maracaibo Basin within this study region; the Basin is limited to the west by the Serranía de Perijá, to the north by the coastline, and to the south by the Cordillera de Mérida (not shown). Black circles represent localities of *M. robinsoni*; white circles represent localities of *M. xerophila*.

Tests for competitive exclusion and release

Marmosa xerophila predominated in areas of potential sympatry along its known contact zone with *M. robinsoni* (Fig. 3c; Supplementary material Appendix 1). Given their frequency overall in the greater Maracaibo Basin, the number of occurrences expected by chance on the Península de Paraguaná was 5 for *M. robinsoni* and 2 for *M. xerophila*. However, the observed localities on the peninsula – 2 for *M. robinsoni* and 5 for *M. xerophila* – deviated significantly from the theoretical expectation (binomial probability, $p = 0.016$).

On the Península de Paraguaná, in areas of potential sympatry surrounding the known contact zone, localities of each species fell in either areas (pixels) more strongly predicted for that same species or extremely close to them (i.e. in adjacent pixels; see below). *Marmosa xerophila* was more strongly predicted throughout most of the Península de Paraguaná, whereas *M. robinsoni* was more strongly predicted in only 2 areas of the peninsula: the Cerro Santa Ana and the Fila de Monte Cano (Fig. 4). All 5 peninsular localities of *M. xerophila* fell in areas more strongly predicted

for that species. The 2 peninsular localities of *M. robinsoni* corresponded to sites barely more suitable for *M. xerophila* (at Fila de Monte Cano, locality 101; and Cerro Santa Ana, locality 100; Supplementary material Appendix 1; Fig. 4; Supplementary material Appendix 3, Fig. A7). However, the 2 records fell in pixels adjacent to 1 or more pixels more strongly predicted for *M. robinsoni*. In the case of the record from Fila de Monte Cano, this exceptional locality corresponds to a tiny area of gallery forest habitat along a stream (J. Ochoa-G. in litt.), a case of local conditions not reflected in the climatic variables employed here (Soley-Guardia et al. in press; see Austin and Van Niel 2011). In the case of the record in the lower part of Cerro Santa Ana, the presence of this species in the Cerro Santa Ana has been demonstrated with numerous records at various elevations (Anderson et al. 2012) that indeed fall in areas more strongly predicted for that species, but these records were excluded from the model calibration process because of the filtering procedure that we accomplished to reduce the effects of sampling bias (Material and methods).

These results suggest that *Marmosa xerophila* may be a superior competitor to *M. robinsoni* in most of the areas

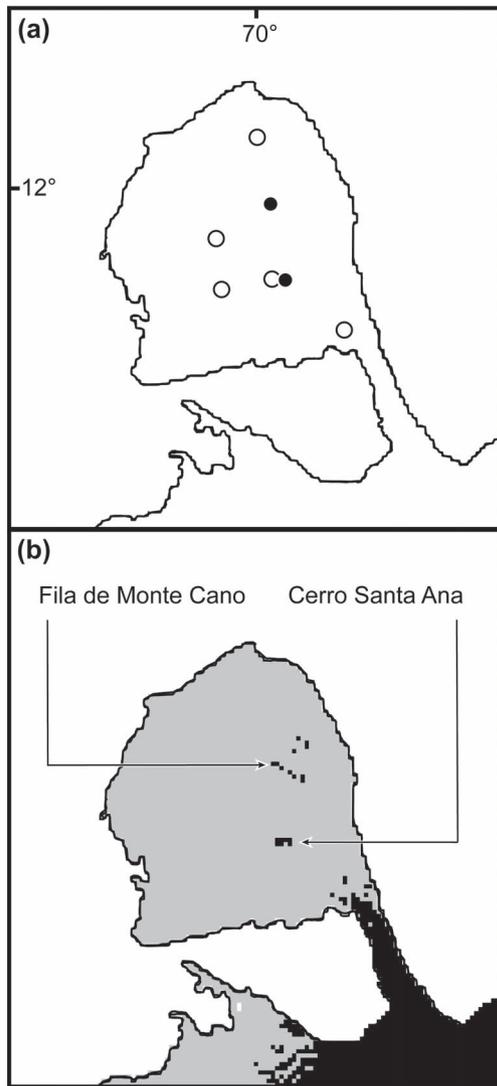


Figure 4. Areas of potential sympatry for *Marmosa robinsoni* and *M. xerophila* in northern Estado Falcón (Venezuela) showing areas more strongly predicted for each species. (a) Occurrence records of focal species. Black circles represent localities of *M. robinsoni*; white circles represent localities of *M. xerophila*. (b) Pixels more strongly predicted suitable for either species: pixels in which the species that had higher suitability values was *M. robinsoni* are indicated with black shading, whereas pixels in which the species with higher suitability values was *M. xerophila* are indicated with grey shading. Notice the two geographic features more strongly predicted for, and occupied by *M. robinsoni* (Cerro de Santa Ana and Fila de Monte Cano) in the Península de Paraguaná. Populations of *M. robinsoni* present at these geographic features are isolated from areas with similar environmental conditions on the adjacent mainland by areas more strongly predicted for, and occupied by, *M. xerophila*.

that are suitable for both species in the Península de Paraguaná. In fact, areas on the peninsula suitable for and occupied by *M. robinsoni* appear to be disjunct from populations found in suitable areas on the mainland not because intervening regions harbor unsuitable climatic conditions, but rather because they constitute environments even more suitable for and occupied by *M. xerophila*. In contrast, the models (and available locality records) did not provide

strong evidence for competitive release. In regions far from the range of *M. xerophila*, few localities of *M. robinsoni* exist in regions of potential sympatry. However, none of those sites was more strongly predicted for *M. xerophila* (a strict test of the hypothesis of competitive release). Nevertheless, *M. robinsoni* is commonly found in highly xeric habitats (typical of *M. xerophila*) in regions where *M. xerophila* is absent (Fig. 5), but overall it occupies more mesic conditions in regions where *M. xerophila* also occurs (Fig. 4; Supplementary material Appendix 3, Fig. A7).

Discussion

Competitive exclusion and allopatry

The results suggest that competition may maintain (and may even have created) allopatric conditions among populations of *Marmosa robinsoni* on the Península de Paraguaná and those on the adjacent mainland. If so, to our knowledge this study documents 1 of only 2 cases of such a phenomenon in the literature (Jaeger 1971). Nevertheless, we clarify that a similar phenomenon, competition maintaining interspecific parapatric ranges, is well documented in the literature (Lomolino et al. 2006, Peterson et al. 2011, Wisz et al. 2012 and references therein). The statistically significant predominance of localities of *M. xerophila* in areas of potential sympatry along its known contact zone with *M. robinsoni* is congruent with the prediction of competitive exclusion. Furthermore, it suggests that *M. xerophila* may be a superior competitor in most areas suitable for both. The latter is consistent with a previous study that provided support to the hypothesis that geographically restricted species of small mammals are competitively dominant over related widespread species (Glazier and Eckert 2002). However, in the 2 *Marmosa* studied here, the outcome of the competition (i.e. which species becomes excluded) appears to depend on the relative suitability of environmental conditions at each site. Each species seems to be a superior competitor at sites more strongly predicted as suitable for that species.

Specifically, close examination of the Península de Paraguaná revealed the striking existence of small areas more strongly predicted for *Marmosa robinsoni* embedded within a matrix of sites with more suitable conditions for (and occupied by) *M. xerophila* (Fig. 4; Supplementary material Appendix 3, Fig. A7). These ‘islands’ more favorable for *M. robinsoni* corresponded to the Cerro de Santa Ana and the Fila de Monte Cano, each of which harbors localities of *M. robinsoni*. The possibility that competition may maintain (and possibly may even have created) allopatric conditions for populations of *M. robinsoni* is supported by 3 observations: 1) the models identified suitable conditions for both species in the peninsula, the adjacent mainland, and the isthmus connecting the 2; 2) in geographic regions where *M. xerophila* is absent, *M. robinsoni* is commonly found in xeric habitat, perhaps as a result of competitive release; 3) in the relatively well-sampled Península de Paraguaná (where both species are present), *M. xerophila* is always present in sites more strongly predicted suitable for it,

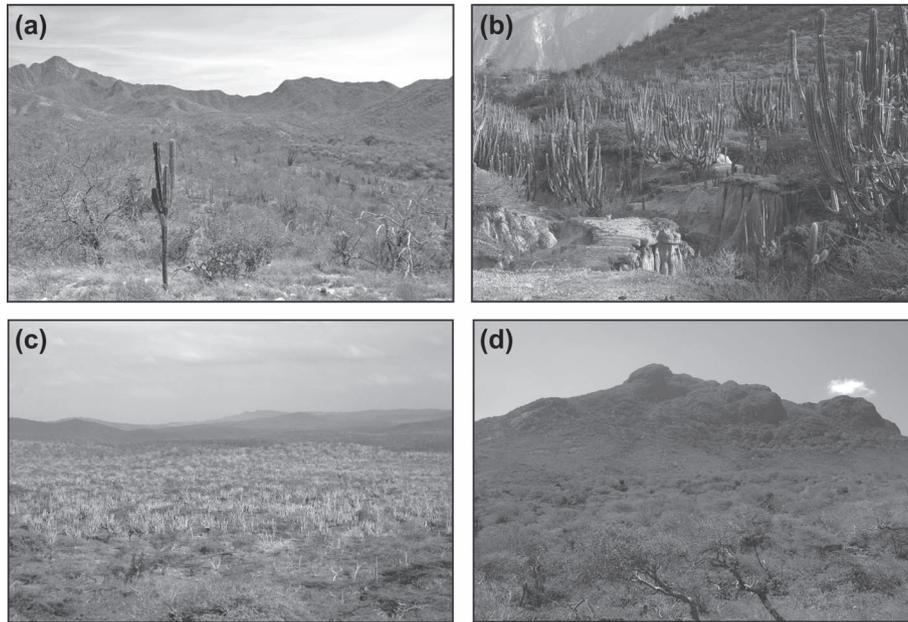


Figure 5. Examples of Venezuelan regions with suitable conditions for both of the focal species but occupied by *Marmosa robinsoni*. The first three represent xeric landscapes in areas far from the documented distribution of *M. xerophila*. The last constitutes a more mesic area along the documented zone of contact with *M. xerophila*. (a) Península de Macanao, Isla de Margarita (Estado Nueva Esparta; photo by Jesús Molinari). (b) Near Lagunillas (Estado Mérida; photo by Pascual Soriano). (c) Near the southern versant of the Serranía de San Luis (Estado Falcón; photo by Robert Anderson). (d) Cerro Santa Ana, Península de Paraguaná and adjacent lowlands (Estado Falcón; photo by Robert Anderson). At the first three sites (in biogeographic regions where *M. xerophila* is not present), *M. robinsoni* is commonly found in xerophytic shrublands. In contrast, on the Península de Paraguaná, *M. robinsoni* occurs predominately in the more mesic habitat in Cerro Santa Ana, likely due to exclusion from the xeric lowlands by *M. xerophila*.

whereas *M. robinsoni* is restricted to more mesic areas on Cerro Santa Ana and the Fila de Monte Cano.

Revisiting the concept of ecological vicariance

The possibility of allopatry driven by a biotic interaction could have strong implications for studies of population differentiation and even speciation, as similar cases might be taxonomically and geographically widespread (see below). This invites a reconsideration of the mechanisms that lead to ecological vicariance. As conceived by most authors, ecological vicariance is currently understood as the result of intrinsic organismal response to large-scale ecological variation, via the fragmentation of a single population into areas divided by ecologically, but not physically, unsuitable habitat (Pyron and Burbrink 2010; see also Haffer 1969, 1997, 2008, Vuilleumier 1971, Cracraft and Prum 1988, Hardy and Linder 2005, Escudero et al. 2009). Whereas this mechanism indeed leads to geographic isolation (Moritz et al. 2000, Wiens 2004, Kozak and Wiens 2006, Waltari et al. 2007), we argue that limiting the notion of ecological vicariance only to those cases in which large-scale habitat-related changes have occurred excludes the possibility that important (likely local-scale; Peterson et al. 2011) biotic interactions might also isolate populations in the absence of physical or habitat-related barriers. In fact, we argue that biotic interactions are capable of creating and maintaining geographic isolation at a local scale (i.e. at particular sites), and also likely across a larger geographic extent (e.g. along

extensive portions of their distributions). This redefinition of ecological vicariance should not be confused with the term soft vicariance, which applies to cases in which isolation is incomplete, regardless of whether the implied barrier is physical, climatic or, as suggested in the present study (see below), driven by a biotic interaction (Fransen 2007, see also Fransen 2002, Hickerson and Meyer 2008; not Pyron and Burbrink 2010).

The possibility that biotic interactions could create or maintain allopatry is indirectly, but unequivocally supported by results of numerous studies that have shown that such interactions can affect species' distributions even at a large geographic scale (see Wisz et al. 2012 for a review). Studies have documented that local interspecific competition between plant species can lead to extirpation of populations at a large scale (Bullock et al. 2000, Leathwick and Austin 2001). Similarly, some displacements of animal species have been shown to occur as a result of either the invasion or the introduction of superior competitors (Reitz and Trumble 2002, Bertolino 2008). Competition has also been implicated in maintaining parapatric range boundaries at a large scale (Anderson et al. 2002, Lomolino et al. 2006, Peterson et al. 2011, Pasch et al. 2013), possibly being a particularly important phenomenon in suture zones (Swenson 2006, Sacks et al. 2011) – i.e. in areas of contact between recently joined biotas (Remington 1968). Furthermore, a number of studies on aquatic organisms have documented the existence of phylogenetic divergences between parapatrically distributed taxa, even in cases in which the implied taxa have remained parapatrically distributed for long periods of

time and in the face of high dispersal potential (Waters 2011 and references therein). According to Waters (2011), this likely is explained by a density-dependent competitive effect, in which dispersing individuals represent a tiny minority relative to the resident population, and might be selected against because of their rarity.

Other negative biotic interactions – parasitism and predation – also are capable of affecting species’ distributions either by themselves or in interplay with competition. One example of the latter is the parasite-mediated competition between *Anolis* lizards in the island of St Maarten (Schall 1992). In addition, it is well known that the distributions of parasites and predators can be modified – reduced, expanded, or fragmented – by virtue of changes in the distributions of their hosts and prey (Anderson 1972, Case et al. 2005, Holt and Barfield 2009, Kelehear et al. 2012). Inversely, the distributions of prey and hosts can be severely constrained by the presence of generalist predators and parasites (Grinnell 1917, Holt 1997, Alexander et al. 2007; but see Holt et al. 2011).

Positive interactions, be they mutualism or facilitation, can also affect species distributions, as the range of the

beneficiary species might be modified as a consequence of changes in the range of benefactor species (Bertness and Callaway 1994, Bond 1994, Choler et al. 2001, Bruno et al. 2003, Pauw and Bond 2011, le Roux et al. 2012). For example, species-specific facilitation among epiphytes and trees suggests that epiphyte distributions can be strongly influenced by tree distributions (Callaway et al. 2002). Similarly, for lycaenid butterflies that have mutualistic interactions with ants, mutualistic relationships not only can affect species distributions, but also promote allopatry (Pellissier et al. 2012). Finally, paleontological evidence also suggests that biotic interactions have shaped species ranges at a large scale in the past, and for long periods of time (see Wisz et al. 2012 and references therein). In summary, a plethora of cases in which biotic interactions affect species distributions – at spatial scales from local to continental – have been documented; hence, the idea that such interactions could create and/or maintain allopatry should be seen as likely to be taxonomically and geographically widespread.

Two major classes of mechanisms explain how biotic interactions can lead to allopatry. In the first, which we term intrusion, the arrival of a species (e.g. invasive species) into

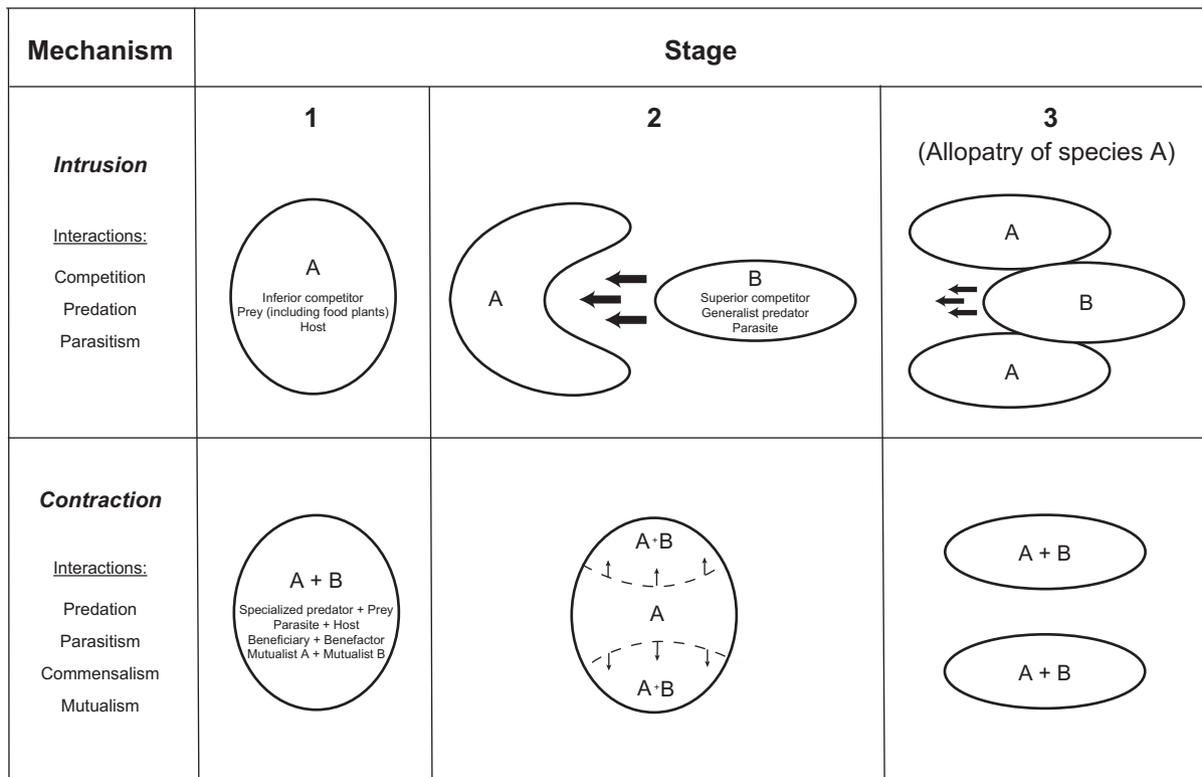


Figure 6. Schematic view of the classes of mechanisms by which biotic interactions can lead to allopatry. Species A experiences division of its original range as a consequence of its interaction with species B, and its resulting distributional areas are allopatric. Range intrusion: the intrusion of species B into the range of species A causes the disappearance of species A in the area newly occupied by species B; the driving biotic interactions include competitive exclusion (species A being an inferior competitor to species B), predation (species A being the prey of species B, a generalist and highly effective predator of species A), and parasitism (species A being the host of species B, a generalist and lethal parasite). Range contraction: the contraction of the range of species B causes the concomitant reduction of the range of species A, which becomes divided; the driving biotic interactions include predation (species B being the prey of species A, a predator specialized on species B), parasitism (species B being the host of species A, a specialized parasite), commensalism (species B being the benefactor of species A, a specialized commensalist), mutualism (species B being an obligate mutualist of species A). Each mechanism follows the same progression. Stage 1: before the biotic interaction had a disruptive effect on the range of species A; stage 2: biotic interaction divides the range of species A; stage 3: allopatry in species A resulting from the interaction between the two species. For simplicity, the term predation in this figure includes phytophagy.

the range of another causes the disappearance of the latter in the area newly occupied by the arriving species. This can occur when the arriving species is a superior competitor to, a generalist and highly effective predator of, or a generalist and lethal parasite of the species whose range becomes divided (Fig. 6). In the second, which we term contraction, the reduction of the range of 1 species causes the concomitant division of that of another species. This mechanism can act when the species that experiences the original range reduction is the prey of a specialized predator, the host of a specialized parasite, the benefactor of a specialized commensalist (beneficiary), or the obligate mutualist of the focal species (Fig. 6).

Together with findings from 2 previous studies (Jaeger 1971, Pellissier et al. 2012), our results imply that biotic interactions have the potential to directly promote genetic differentiation, and eventually speciation via geographic isolation. This possibility depends at least on the degree by which biotic interactions prevent gene flow between the populations involved, and on the length of time these interactions operate. Analogous to speciation events regarding insular populations far from continents (Heaney 2000, Whittaker et al. 2008, Kisel and Barraclough 2010), low levels of gene flow and long periods of isolation caused by biotic interactions would promote speciation. Given the dynamic nature of biotic interactions, it is expected that often they will not persist as long as some physical or habitat-related barriers; however, some might still prevent gene flow long enough to lead to speciation. Thus, biotic interactions represent alternative causal explanations for divergence events in phylogeographic trees that cannot be plausibly explained by geologic or other habitat-related events. Transferring models to different climate scenarios is challenging, ideally requiring previous cross-space demonstrations of transferability in present-day climatic conditions (Araújo and Rahbek 2006, Radosavljevic and Anderson 2013). Although such tests are not realistic in our study given the restricted distribution of *M. xerophila*, projections of ecological niche models onto reconstructions of past climatic scenarios could be helpful to investigate the possible role of competition not only maintaining but also creating allopatry (i.e. acting as a vicariant agent). More importantly, projections of these models onto future climatic scenarios – along with further methodological developments to study species interactions (Wisz et al. 2012, Blois et al. 2013) – should prove insightful to study future species distributions, risks of extinction, and speciation via allopatry (Memmott et al. 2007, Hegland et al. 2009, Aguirre et al. 2011, Norberg et al. 2012, Anderson 2013).

Acknowledgements – We thank the curators and support staffs of institutions that allowed access to voucher material, especially Nancy Simmons, Robert Voss, Patricia Brunauer, and Eileen Westwig (AMNH); Pascual Soriano (CVULA); Francisco Bisbal-E. and Javier Sánchez-H. (EBRG); Carmen Ferreira, Sandra Giner, and Mercedes Salazar (MBUCV); Belkis Rivas (MHNLS); and Michael Carleton, Alfred Gardner, Linda Gordon, and Kristofer Helgen (USNM). Amy Berkov, Corentin Bohl, Sharon Jansa, Jason Munshi-South, Aleksandar Radosavljevic, Ali Raza, Mariano Soley-Guardia, and Robert Voss read one or more versions of this manuscript and made helpful comments. Similarly, Sara Varela,

and our subject matter editor, Douglas Kelt, who remained anonymous during the review process, provided comments that improved the quality of the manuscript. Jesús Molinari and Pascual Soriano provided habitat photographs. Franziska Bauer provided critically relevant literature and assisted with Fig. 3. This work was funded, in part, by awards provided to EEG from the American Museum of Natural History (Theodore Roosevelt Memorial Fund), the City College of City Univ. of New York (Graduate Student Award), and the American Society of Mammalogists (Grants in Aid of Research), as well as by National Science Foundation grants DEB-0717357 and DEB-1119915 (both to RPA), DEB-743062 (to Sharon Jansa), and DEB-743039 (to Robert Voss). Additional support to EEG was provided by the Graduate Center of the City Univ. of New York (Science Fellowship, University Fellowship, Tuition Fellowship, and Sue Rosenberg Zalk Student Travel and Research Fund), and the Smithsonian Inst. (Buck Postdoctoral Fellowship Program and the Division of Mammals). Support from the Luis Stokes Alliance for Minority Participation and the City College Academy for Professional Preparation was provided to RAB (Bridge to Doctorate Fellowship).

References

- Abrams, P. 1983. The theory of limiting similarity. – *Annu. Rev. Ecol. Syst.* 14: 359–376.
- Aguirre, L. F. et al. 2011. Phenology and interspecific ecological interactions of Andean biota in the face of climate change. – In: Herzog, S. K. et al. (eds), *Climate change and biodiversity in the tropical Andes*. Inter-American Inst. for Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE), pp. 68–92.
- Alexander, H. M. et al. 2007. Is there reduction in disease and pre-dispersal seed predation at the border of a host plant's range? Field and herbarium studies of *Carex blanda*. – *J. Ecol.* 95: 446–457.
- Alvizu, P. E. and Aguilera, M. 1998. Uso del espacio de *Marmosa robinsoni* (Didelphidae: Marsupialia) en una zona xerófila de los Andes venezolanos. – *Ecotropicos* 1: 81–92.
- Anderson, R. C. 1972. The ecological relationships of meningeal worm and native cervids in North America. – *J. Wildl. Dis.* 8: 304–310.
- Anderson, R. P. 2012. Harnessing the world's biodiversity data: promise and peril in ecological niche modeling of species distributions. – *Ann. N. Y. Acad. Sci.* 1260: 66–80.
- Anderson, R. P. 2013. A framework for using niche models to estimate impacts of climate change on species distributions. – *Ann. N. Y. Acad. Sci.* 1297: 8–28.
- Anderson, R. P. and Martínez-Meyer, E. 2004. Modeling species' geographic distributions for conservation assessments: an implementation with the spiny pocket mice (*Heteromys*) of Ecuador. – *Biol. Conserv.* 116: 167–179.
- Anderson, R. P. and Raza, A. 2010. The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: preliminary tests with montane rodents (genus *Nephelomys*) in Venezuela. – *J. Biogeogr.* 37: 1378–1393.
- Anderson, R. P. and Gonzalez, I. Jr 2011. Species-specific tuning increases robustness to sampling bias in models of species distributions: an implementation with Maxent. – *Ecol. Model.* 222: 2796–2811.
- Anderson, R. P. et al. 2002. Using niche-based GIS modeling to test geographic predictions of competitive exclusion and competitive release in South American pocket mice. – *Oikos* 98: 3–16.
- Anderson, R. P. et al. 2012. Faunal nestedness and species–area relationship for small non-volant mammals in “sky islands”

- of northern Venezuela. – *Stud. Neotrop. Fauna Environ.* 47: 157–170.
- Araújo, M. B. and Rahbek, C. 2006. How does climate change affect biodiversity. – *Science* 313: 1396–1397.
- Arif, S. et al. 2007. Bioclimatic modelling, morphology, and behaviour reveal alternative mechanisms regulating the distributions of two parapatric salamander species. – *Evol. Ecol. Res.* 9: 843–854.
- Austin, M. P. and Van Niel, K. P. 2011. Improving species distribution models for climate change studies: variable selection and scale. – *J. Biogeogr.* 38: 1–8.
- Banks, W. E. et al. 2008. Neanderthal extinction by competitive exclusion. – *PLoS One* 3: e3972.
- Barve, N. et al. 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. – *Ecol. Model.* 222: 1810–1819.
- Berlocher, S. H. and Feder, J. L. 2002. Sympatric speciation in phytophagous insects: moving beyond controversy? – *Annu. Rev. Entomol.* 47: 773–815.
- Bertness, M. D. and Callaway, R. 1994. Positive interactions in communities. – *Trends Ecol. Evol.* 9: 191–193.
- Bertolino, S. 2008. Introduction of the American grey squirrel (*Sciurus carolinensis*) in Europe: a case study in biological invasion. – *Curr. Sci.* 95: 903–906.
- Bisbal-E., F. J. 1990. Inventario preliminar de la fauna del Cerro Santa Ana, Península de Paraguán – Estado Falcón, Venezuela. – *Acta Cient. Venez.* 41: 177–185.
- Blois, J. L. et al. 2013. Climate change and the past, present, and future of biotic interactions. – *Science* 341: 499–504.
- Bond, W. J. 1994. Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. – *Phil. Trans. R. Soc. B* 344: 83–90.
- Boria, R. A. et al. 2014. Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. – *Ecol. Model.* 275: 73–77.
- Brito, J. C. and Crespo, E. G. 2002. Distributional analysis of two vipers (*Vipera latastei* and *V. seoanei*) in a potential area of sympatry in the northwestern Iberian Peninsula. – In: Schuett, G. W. et al. (eds), *Biology of the vipers*. Eagle Mountain Publishing, LC, UT, pp. 129–138.
- Brito, J. C. et al. 2011. Biogeography and conservation of viperids from north-west Africa: an application of ecological niche-based models and GIS. – *J. Arid Environ.* 75: 1029–1037.
- Brown, J. H. 1971. Mechanisms of competitive exclusion between two species of chipmunks. – *Ecology* 52: 305–311.
- Bruno, J. F. et al. 2003. Inclusion of facilitation into ecological theory. – *Trends Ecol. Evol.* 18: 119–125.
- Bullock, J. M. et al. 2000. Geographical separation of two *Ulex* species at three spatial scales: does competition limit species' ranges? – *Ecography* 23: 257–271.
- Burns, J. H. and Strauss, S. Y. 2011. More closely related species are more ecologically similar in an experimental test. – *Proc. Natl Acad. Sci. USA* 108: 5302–5307.
- Callaway, R. M. et al. 2002. Epiphyte host preferences and host traits: mechanisms for species-specific interactions. – *Oecologia* 132: 221–230.
- Case, T. J. et al. 2005. The community context of species' borders: ecological and evolutionary perspectives. – *Oikos* 108: 28–46.
- Choler, P. et al. 2001. Facilitation and competition on gradients in alpine plant communities. – *Ecology* 82: 3295–3308.
- Cooper, N. et al. 2008. A common tendency for phylogenetic overdispersion in mammalian assemblages. – *Proc. R. Soc. B* 275: 2031–2037.
- Costello, M. J. et al. 2013. Biodiversity data should be published, cited, and peer reviewed. – *Trends Ecol. Evol.* 28: 454–461.
- Coyne, J. A. and Orr, H. A. 2004. *Speciation*. – Sinauer Associates.
- Cracraft, J. and Prum, R. O. 1988. Patterns and processes of diversification: speciation and historical congruence in some Neotropical birds. – *Evolution* 42: 603–620.
- de Queiroz, K. 2007. Species concepts and species delimitation. – *Syst. Biol.* 56: 879–886.
- Elith, J. et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. – *Ecography* 29: 129–151.
- Elith, J. et al. 2010. The art of modelling range-shifting species. – *Methods Ecol. Evol.* 1: 330–342.
- Elith, J. et al. 2011. A statistical explanation of MaxEnt for ecologists. – *Divers. Distrib.* 17: 43–57.
- Escudero, M. et al. 2009. Significance of ecological vicariance and long distance dispersal in the diversification of *Carex* sect. *spirostachyae* (Cyperaceae). – *Am. J. Bot.* 96: 2100–2114.
- Fitzpatrick, B. M. and Turelli, M. 2006. The geography of mammalian speciation: mixed signals from phylogenies and range maps. – *Evolution* 60: 601–615.
- Fransen, C. H. J. M. 2002. Taxonomy, phylogeny, historical biogeography, and historical ecology of the genus *Pontonia* Latreille (Crustacea: Decapoda: Caridea: Palaemonidae). – National Museum of Natural History, Leiden.
- Fransen, C. H. J. M. 2007. The Influence of land barriers on the evolution of Pontoniine shrimps (Crustacea, Decapoda) living in association with molluscs and solitary ascidians. – In: Renema, W. (ed.), *Biogeography, time and place: distributions, barriers, and islands*. Springer, pp. 103–115.
- Futuyma, D. J. 1998. *Evolutionary biology*, 3rd. – Sinauer Associates.
- Gause, G. F. 1934. *The struggle for existence*. – Williams and Wilkin.
- Gavrilets, S. 2003. Models of speciation: what have we learned in 40 years? – *Evolution* 57: 2197–2215.
- Gifford, M. E. and Kozak, K. H. 2012. Islands in the sky or squeezed at the top? Ecological causes of elevational range limits in montane salamanders. – *Ecography* 35: 193–203.
- Glazier, D. S. and Eckert, S. E. 2002. Competitive ability, body size and geographical range size in small mammals. – *J. Biogeogr.* 29: 81–92.
- Grinnell, J. 1917. The niche-relationships of the California thrasher. – *Auk* 34: 427–433.
- Gutiérrez, E. E. et al. 2010. Molecular systematics of mouse opossums (Didelphidae: *Marmosa*): assessing species limits using mitochondrial DNA sequences, with comments on phylogenetic relationships and biogeography. – *Am. Mus. Novitates* 3692: 1–22.
- Gutiérrez, E. E. et al. 2011. Occurrence of *Marmosa waterhousei* in the Venezuelan Andes, with comments on its biogeographic significance. – *Mammalia* 75: 381–386.
- Haffer, J. 1969. Speciation in Amazonian forest birds. – *Science* 165: 131–137.
- Haffer, J. 1997. Alternative models of vertebrate speciation in Amazonia: an overview. – *Biodivers. Conserv.* 6: 451–476.
- Haffer, J. 2008. Hypotheses to explain the origin of species in Amazonia. – *Braz. J. Biol.* 68: 917–947.
- Handley, C. O. Jr 1976. *Mammals of the Smithsonian Venezuelan Project*. – Brigham Young Univ. Sci. Bull. [Biol]. 20: 1–91.
- Hardin, G. 1960. The competitive exclusion principle. – *Science* 131: 1292–1297.
- Hardy, C. R. and Linder, H. P. 2005. Intraspecific variability and timing in ancestral ecology reconstruction: a test case from the Cape Flora. – *Syst. Biol.* 54: 299–316.
- Heaney, L. R. 2000. Dynamic disequilibrium: a long-term, large-scale perspective on the equilibrium model of island biogeography. – *Global Ecol. Biogeogr.* 9: 59–74.
- Hegland, S. J. et al. 2009. How does climate warming affect plant-pollinator interactions? – *Ecol. Lett.* 12: 184–195.

- Hernandez, P. A. et al. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. – *Ecography* 29: 773–785.
- Hickerson, M. J. and Meyer, C. P. 2008. Testing comparative phylogeographic models of marine vicariance and dispersal using a hierarchical Bayesian approach. – *BMC Evol. Biol.* 8: 322.
- Hijmans, R. J. et al. 2005. Very high resolution interpolated climate surfaces for global land areas. – *Int. J. Climatol.* 25: 1965–1978.
- Holt, R. D. 1997. From metapopulation dynamics to community structure: some consequences of spatial heterogeneity. – In: Hanski, I. and Gilpin, M. (eds), *Metapopulation biology*. Academic Press, pp. 149–164.
- Holt, R. D. and Barfield, M. 2009. Trophic interactions and range limits: the diverse roles of predation. – *Proc. R. Soc. B* 276: 1435–1442.
- Holt, R. D. et al. 2011. Predation and the evolutionary dynamics of species ranges. – *Am. Nat.* 178: 488–500.
- Holycross, A. T. and Douglas, M. E. 2007. Geographic isolation, genetic divergence, and ecological non-exchangeability define ESUs in a threatened sky-island rattlesnake. – *Biol. Conserv.* 134: 142–154.
- Hone, D. W. E. and Benton, J. M. 2005. The evolution of large size: how does Cope's Rule work? – *Trends Ecol. Evol.* 20: 4–6.
- Hortal, J. et al. 2008. Historical bias in biodiversity inventories affects the observed environmental niche of the species. – *Oikos* 117: 847–858.
- Hutchinson, G. E. 1959. Homage to Santa Rosalia, or why are there so many kinds of animal? – *Am. Nat.* 93: 145–159.
- Jaeger, R. G. 1971. Competitive exclusion as a factor influencing the distribution of two species of terrestrial salamanders. – *Ecology* 52: 632–637.
- Juliano, S. A. and Lawton, J. H. 1990. The relationship between competition and morphology. I. Morphological patterns among co-occurring dytiscid beetles. – *J. Anim. Ecol.* 59: 403–419.
- Kamilar, J. K. and Ledogar, J. A. 2011. Species co-occurrence patterns and dietary resource competition in primates. – *Am. J. Phys. Anthropol.* 144: 131–139.
- Kelehear, C. et al. 2012. Rapid evolution of parasite life history traits on an expanding range-edge. – *Ecol. Lett.* 15: 329–337.
- Kisel, Y. and Barraclough, T. G. 2010. Speciation has a spatial scale that depends on levels of gene flow. – *Am. Nat.* 175: 316–334.
- Kozak, K. H. and Wiens, J. J. 2006. Does niche conservatism drive speciation? A case study in North American salamanders. – *Evolution* 60: 2604–2621.
- le Roux, P. C. et al. 2012. Biotic interactions affect the elevational ranges of high-latitude plant species. – *Ecography* 35: 1048–1056.
- Leathwick, J. R. 2002. Intra-generic competition among *Nothofagus* in New Zealand's primary indigenous forests. – *Biodivers. Conserv.* 11: 2117–2187.
- Leathwick, J. R. and Austin, M. P. 2001. Competitive interactions between tree species in New Zealand's old-growth indigenous forests. – *Ecology* 82: 2560–2573.
- LeBrun, E. G. et al. 2007. An experimental study of competition between fire ants and Argentine ants in their native range. – *Ecology* 88: 63–75.
- Lomolino, M. V. et al. 2006. *Biogeography*, 3rd ed. – Sinauer Associates.
- MacArthur, R. H. and Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. – *Am. Nat.* 101: 377–385.
- Martínez-Freiría, F. et al. 2008. GIS-based niche models identify environmental correlates sustaining a contact zone between three species of European vipers. – *Divers. Distrib.* 14: 452–461.
- Memmott, J. et al. 2007. Global warming and the disruption of plant–pollinator interactions. – *Ecol. Lett.* 10: 710–717.
- Moen, D. S. and Wiens, J. J. 2009. Phylogenetic evidence for competitively driven divergence: body-size evolution in Caribbean treefrogs (Hylidae: *Osteopilus*). – *Evolution* 63: 195–214.
- Mooney, H. A. and Cleland, E. E. 2001. The evolutionary impact of invasive species. – *Proc. Natl Acad. Sci. USA* 98: 5446–5451.
- Moritz, C. et al. 2000. Diversification of rainforest faunas: an integrated molecular approach. – *Annu. Rev. Ecol. Syst.* 31: 533–563.
- Murie, J. O. 1971. Behavioral relationships between two sympatric voles (*Microtus*): relevance to habitat segregation. – *J. Mammal.* 52: 181–186.
- Norberg, J. et al. 2012. Eco-evolutionary responses of biodiversity to climate change. – *Nature* doi: 10.1038/nclimate1588
- Pasch, B. et al. 2013. Interspecific dominance via vocal interactions mediates altitudinal zonation in Neotropical singing mice. – *Am. Nat.* 182: E161–E173.
- Pauw, A. and Bond, W. J. 2011. Mutualisms matter: pollination rate limits the distribution of oil-secreting orchids. – *Oikos* 120: 1531–1538.
- Pearson, R. G. et al. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. – *J. Biogeogr.* 34: 102–117.
- Pellissier, L. et al. 2010. Species distribution models reveal apparent competitive and facilitative effects of a dominant species on the distribution of tundra plants. – *Ecography* 33: 1004–1014.
- Pellissier, L. et al. 2012. Molecular substitution rate increases in myrmecophilous lycaenid butterflies (Lepidoptera). – *Zool. Scripta* doi: 10.1111/j.1463-6409.2012.00556.x
- Peterson, A. T. et al. 2011. Ecological niches and geographic distributions. – *Monographs in Population Biology*, Princeton Univ. Press.
- Phillips, S. J. 2008. Transferability, sample selection bias and background data in presence-only modelling: a response to Peterson et al. (2007). – *Ecography* 31: 272–278.
- Phillips, S. J. and Dudík, M. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. – *Ecography* 31: 161–175.
- Phillips, S. J. et al. 2006. Maximum entropy modeling of species geographic distributions. – *Ecol. Model.* 190: 231–259.
- Polechová, J. and Barton, N. H. 2005. Speciation through competition: a critical review. – *Evolution* 59: 1194–1210.
- Pyron, R. A. and Burbrink, F. T. 2010. Hard and soft allopatry: physically and ecologically mediated modes of geographic speciation. – *J. Biogeogr.* 37: 2005–2015.
- Radosavljevic, A. and Anderson, R. P. 2013. Making better Maxent models of species distributions: complexity, overfitting, and evaluation. – *J. Biogeogr.* [Early view] doi: 10.1111/jbi.12227
- Reddy, S. and Dávalos, L. M. 2003. Geographical sampling bias and its implications for conservation priorities in Africa. – *J. Biogeogr.* 30: 1719–1727.
- Reitz, S. R. and Trumble, J. T. 2002. Competitive displacement among insects and arachnids. – *Annu. Rev. Entomol.* 47: 435–465.
- Remington, C. L. 1968. Suture-zones of hybrid interaction between recently joined biotas. – *Evol. Biol.* 2: 321–428.
- Rossi, R. V. et al. 2010. A revision of the didelphid marsupial genus *Marmosa*. Part 1. The species in Tate's "Mexicana" and "Mitis" sections and other closely related forms. – *Bull. Am. Mus. Nat. Hist.* 334: 1–83.

- Sacks, B. N. et al. 2011. A restricted hybrid zone between native and introduced red fox (*Vulpes vulpes*) populations suggests reproductive barriers and competitive exclusion. – *Mol. Ecol.* 20: 326–341.
- Salomon, M. 2001. Evolutionary biogeography and speciation: essay on a synthesis. – *J. Biogeogr.* 28: 13–27.
- Schall, J. J. 1992. Parasite-mediated competition in *Anolis* lizards. – *Oecologia* 92: 58–64.
- Shcheglovitova, M. and Anderson, R. P. 2013. Estimating optimal complexity for ecological niche models: a jackknife approach for species with small sample sizes. – *Ecol. Model.* 269: 9–17.
- Sobel, J. M. et al. 2009. The biology of speciation. – *Evolution* 64: 295–315.
- Soley-Guardia, M. et al. in press. The effect of spatially marginal localities in modelling species' niches and distributions. – *J. Biogeogr.*
- Swenson, N. G. 2006. GIS-based niche models reveal unifying climatic mechanisms that maintain the location of avian hybrid zones in a North American suture zone. – *J. Evol. Biol.* 19: 717–725.
- Thielen, D. R. et al. 1997. Food availability and population dynamics of *Marmosa xerophila* Handley and Gordon 1979 (Marsupialia: Didelphidae). – *Zoocriaderos* 2: 1–15.
- Thielen, D. R. et al. 2009. Rearing cycle and other reproductive parameters of the xerophitic mouse opossum *Marmosa xerophila* (Didelphimorphia: Didelphidae) in the Peninsula of Paraguaná, Venezuela. – *Interciencia* 34: 195–198.
- Thompson, P. and Fox, B. J. 1993. Asymmetric competition in Australian heathland rodents: a reciprocal removal experiment demonstrating the influence of size-class structure. – *Oikos* 67: 264–278.
- Violle, C. D. et al. 2011. Phylogenetic limiting similarity and competitive exclusion. – *Ecol. Lett.* 14: 782–787.
- Vuilleumier, B. S. 1971. Pleistocene changes in the fauna and flora of South America. – *Science* 173: 771–780.
- Waltari, E. et al. 2007. Locating Pleistocene refugia: comparing phylogeographic and ecological niche model predictions. – *PLoS One* 2: e563.
- Warren, D. L. and Seifert, S. N. 2011. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. – *Ecol. Appl.* 21: 335–342.
- Waters, J. M. 2011. Competitive exclusion: phylogeography's 'elephant in the room'? – *Mol. Ecol.* 20: 4388–4394.
- Whittaker, R. J. et al. 2008. A general dynamic theory of oceanic island biogeography. – *J. Biogeogr.* 35: 977–994.
- Wiens, J. J. 2004. Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. – *Evolution* 58: 193–197.
- Wisz, M. S. et al. 2008. Effects of sample size on the performance of species distribution models. – *Divers. Distrib.* 14: 763–773.
- Wisz, M. S. et al. 2012. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. – *Biol. Rev.* 88: 15–30.
- Yesson, C. et al. 2007. How global is the Global Biodiversity Information Facility? – *PLoS One* 2: e1124.
- Zambrano, Z. 2001. Impacto del marsupial *Marmosa robinsoni* sobre la reproducción de dos cactáceas columnares en un enclave interandino venezolano. – Unpubl. thesis, Univ. de los Andes, Mérida, Venezuela.

Supplementary material (Appendix ECOG-00620 at <www.ecogeography.org/readers/appendix>). Appendix 1–3.

Ecography

ECOG-00620

Gutiérrez, E. E., Boria, R. A. and Anderson, R. P. 2014.
Can biotic interactions cause allopatry? niche models,
competition, and distributions of South American
mouse opossums. – *Ecography* doi: 10.1111/
ecog.00620

Supplementary material

1 **APPENDIX 1.**—Gazetteer and specimens examined. Below we list the localities and specimens of
2 *Marmosa robinsoni* and *M. xerophila* employed in this study. We report data verbatim from specimen
3 tags for cases in which specimens were examined ourselves and follow Rossi et al. (2010) otherwise.
4 Elevation, geographic coordinates, and sources for coordinates are indicated in brackets. Elevational
5 data (if any) are reproduced verbatim from either specimen tags or Rossi et al. (2010) in meters (m).
6 For each entry, boldface type indicates the place name to which geographic coordinates correspond.
7 Literature, maps, and other sources used to georeference localities are indicated within brackets,
8 and the corresponding citations appear in Appendix 2. Estimated georeferencing error is indicated
9 for each entry in kilometers (km). Note that most historical collectors typically collected specimens
10 1–2 km from their camp, despite providing a single locality description for that site. Hence, in
11 addition to the estimated georeferencing error noted here, specimens likely came from somewhere
12 within a slightly larger radius (in contrast to estimated errors including such “roaming distance,” e.g.
13 Anderson 2003; Anderson and Gutiérrez 2009). Museum catalog numbers for specimens examined
14 (either by us or by Rossi et al. 2010) follow each locality, using the following institutional
15 abbreviations: AMNH, American Museum of Natural History (New York); BMNH, Natural History
16 Museum (London); CVULA, Colección de Vertebrados de la Universidad de los Andes (Mérida);
17 EBRG, Museo de la Estación Biológica de Rancho Grande (Maracay); FMNH, Field Museum of
18 Natural History (Chicago); MHNLS, Museo de Historia Natural La Salle (Caracas); MBUCV, Museo
19 de Biología de la Universidad Central de Venezuela (Caracas); MCZ, Museum of Comparative
20 Zoology, Harvard University (Cambridge); MVZ, Museum of Vertebrate Zoology, University of
21 California (Berkeley); USNM, United States National Museum of Natural History (Washington,
22 DC). Early specimens in the AMNH for which the osteological portion was cataloged in a separate
23 numbering sequence from the skin are indicated as skin number/osteological number. Localities that
24 were not used in analyses because they fell outside the environmental grids (numbers: 29, 37, 99,

25 150, 151, 186) or because of their large georeferencing error (numbers: 48, 79, 94, 105, 146, 162) are
26 listed here as well.

27

28 *Marmosa robinsoni*

29 COLOMBIA

30 ATLÁNTICO

31 1. **Barranquilla** [ca. 100 m, 10°59'N, 74°48'W; Paynter 1997], MVZ 135234–135243;

32 "**Barranquilla**" [place of shipment]: MVZ 183339; Vicinity **Barranquilla**: MVZ 183334–
33 183338. Georeference error: ca. 2 km.

34

35 BOLÍVAR

36 2. **San Juan Nepomuceno** [167 m, 09°57'N, 75°05'W; Paynter 1997], FMNH 69315.

37 Georeference error: ca. 2 km.

38

39 CESAR

40 3. Río Cesar [=El **Orinoco**; 158 m, 10°13'N, 73°23'W; Hershkovitz 1960], USNM 280820,

41 280886–280888; Río Guaimaral [=El Guaimaral, 5 km from **El Orinoco**; coordinates

42 correspond to **El Orinoco**, which is located 5 km from El Guaimaral; see Hershkovitz 1960;

43 Anderson 2003], USNM 280817, 280819. Georeference error: ca. 1 km.

44 4. **Colonia Agrícola de Caracolicito** [400 m, 10°18'N, 74°00'W; Hershkovitz 1947], USNM

45 280806. Georeference error: ca. 1 km.

46 5. **El Salado** [430 m, 10°22'N, 73°29'W; Hershkovitz 1947], USNM 280814–280816. Georeference

47 error: ca. 1 km.

48 6. **Pueblo Bello** [1067 m, 10°24'N, 73°39'W; Hershkovitz 1947], USNM 280807–280813.

49 Georeference error: ca. 1 km.

50 7. **San Sebastián** [1900–2000 m, 10°37'N, 73°34'W; Hershkovitz 1947], FMNH 69320, 69321.

51 Georeference error: ca. 1 km.

52

53

CUNDINAMARCA

54 8. **Bogotá** [2590 m, 05°26'N, 74°34'W; Hernández-Camacho, 1956 (but see Anderson, 1999;

55 Anderson 2003) clarified that this locality corresponded to "*Volcanes, cerca a la cabecera del*
56 *corregimiento de Córdoba, Municipio de Caparrapí, Departamento de Cundinamarca; vertiente occidental de*
57 *la Cordillera Oriental. Colombia. Alt. 250 metros*"; not Rossi et al. 2010, who provided
58 coordinates for Bogotá (at an elevation of 2590 m) missing the mention of "*Volcanes*" on the
59 oldest museum tag tied to the specimen], AMNH 143521. Georeference error: ca. 2 km.

60

61

HUILA

62 9. Valle de Suaza, **Naranjal** [02°01'N, 75°51'W; NGA 2010], USNM 541857–541861, 543120.

63 Georeference error: ca. 2 km.

64 10. **7.5 km E Villavieja** [488 m, 03°14'N, 75°10'W; GE 2010], specimens from this locality were

65 reported by Rossi et al. 2010 under locality "*16 km NE Villavieja*" (see below). Georeference
66 error: ca. 1 km.

67 11. **5 km N Villavieja** [488 m, 03°16'N, 75°12'W; IGAC 1985a], specimens from this locality were

68 reported by Rossi et al. 2010 under locality "*16 km NE Villavieja*" (see below). Georeference
69 error: ca. 1 km.

70 12. **16 km NE Villavieja** [488 m, 03°21'N, 75°10'W; IGAC 1985a], MVZ 113366, 113367,

71 113833–113840. Georeference error: ca. 1 km.

72

73

LA GUAJIRA

74 13. Sierra Negra, **Villanueva**, Valledupar District [274 m, 10°37'N, 72°58'W; Hershkovitz 1960],

75 USNM 280821–280852; **Villanueva**, Valledupar District, USNM 280853–280875.

76 Georeference error: ca. 1 km.

77 14. **Las Marimondas**, Fonseca District [1000 m, 10°52'N, 72°43'W; Hershkovitz 1947],

78 USNM280876–280880, 280882, 280883, 280885. Georeference error: ca. 1 km.

79 15. **San Miguel** [1700 m, 10°58'N, 73°29'W; Paynter 1997], FMNH 18506. Georeference error: ca.

80 1 km.

81 16. Santa Marta, **Pueblo Viejo** [610 m, 10°59'N, 73°10'W; IGAC 1988; see Anderson 2003],

82 FMNH 18508. Georeference error: ≤ 5 km.

83 17. **Pueblo Viejo [=El Pueblito]**; 610 m, 10°59'N, 73°27'W; IGAC 1988; see Anderson 2003],

84 FMNH 18509; BMNH 9.4.15.18–9.4.15.20; MCZ B8117–B8122, B8123, B8125–B8127,

85 B8132, B8143; USNM 85531, 85532. Georeference error: ≤ 5 km.

86 18. **La Concepción** [ca. 800 m, 11°03'N, 73°27'W; Paynter 1997; not Rossi et al. 2010], FMNH

87 18507. Georeference error: ca. 1 km.

88

89

MAGDALENA

90 19. **Palomino** [ca. 600 m, 11°02'N, 73°39'W; Paynter 1997], USNM 85533. Georeference error: ca.

91 1 km.

92 20. **Minca** [670 m, 11°09'N, 74°07'W; Paynter 1997], AMNH 23293. Georeference error: ca. 1 km.

93 21. **Bonda** [46 m, 11°14'N, 74°08'W; Paynter 1997], AMNH 14610, 14611, 15357–15361, 23273–

94 23276, 23280, 23281, 23292, 23627. Georeference error: ca. 1 km.

95 22. **Mamatoco** [ca. 25 m, 11°14'N, 74°10'W; Paynter 1997], AMNH 15362. Georeference error: ca.
96 1 km.

97 23. **Taganga** [0 m, 11°16'N, 74°12'W; Paynter 1997], AMNH 15363. Georeference error: ca. 1 km.

98

99

NORTE DE SANTANDER

100 24. Cucuta, 10 mi N [=10 miles N **Cúcuta**; 215 m, 08°02'N, 72°08'W; IGAC 1985b], FMNH

101 18692. Georeference error: ca. 1 km.

102

103

TOLIMA

104 25. Madalegna River, **Honda** [183 m, 05°12'N, 74°45'W; Paynter 1997], AMNH 34602–34604.

105 Georeference error: ca. 1 km.

106 26. **Mariquita** [535 m, 05°12'N, 74°54'W; Paynter 1997], AMNH 207766. Georeference error: ca. 1

107 km.

108

109

GRENADA

110

SAINT GEORGE

111 27. Annandale [=Annandale waterfalls; 12°05'N, 61°43'W; NGA 2010], BMNH 87.6.30.5.

112 Georeference error: ca. 1 km.

113

114

PANAMA

115

CANAL ZONE

116 28. **Fort Kobbe** [08°54'N, 79°36'W; Fairchild and Handley 1966], USNM 298697, 298698, 300329,

117 300330, 301141, 303049. Georeference error: ca. 1 km.

118 29. **Quarry Heights** [08°57'N, 79°34'W; Fairchild and Handley 1966], USNM 303281–303283.

119 Georeference error: ca. 1 km.

120 30. 8 km W Balboa, **Rodman Naval Ammo** [=Ammunition] **Depot** [=Rodman Naval Station;

121 08°57'N, 79°37'W; Fleming 1970], USNM 456818, 456822. Georeference error: ca. 1 km.

122 31. **Miraflores** [08°59'N, 79°36'W; Fairchild and Handley 1966], USNM 396415. Georeference

123 error: ca. 1 km.

124

125 CHIRIQUÍ

126 32. **2 mi NE Tolé** [08°15'N, 81°39'W; GE 2010], USNM 331071. Georeference error: ca. 2 km.

127 33. **Colorado Camp.** [=Campamento Cerro Colorado; 08°29'N, 81°48'W; GE 2010], USNM

128 541324. Georeference error: ca. 2 km.

129 34. **23–25 km NNE San Felix** [=Near Escopeta Camp; 08°30'N, 81°47'W; Rossi et al. 2010],

130 USNM 541000, 541002. Georeference error: ca. 4 km.

131 35. **Finca Santa Clara, 14.5 km NW El Volcán** [08°51'N, 82°45'W; GE 2010], USNM 520772.

132 Georeference error: ca. 2 km.

133

134 COCLÉ

135 36. **2 mi E Río Hato** [08°23'N, 80°08'W; GE 2010; also see Fairchild and Handley 1966], USNM

136 331069. Georeference error: ca. 2 km.

137

138 PANAMÁ

139 37. **Saboga Island** [08°37'N, 79°04'W; GE 2010], MCZ 10809. Georeference error: ca. 2 km.

140 38. **4 mi E, 1 mi S Pacora** [09°04'N, 79°14'W; GE 2010], USNM 305146. Georeference error: ca.

141 4 km.

142

143

VERAGUAS

144 39. **Río Santa María, Santa Fé** [08°31'N, 81°04'W; Fairchild and Handley 1966], USNM 304696–

145 304709. Georeference error: ca. 1 km.

146

147

TRINIDAD & TOBAGO

148

TOBAGO

149 40. **Speyside** [11°18'N, 60°32'W; Anderson and Gutiérrez 2009], AMNH 184845, 184846, 184848,

150 184849. Georeference error: ca. 3 km.

151 41. **1 km E Charlotteville** [11°19'N, 60°32'W; GE 2010; Rossi et al. 2010 combined this locality

152 with "Near Charlotteville"], AMNH 259973, 259983; USNM 537898, 537899, 538075–

153 538078. Georeference error: ca. 1 km.

154

155

TRINIDAD

156 42. **Brazil village** [10°33'N, 61°17'W; GE 2010], AMNH 208997, 208998. Georeference error: ca.

157 3 km.

158 43. **Bush Bush Forest** [10°24'N, 61°03'W; Downs et al. 1968; Rossi et al. 2010 combined this

159 locality with "Nariva Swamp, **Bush Bush Forest**"; Nariva Swamp, **Bush Bush Forest**]

160 AMNH 188357, 189314–189316, 204855–204857, 206595–206597, 206761, 206762,

161 206764–206768. Georeference error: ca. 2 km.

162 44. **Caparo** [10°27'N, 61°19'W; Anderson and Gutiérrez 2009], AMNH 7426, 7429, 7660/6046–

163 7664/6050. Georeference error: ca. 3 km.

- 164 45. **Caura** [10°43'N, 61°21'W; Anderson and Gutiérrez 2009], AMNH 7665/6051, 7666/6052,
165 7667/6053–7670/6056, 7672/6058, 7674/6060–7676/6062; USNM 85556; **Caura** Mts.,
166 AMNH 7430. Georeference error: ca. 3 km.
- 167 46. Cedros [10°05'N, 61°51'W; O.S. 1930; coordinates correspond to **Bonasse**, near Cedros Bay],
168 AMNH 234960, 234961; Cedros Ward, Cedros, St. Patrick Co, AMNH 214424.
169 Georeference error: ca. 5 km.
- 170 47. **Cumaca** [10°42'N, 61°10'W; Anderson and Gutiérrez 2009; Rossi et al. 2010 lumped this
171 locality with "Valencia Ward, **Cumaca**, St. Andrew"], AMNH 188354, 208996, 208999–
172 209003, 212128–212130, 214425–214438, 214444, 234963–234970. Georeference error: ca.
173 4 km.
- 174 48. El Cerro del Oropuche [10°46'N, 61°09'W; NGA 2010], AMNH 31229–31231. Georeference
175 error: ca. 12 km.
- 176 49. **Fishing Pond** [10°35'N, 61°03'W; Anderson and Gutiérrez 2009], AMNH 173997.
177 Georeference error: ca. 4 km.
- 178 50. **Prinestown [=Princes Town; 10°16'N, 61°23'W; Anderson and Gutiérrez 2009], AMNH**
179 4799–4802, 6046, 6049, 6121, 6123, 6045/4767, 6047/4768, 6048/47669, 6050/4770–
180 6053/4773, 6055/4775, 6056/4776, 6058/4778. Georeference error: ca. 4 km.
- 181 51. **Sangre Grande** [10°35'N, 61°07'W; Anderson and Gutiérrez 2009], AMNH 173984, 173996,
182 174000, 174007, 174008, 174012, 174162, 188356; El Reposo Rd., **Sangre Grande**, AMNH
183 173990; Maingot Estate, 5 miles from **Sangre Grande**, AMNH 173998. Georeference error:
184 ca. 10 km.
- 185 52. Tamana Ward, **Cumuto**, St. Andrew [10°35'N, 61°12'W; Anderson and Gutiérrez 2009],
186 AMNH 212303–212305. Georeference error: ca. 3 km.
187

188 VENEZUELA

189 ANZOÁTEGUI

190 53. **Mamo** [08°28'N, 63°06'W; Gardner 2008], MHNLS 6463. Georeference error: ca. 2 km.

191 54. Paso "**Los Cocos**" Río Caris S de El Trigre [08°36'N, 64°04'W; Anderson and Gutiérrez 2009],
192 MBUCV 3131–3134; Sabana "**Los Cocos**", Río Caris, S El Tigre, MBUCV 3135.

193 Georeference error: ca. 2 km.

194 55. **Morichal Largo [=Río Morichal Largo]**, límite de los Estados Anzoátegui y Monagas

195 [08°46'N, 63°13'W; SAGCN 1996], MHNLS 5611, 5612. Georeference error: ca. 5 km.

196 56. **Hato Real Campo Matas** [09°22'N, 64°02'W; collector's label], EBRG 24174. Georeference
197 error: < 5 km.

198 57. **Complejo De Joces, 15 km E Puerto Piritu** [10°05'N, 64°53'W; collector's label], EBRG

199 22811, 22812; **Quebrada Hoces 15 km E Puerto Piritu**, EBRG 22231, 22232.

200 Georeference error: < 5 km.

201

202 APURE

203 58. **Caño la Guardia, afluente del Río Capanaparo** [90 m, 06°40'N, 67°35'W; collector's label],

204 MHNLS 7600, 7601, 7984, 7985. Georeference error: < 5 km.

205 59. "Mata Salado", **Hato Acapulco**, entre Capanaparo y Arauca [07°00'N, 67°07'W; Gardner
206 2008], MBUCV 1423, 1424. Georeference error: ca. 5 km.

207 60. La Trinidad (**Hato La Trinidad de Arauca**) [07°11'N, 69°04'W; Voss 1991], MBUCV 1414,
208 1415. Georeference error: ca. 5 km.

209 61. **El Mantecal** [07°33'N, 69°09'W; Paynter 1982], CVULA I-952. Georeference error: ca. 5 km.

210 62. **Hato El Frío, 30 km W del Saman de Apure** [60 m, 07°43'N, 68°58'W; collector's label],

211 MHNLS 8234. Georeference error: < 5 km.

212 63. **Hato El Frío** [60 m, 07°49′N, 68°54′W; collector's label], MHNLS 7942; USNM 448524.

213 Georeference error: < 5 km.

214

215 ARAGUA

216 64. **Fundo Paso del Medio, 10 km ENE San Juan de los Morros** [400–458 m, 09°56′N,

217 67°16′W; collector's label], EBRG 24083–24086. Georeference error: < 5 km.

218 65. **Hacienda Macapo, Lago de Valencia** [10°08′N, 67°39′W; collector's label], EBRG 22154,

219 22158, 22159, 22390. Georeference error: < 5 km.

220 66. **Camp Rangel** [10°09′N, 67°09′W; Anderson and Gutiérrez 2009], USNM 314171.

221 Georeference error: ca. 5 km.

222 67. **Rancho Grande** [1050–1100 m, 10°21′N, 67°40′W; Anderson and Gutiérrez 2009], USNM

223 517262–517270; Parque Nacional Henri Pittier, **Rancho Grande**, Guamitas, EBRG 16903.

224 Georeference error: ca. 2 km.

225 68. **2 km NE Ocumare de La Costa** [183 m, 10°28′N, 67°45′W; DCN 1971], USNM 517271–

226 517280. Georeference error: ca. 1 km.

227

228 BARINAS

229 69. **Reserva Forestal Caparo, 30 km E del Cantón** [200 m, 07°28′N, 71°00′W; GE 2010],

230 CVULA I-6539. Georeference error: ca. 3 km.

231 70. **Reserva Forestal Ticoporo Unidad II**, Compartimiento 23 [200 m, 08°07′N, 70°50′W; Ochoa

232 *et al.* 1988; GE 2010], EBRG 15757, 15758, 15761; **Reserva Forestal Ticoporo Unidad II**,

233 Compartimiento 16, EBRG 10151, 10274; **Reserva Forestal Ticoporo Unidad II**, área

234 intervenida, EBRG 6386; **Reserva Forestal Ticoporo Unidad II**, 8 km ESE Miri, EBRG

235 15789; **Reserva Forestal Ticoporo Unidad II**, Compartimiento 23 Río Quiu, EBRG

- 236 10133–10135, 10251, 10252; **Reserva Forestal Ticoporo Unidad II**, Compartimiento 9,
237 EBRG 10284, 15762; **Reserva Forestal Ticoporo Unidad II**, Parcela 15, EBRG 6387.
238 Georeference error: ca. 5 km.
- 239 71. La Erika [=La Erica], 20 km SW Barinas [08°29'N, 70°22'W; DCN 1970], CVULA I-073.
240 Georeference error: ca. 3 km.
- 241 72. **El Irel** [90 m, 08°46'N, 70°06'W; GPS coordinates taken by T. Paparoni in 2010], CVULA I-
242 3375. Georeference error: ca. 1 km.
- 243 73. **Río Barragán [=Quebrada Barragán]**, Barinitas [440 m, 08°48'N, 70°27'W; coordinates
244 correspond to a place along the river with the indicated elevation; DCN 1975a], CVULA I-
245 0347. Georeference error: ca. 1 km.
- 246 74. La Quinta, **5 km SW Altamira** [697 m, 08°48'N, 70°32'W; DCN 1976a], USNM 418540.
247 Georeference error: ca. 1 km.
- 248 75. **Altamira de Caceres** [830 m, 08°50'N, 70°30'W; DCN 1976a], CVULA I-0847. Georeference
249 error: ca. 1 km.
- 250
- 251 BOLÍVAR
- 252 76. **Ciudad Bolívar** [ca. 100 m, 08°08'N, 63°33'W; Paynter 1982], AMNH 16132. Georeference
253 error: ca. 1 km.
- 254
- 255 CARABOBO
- 256 77. **Pira-Pira [=Pirapira]**; 09°57'N, 68°04'W; Paynter 1982], EBRG 47. Georeference error: ca. 2
257 km.
- 258 78. **El Trompillo** [ca. 500 m, 10°04'N, 67°46'W; Paynter 1982], BMNH 14.9.1.86–14.9.1.97.
259 Georeference error: ca. 1 km.

- 260 79. **Valencia** [10°11'N, 68°00'W; Paynter 1982], EBRG 125. Georeference error: > 10 km.
- 261 80. **6 km SSE Montalban, Sabana Aguirre** [562 m, 10°11'N, 68°18'W; DCN 1976b; A. L. Tuttle's
262 field notes (1967); Tuttle's corrected elevation is 562 m, not 1055 m as indicated on
263 specimen label], EBRG 3972. Georeference error: ca. 1 km.
- 264 81. **Punta Cabito**; Lago de Valencia [420 m, 10°12'N, 67°50'W; Mavárez et al. 2002], MHNLS
265 2979, 2980, 3188–3194, 3295. Georeference error: ca. 1 km.
- 266 82. **1 km E Montalban, Sanjon** [579–598 m, 10°12'N, 68°20'W; DCN 1976b; A. L. Tuttle's field
267 notes (1967); Tuttle's corrected elevation is 598 m, not 1091 m as previously indicated on
268 specimen label], EBRG 3975; 2.5 km SE Montalban, El Castaño, EBRG 3977; Montalban,
269 Potrerito, EBRG 3973, 3974, 3976, 3978. Georeference error: ca. 1 km.
- 270 83. Embalse Río Moron, **Campamento Palmichal** [10°18'N, 68°14'W; Anderson and Gutiérrez
271 2009], EBRG 17081. Georeference error: ca. 2 km.
- 272 84. Bahía de **Patanemo** [10°26'N, 67°55'W; Anderson and Gutiérrez 2009], MHNLS 3732.
273 Georeference error: ca. 3 km.
- 274 85. **San Esteban** [ca. 200 m, 10°26'N, 68°01'W; Paynter 1982], AMNH 31532; BMNH
275 11.5.25.178–11.5.25.183, 11.5.25.184, 11.5.25.185, 11.5.25.187; **San Esteban** Valley: BMNH
276 11.5.25.186. Georeference error: ca. 1 km.
- 277 86. **Caño Alpargatón**, Petroquímica de Moron [10°28'N, 68°15'W; DCN 1976a], MBUCV 4078;
278 La Batea, 5 km SO [SW] de Moron, MBUCV 4097, 4101–4104. Georeference error: ca. 3
279 km.
- 280 87. **10 km NO [NW] Urama, Río Yaracuy** [125 m, 10°32'N, 68°23'W; DCN 1983; not Rossi et
281 al. 2010], EBRG 3959. Georeference error: ca. 2 km.

282 88. **El Central**, 10 km NW Urama, Río Yaracuy [25 m, 10°33'N, 68°25'W; Gardner 2008; see also
283 Handley 1976], USNM372938–372940, 372942–372944, 372947. Georeference error: ca. 1
284 km.

285

286 COJEDES

287 89. **Finca El Piñero, 25 km E El Baul** [08°59'N, 68°09'W; GE 2010; see also Polisar et al. 2003],
288 EBRG 8174. Georeference error: ca. 5 km.

289 90. **Hato El Piñero a 20 km N de El Baul** [09°00'N, 68°10'W; GE 2010], MBUCV 5157.
290 Georeference error: ca. 5 km.

291 91. Hato El **Tirado** [100 m, 09°05'N, 68°25'W; Anderson and Gutiérrez 2009], MHNLS 3812,
292 3889, 3890. Georeference error: ca. 2 km.

293 92. **Hato Nuevo** [09°13'N, 68°05'W; Gardner 2008], EBRG 364, 458–461, 464, 465. Georeference
294 error: ca. 2 km.

295 93. **Hato de Itabana** [80 m, 09°28'N, 68°27'W; Paynter 1982], MHNLS 4405. Georeference error:
296 ca. 5 km.

297

298 DISTRITO CAPITAL

299 94. **Caracas** [950 m, 10°30'N, 66°55'W; Paynter 1982], AMNH 130586–130589. Georeference
300 error: ca. 15 km.

301

302 FALCÓN

303 95. 20 km S and 98 km E Maracaibo (**Hacienda Socopito**) [470–480 m, 10°30'N, 70°44'W;
304 Handley 1976; see also Anderson 2003], USNM 443801; 24 km S and 94 km E Maracaibo
305 (**Hacienda Socopito**), USNM 418531, 418532. Georeference error: ≤ 5 km.

- 306 96. **Near Mirimire** [250 m, 11°10'N, 68°44'W; Handley 1976; coordinates correspond to the
307 nearest site to Mirimire visited by collector at indicated elevation], USNM 406953.
308 Georeference error: ca. 8 km.
- 309 97. 5 km N and 13 km E Mirimire (cerca **La Pastora**) [122 m, 11°11'N, 68°35'W; Anderson 2003],
310 EBRG 3979. Georeference error: ≤ 5 km.
- 311 98. **Parque Nacional Juan Cristófono Falcón, sector Acurigua** [650 m, 11°17'N, 69°28'W;
312 collector's label], EBRG 23773, 23887, 23888. Georeference error: ca. 2 km.
- 313 99. **Campechano cerca Boca Río Hueque, Municipio Píritu** [0 m, 11°27'N, 68°57'W;
314 collector's label], EBRG 22549, 22556, 22558, 22560. Georeference error: < 5 km.
- 315 100. **Cerro Santa Ana**, Península de Paraguaná [300–615 m, 11°49'N, 69°57'W; Anderson 2003;
316 SAGCN 1990], EBRG 3698, 3707, 15977, 15982, 15986; 49 km N and 32 km W Coro,
317 **Cerro Santa Ana**, EBRG 3993–3997; Península de Paraguaná, **Cerro Santa Ana**, 4 km N
318 Santa Ana, AMNH 276478, 276479, 276487, 276489, 276496, 276502, 276530, 276531,
319 276537, 276541, 276543, 276562; EBRG 25346–25351, 25357, 25359, 25367, 25371, 25465,
320 25496, 25498, 25512, 25514; 15 km SSW Pueblo Nuevo [=49 km and 32 km of Coro],
321 **Cerro Santa Ana**, Península de Paraguaná, USNM 442907; 49 km N and 32 km W Coro
322 (**Cerro Santa Ana**), USNM 443870–443874, 443877, 443880–443888, 443890–443896.
323 Georeference error: ca. 1 km.
- 324 101. **Reserva Biológica Monte Cano**, 5 km de Pueblo Nuevo Península de Paraguaná [200 m,
325 11°58'N, 69°59'W; GPS coordinates taken by M. Soley-Guardia in 2009], EBRG 23557–
326 23566; Estación Biológica Monte Cano, San José de Cocodite, EBRG 24097–24099;
327 Montecano Pueblo Nuevo Península Paraguaná, EBRG 20677–20679; San José de Cocodite
328 Estación Biológica de Monte Cano Municipio Falcón Península de Paraguaná, EBRG
329 23585–23591. Georeference error: ca. 1 km.

330 102. Reserva de Fauna Silvestre Tucurere, **Hacienda Somosagua** [near Boca de Tocuyo],
331 Municipio Acosta [40 m, 11°03'N, 68°26'W; GE 2010], EBRG 24923. Georeference error:
332 ca. 3 km.

333 103. Península de Paraguaná, **Cerro Santa Ana, 3 km N Santa Ana** [120–200m, 11°48'N,
334 69°57'W; collectors' label], AMNH 276533 (previously EBRG 25354); EBRG 25366; Cerro
335 Santa Ana, Península Paraguaná, EBRG 12342. Georeference error: ca. 1 km.

336

337 GUÁRICO

338 104. **Santa Rita, cerca Río Manapiare** [08°08'N, 66°15'W; Gardner 2008], MBUCV 2435.
339 Georeference error: ca. 2 km.

340 105. Paso Mereyal, **Hato La Muerta**, Espino [08°17'N, 65°46'W; www.fallingrain.com .
341 Specifically: http://www.fallingrain.com/world/VE/12/Hato_La_Muerta.html], MBUCV
342 1469. Georeference error: ca. 12 km.

343 106. **Hato La Fé**, Caserio Corozopando [90 m, 08°30'N, 67°35'W; Voss 1991], MHNLS 6723.
344 Georeference error: ca. 5 km.

345 107. **Carretera Calabozo-San Fernando, nivel Hato Flores Moradas** [08°34'N, 67°33'W;
346 Anderson and Gutiérrez 2009; not Paynter 1982], EBRG 8078. Georeference error: ca. 4
347 km.

348 108. **Estación Biológica de los Llanos** [110–115 m, 08°52'N, 67°23'W; Handley 1976], USNM
349 385052; Estación Biológica de Calabozo, MBUCV 1416–1422; **Estación Biológica de Los**
350 **Llanos**, Calabozo, MBUCV 1429–1433, 1934–1937, 1952, 2032; 7 km S and 5 km E
351 Calabozo [=Estación Biológica de los Llanos], USNM 443897, 443901–443905, 443911;
352 9 km SE Calabozo, **Estación Biológica de los Llanos**, USNM 442908, 443906, 443908,
353 443910. Georeference error: ca. 2 km.

354 109. **Dos Caminos** (50 km S, San Juan de Los Morros) [09°35'N, 67°18'W; Gardner 2008],
355 CVULA I-0261, I-0117. Georeference error: ca. 2 km.
356 110. **Hato Las Palmitas** [181 m, 09°36'N, 67°27'W; Handley 1976], EBRG 3980; 34 km S and 12
357 km O [W] San Juan de Los Morros, **Hato Las Palmitas**, EBRG 3971, 3981–3992; Hato
358 La Palmita [=Hato Las Palmitas], San Francisco de Tiznados, MBUCV 1557; 34 km S
359 and 12 km W San Juan de los Morros, **Hto. Las Palmitas**, USNM 385053–385056,
360 418518, 418519, 443794, 443797, 443798, 443800. Georeference error: ca. 5 km.

361 111. **Río Portuguesa 18 km NO [NW] Camaguan, Municipio Camaguan** [69 m, 08°11'N,
362 67°42'W; collector's label], EBRG 24980. Georeference error: ca. 2 km.

363

364 LARA

365 112. 14 km NE El Tocuyo, **Puerta Vieja** [616 m, 09°51'N, 69°41'W; DCN 1975b; see also Handley
366 1976], USNM 443914. Georeference error: ca. 1 km.

367 113. 10 km N El Tocuyo, **caserio Boro** [528 m, 09°53'N, 69°47'W; Handley 1976; DCN 1975b],
368 USNM 443913. Georeference error: ca. 2 km.

369 114. 8 km SW Barquisimeto, **La Concordia** [592 m, 10°01'N, 69°29'W; NGA 2010; see also
370 Handley 1976], USNM 443912. Georeference error: ca. 1 km.

371 115. **Río Tocuyo** [500 m, 10°16'N, 69°56'W; Voss 1991], AMNH 130577–130585, 130600.
372 Georeference error: ca. 1 km.

373

374 MÉRIDA

375 116. **Laguna de Caparú, 3 km SE San Juan de Lagunillas** [900 m, 08°29'N, 71°20'W; Sosa and
376 Soriano 1996], CVULA I-2964, I-3863, I-3867, I-3868. Georeference error: ca. 2 km.

377 117. **Las Gonzalez** [800–900 m, 08°30′N, 71°19′W; DCN 1977], CVULA I-1218, I-1223, I-1318, I-
378 1319, I-1515. Georeference error: ca. 1 km.

379 118. **Lagunillas** [08°30′N, 71°22′W; Handley 1976], CVULA I-1760. Georeference error: ca. 3 km.

380 119. Cafetos de **Milla** [ca. 1100 m, 08°36′N, 71°08′W; DCN 1977; elevation likely wrong in Rossi et
381 al. 2010; see Gardner 2008], BMNH 98.7.1.21; USNM 149005. Georeference error: ca. 1 km.

382 120. **Pedregosa** [=Quebrada La Pedregosa; 1630 m, 08°36′N, 71°12′W; Paynter 1982], BMNH
383 98.7.1.19. Georeference error: ca. 1 km.

384

385 MIRANDA

386 121. **Turgua** [10°22′N, 66°45′W; DCN 1964], MBUCV 1411, 1412. Georeference error: ca. 1 km.

387 122. **8 km S Caracas, cerca Turagua** [=Turgua; 1144 m, 10°22′N, 66°50′W; Anderson and
388 Gutiérrez 2009], EBRG 3960, 3961. Georeference error: ca. 2 km.

389 123. **8 km SSE Caracas** [1144 m, 10°25′N, 66°51′W; DCN 1964; see also Handley 1976], USNM
390 385047–385049. Georeference error: ca. 1 km.

391 124. **19 km E Caracas (Curapao)** [1160–1630 m, 10°31′N, 66°38′W; Anderson and Gutiérrez
392 2009], EBRG 3962–3965; Estanque de Curupao, N. de Guarenas, MBUCV 2033; **19 km E**
393 **Caracas, Curupao**, USNM 385057–385060. Georeference error: ca. 2 km.

394

395 MONAGAS

396 125. **Los Pozos** [08°28′N, 62°43′W; SAGCN 1996], MHNLS 4727, 4728; Carretera **Los Pozos**,
397 MHNLS 4732. Georeference error: ca. 3 km.

398 126. **Carretera Los Barrancos-Chaguaramas**, km 20 [08°32′N, 62°45′W; SAGCN 1996;
399 coordinates correspond to 20 km N Los Barrancos on the indicated road], MHNLS 4723,
400 4724, 4726, 4729–4731. Georeference error: ca. 5 km.

- 401 127. **Uverito**, 35 km S Temblador Distrito Sotillo [40 m, 08°40'N, 62°37'W; SAGCN 1996], EBRG
402 16226, 16228, 16229, 16232. Georeference error: ca. 6 km.
- 403 128. **Campamento El Merey**, cerca Chaguaramas, 45 km SSO [SSW] Temblador, Distrito Sotillo
404 [30 m, 08°40'N, 62°48'W, GE 2010], EBRG 16863. Georeference error: ca. 2 km.
- 405 129. **Río Ñato, 4 km N Las Gaviotas, Municipio Aguasay** [09°10'N, 63°22'W; collector's label],
406 EBRG 22378. Georeference error: < 5 km.
- 407 130. 55 km SSE Maturín, **Hato Mata de Bejuco** [18 m, 09°19'N, 62°56'W; Handley 1976; Rossi et
408 al. 2010 lumped this locality with “*Hato Mata de Bajuco*”], USNM 443915–443917, 442720.
409 Georeference error: ca. < 5 km.
- 410 131. **47 km SE Maturín**, Hato Santa Barbara [18 m, 09°22'N, 63°01'W; GE 2010; see also Handley
411 1976], USNM 385068–385072. Georeference error: ca. 1 km.
- 412 132. **Campamento MARNR**, Río Guarapiche [09°55'N, 62°55'W; DCN 1978], EBRG 17569.
413 Georeference error: ca. 2 km.
- 414 133. **Entre Arbolito y Buena Vista, Suroeste de San Antonio de Capayacual** [850 m, 10°04'N,
415 63°46'W; collector's label], MHNLS 9912, 9914. Georeference error: < 5 km.
- 416 134. San Antonio [=**San Antonio de Maturín**; 549 m, 10°07'N, 63°43'W; Paynter 1982], AMNH
417 69939, 69940. Georeference error: ca. 1 km.
- 418 135. **Caripe** [860 m, 10°11'N, 63°30'W; DCN 1969], MBUCV 397–400. Georeference error: ca. 2
419 km.
- 420 136. 5 km NW Caripe, **San Agustín** [1150 m, 10°12'N, 63°32'W; Handley 1976], USNM 406951.
421 Georeference error: ca. 2 km.
- 422 137. **Ipuré**, Cumaná [10°22'N, 64°08'W; Anderson and Gutiérrez 2009], BMNH 0.5.1.59.
423 Georeference error: ca. 7 km.
424

425
426
427
428
429
430
431
432
433
434
435
436
437
438
439
440
441
442
443
444
445
446
447
448

NUEVA ESPARTA

138. **Península de Macanao, Quebrada La Chica** [50 m, 10°02′N, 64°16′W; collector's label],
EBRG 24297. Georeference error: < 5 km.
139. Península de Macanao, **Punta Arenas** [10°59′N, 64°24′W; DCN 1979a], EBRG 3133, 3134.
Georeference error: ca. 1 km.
140. **La Sierra**, Isla de Margarita [100 m, 11°01′N, 63°52′W; DCN 1979b], MHNLS 198.
Georeference error: ca. 1 km.
141. **3 km S La Asunción**, Isla Margarita [38 m, 11°01′N, 63°53′W; DCN 1979b; see also Handley
1976], USNM 388398. Georeference error: ca. 1 km.
142. 2 km N and 1 km E La Assunción (**Salamanca**) [38 m, 11°03′N, 63°52′W; DCN 1979b; see
also Handley 1976], USNM 388381, 388388–388397, 388399, 388400. Georeference error: ca.
1 km.

PORTUGUESA

143. Palmarito Curbeleno [=Palmerita Curbelero], near Guanarito [08°24′N, 69°04′W, NGA
2010], AMNH 266951–266954. Georeference error: ca. 1 km.
144. **Refugio de Fauna Silvestre Estero de Chiriguare, Río Guanare** [ca. 60 m, 08°33′N,
68°44′W; collector's label], EBRG 20681–20683. Georeference error: < 5 km.
145. Near **Guanarito** [08°42′N, 69°13′W; Anderson 2003; Rossi et al. 2010 lumped this locality
with “Palmarito Curbeleno, near *Guanarito*”; “La Arenosa, near *Guanarito*”; and “La Hoyada,
near *Guanarito*”]. Catalogue numbers of specimens examined were taken from Rossi et al.
2010, who reported them together for “Palmarito Curbeleno, near *Guanarito*” (see locality 144,
above). Georeference error: ≤ 5 km.

449
450
451
452
453
454
455
456
457
458
459
460
461
462
463
464
465
466
467
468
469
470
471
472

SUCRE

146. **Embalse Turimiquire**, campamento Inos [ca. 300 m, 10°10'N, 64°19'W; GE 2010], EBRG 16814. Georeference error: ca. 11 km.
147. **Cuchivano** [213 m, 10°14'N, 63°56'W; Anderson and Gutiérrez 2009], AMNH 69938. Georeference error: ca. 3 km.
148. **Río Clavellinos abajo, Embalse Clavellinos, Municipio Ribero** [300 m, 10°22'N, 63°36'W; collector's label], EBRG 23204. Georeference error: < 5 km.
149. **Campo Alegre**, Cumaná [411 m, 10°22'N, 64°12'W; Anderson and Gutiérrez 2009], BMNH 0.5.1.58. Georeference error: ca. 4 km.
150. **21 km E Cumaná**, cerca Sotillo [25 m, 10°27'N, 63°58'W; Gardner 2008; see also Handley 1976], EBRG 3967. Georeference error: ca. 2 km.
151. **16 km E Cumaná**, Hacienda Quetepe [0 m, 10°27'N, 64°02'W; Gardner 2008; see also Handley 1976], EBRG 3966, 3968–3970; **16 km E Cumaná** (Quetepe), USNM 388377–388379, 388385, 388386. Georeference error: ca. 2 km.
152. **Finca Vuelta Larga**, 9.7 km (by road) SE Guaraúnos [10–20 m, 10°30'N, 63°07'W; Anderson and Gutiérrez 2009], AMNH 257208–257210; **Finca Vuelta Larga**; 9.7 km SE. de Guaraunos, MHNLS 8805–8813, 8162, 8164, 8181; **Finca Vuelta Larga**, Guaraunos, MHNLS 8802. Georeference error: ca. 2 km.
153. **Carretera Cariaco-Chacopata** [10°39'N, 63°43'W; Anderson and Gutiérrez 2009], MHNLS 6669. Georeference error: ca. 10 km.
154. Península de Araya, **Laguna Chacopata** [10°41'N, 63°48'W; DCN 1990], EBRG 20680. Georeference error: ca. 2 km.

TÁCHIRA

473 155. **Buena Vista** [07°27'N, 72°26'W; Handley 1976], MBUCV 2772. Georeference error: ca. 3 km.

474 TRUJILLO

475 156. **Valera** [645 m, 09°19'N, 70°37'W; Paynter 1982], FMNH 22175. Georeference error: < 5 km.

476 157. 10 km WNW Valera, Nr. **Isnotú** [930 m, 09°22'N, 70°42'W; Anderson 2003], USNM 370050.

477 Georeference error: ≤ 5km.

478 158. **18 km N Valera, Nr. Agua Viva** [164 m, 09°28'N, 70°34'W; GE 2010], USNM 371304.

479 Georeference error: ca. 2 km.

480 159. 30 km NW Valera, Nr. **El Dividive** [90 m, 09°29'N, 70°44'W; Anderson 2003], USNM

481 371305, 371315, 371316. Georeference error: ≤ 5 km.

482 160. **Hacienda Valle Verde** [29 m, 09°29'N, 70°59'W; GE 2010; coordinates in Handley 1976

483 correspond to La Ceiba, which is located ca. 8 km W of Hacienda], USNM 371317; **Hda.**

484 **Valle Verde** [=46 km WNW Valera; see Handley 1976] vía Puerto La Ceiba, CVULA I-

485 3231. Georeference error: ca. 5 km.

486 161. 23 km NW Valera, Nr. **Agua Santa** [90 m, 09°32'N, 70°39'W; Anderson 2003], USNM

487 370048, 370049. Georeference error: ≤ 5 km.

488

489 VARGAS

490 162. **Canales de Naiguatá**, Parque Nacional El Avila, DF [720–750 m, 10°35'N, 66°44'W;

491 Anderson and Gutiérrez 2009], MHNLS 8577; **Canales de Naiguatá**, DF, MHNLS 7166;

492 Los **Canales de Naiguatá**, Naiguata, DF, MBUCV 2971, 2972. Georeference error: > 10

493 km.

494

495 YARACUY

496 163. **Agua Negra** [80 m, 10°04'N, 69°09'W; SAGCN 1994], MHNLS 3294. Georeference error: ca.
497 2 km.

498

499

YARACUY-CARABOBO

500 164. **19 km NO [NW] Urama**, km 40 [5–25 m, 10°33'N, 68°27'W; Anderson 2003], EBRG 3946–
501 3958. Georeference error: ≤ 5 km.

502

503

ZULIA

504 165. **El Tukuko; Perijá** [300 m, 09°45'N, 72°45'W; collector's label], MHNLS 7775. Georeference
505 error: < 5 km.

506 166. **Mene Grande** [70 m, 09°49'N, 70°56'W; Paynter 1982], CVULA I-1320. Georeference error:
507 ca. 2 km.

508 167. 3 km S and 19 km W Machiques [=Novito; 1132 m, 10°02'N, 72°43'W; Handley 1976],
509 USNM 418529, 418530. Georeference error: ca. 1 km.

510 168. **Hato El Mango, 8 km S La Villa** [200 m, 10°15'N, 72°25'W; collector's label], MHNLS
511 7061. Georeference error: < 5 km.

512 169. **La Soledad, Hacienda Grano de Oro, Campo Boscán, Cuenca Baja del Río Palmar**
513 [10°16'N, 72°04'W; collector's label], MHNLS 11929. Georeference error: < 5 km.

514 170. **Planta Ule**, 20 km de Cabimas, carretera Cabimas-Ciudad Ojeda [5 m, 10°17'N, 71°23'W; GE
515 2010], EBRG 24078, 24080, 24081. Georeference error: ca. 2 km.

516 171. **Río Palmar** [110 m, 10°37'N, 72°24'W; DCN 1974a], EBRG 17066. Georeference error: ca. 2
517 km.

518 172. **Refugio de Fauna Silvestre y Reserva de Pesca Los Olivitos, Municipio Miranda** [0 m,
519 10°48'N, 71°26'W; collector's label], EBRG 22568. Georeference error: < 5 km.

520 173. **17 km N and 55 km W Maracaibo (Hacienda El Tigre)** [80 m, 10°48'N, 72°18'W; NGA
521 2010; not Musser *et al.* 1998 who provided coordinates for Maracaibo], USNM 443807; 18
522 km N and 56 km W Maracaibo [=Hda. El Tigre], USNM 443802–443804. Georeference
523 error: ca. 2 km.

524 174. 39 km NW La Paz, Nr. **Cerro Azul** [80 m, 10°51'N, 72°16'W; Anderson 2003], USNM
525 443805, 443806. Georeference error: ≤ 5 km.

526 175. **Refugio de Fauna Silvestre y Reserva de Pesca Los Olivitos, Municipio Miranda** [0 m,
527 10°57'N, 71°23'W; collector's label; note that same collector reported different coordinates
528 for another locality (number 173, above) within the protected area, but described that
529 locality in the same way as this one], EBRG 22545. Georeference error: < 5 km.

530

531 *Marmosa xerophila*

532 COLOMBIA

533 LA GUAJIRA

534 176. 114 km N and 32 km O [W] Maracaibo (**Cojoro**) [15 m, 11°39'N, 71°51'W; GE 2010; not
535 Handley 1976], EBRG 4003, 4005; 114 km N and 32 km W Maracaibo (La Isla) [=37 km
536 NNE Paraguaipoa; =**Cojoro**], USNM 443810, 443811, 443832; 37 km NNE Paraguaipoa,
537 near **Cojoro**, USNM 443812–443818, 443819, 443820–443831. Georeference error: ca. 2
538 km.

539

540 VENEZUELA

541 FALCÓN

542 177. **18 km WSW Capatárida**, Capatárida [75 m, 11°02'N, 70°40'W; DCN 1963], USNM 442728.

543 Georeference error: ca. 3 km.

- 544 178. **Capatárida** [40–75m, 11°10′N, 70°37′W; DCN 1963; A. L. Tuttle's field notes (1968); see also
545 Handley (1976), who reported the same coordinates], EBRG 4004, 4006–4031; USNM
546 442721–442727, 442729–442731, 442733–442735, 442744, 443918–443925, 443927–443929,
547 443931, 443936–443938, 443940–443942, 443946, 443947, 443951, 443952, 443955–443957,
548 443959, 443960, 443963–443972, 443974–443978. Georeference error: ca. 2 km.
- 549 179. Serranía de San Luis, **La Chapa**, 15 km N Cabure [350–380 m, 11°17′N, 69°36′W; collectors'
550 label], AMNH 276582 (previously EBRG 25427), 276586 (previously EBRG 25433); EBRG
551 25432, 25437, 25439. Georeference error: ca. 1 km.
- 552 180. **Tacuato**, N Península Paraguaná [11°43′N, 69°50′W; DCN 1974b], EBRG 20670.
553 Georeference error: ca. 3 km.
- 554 181. 48 km N and 46 km W Coro, **Yabuquiva** [13 m, 11°48′N, 70°04′W; N. E. Peterson field
555 notes, 1968; SAGCN 1990; DCN 1962; =25 km SW Pueblo Nuevo in Handley 1976],
556 EBRG 4035–4045; 25 km SW Pueblo Nuevo, **Yabuquiva**, Península de Paraguaná, USNM
557 442906; 48 km N and 46 km W Coro (**Yabuquiva**), USNM 443852, 443854–443856,
558 443862, 443863, 443868–443869. Georeference error: < 5 km.
- 559 182. 49 km N and 33 km W Coro (**Moruy**) [80–90m, 11°49′N, 69°58′W; N. E. Peterson field notes,
560 1968; M. Soley-G. in litt.; not Anderson 2003], EBRG 4032, 4033; USNM 443834–443848,
561 443851. Georeference error: ca. 2 km.
- 562 183. 49 km N and 34 km W Coro (**Moruy**) [55 m, 11°50′N, 69°59′W; Anderson 2003], EBRG
563 4034. Georeference error: ≤ 5 km.
- 564 184. San Pedro, **Jadacaquiva**, Península de Paraguaná [11°54′N, 70°05′W; DCN 1962], EBRG
565 22111. Georeference error: ca. 3 km.
- 566 185. **Guaidabacoa**, 22 km NW Pueblo Nuevo, Paraguaná [60 m, 12°06′N, 70°00′W; Díaz and
567 Granadillo, 2005], CVULA I-3498, I-3499; **Guaidabacoa**, Península de Paraguaná, EBRG

568 22112, 22115–22117, 22119; Hato **Guaidabacoa**, Península Paraguaná, EBRG 20671,
569 22113, 22114, 22118. Georeference error: ca. 2 km.
570 186. La Voz de Venezuela, Puerto Tumatey [=**Punta Tumatey**], Península de Paraguaná [12°10'N,
571 69°56'W; DCN 1974c], EBRG 20668, 20669. Georeference error: ca. 2 km.

572

573 ZULIA

574 187. **Las Mentiras, Municipio Paez** [20–30 m, 11°12'N, 72°02'W; collector's label], EBRG 21810,
575 21817, 21819, 21820. Georeference error: < 5 km

576

577 **Literature cited in Appendix 1 and not cited in the Reference section of the article**

578

579 Anderson, R. P. 1999 (2000). Preliminary review of the systematics and biogeography of the spiny
580 pocket mice (*Heteromys*) of Colombia. *Revista Acad. Colomb. Ci. Exact.* 23: 613–630.

581 Anderson, R. P. 2003. Taxonomy, distribution, and natural history of the genus *Heteromys* (Rodentia:
582 Heteromyidae) in western Venezuela, with the description of a dwarf species from the
583 Península de Paraguaná. – *Amer. Mus. Novitates* 3396: 1–12.

584 Anderson, R. P. and Gutiérrez, E. E. 2009. Taxonomy, distribution, and natural history of the genus
585 *Heteromys* (Rodentia: Heteromyidae) in central and eastern Venezuela, with the description of
586 a new species from the Cordillera de la Costa. – In: Voss R. S. and Carleton M. D. (eds),
587 Systematic mammalogy: contributions in honor of Guy G. Musser. – *Bull. Amer. Mus. Nat.*
588 *Hist.* 331: 33–93.

589 DCN. 1962. Hoja 6151 (Punto Fijo), escala 1:100.000. Caracas: Dirección de Cartografía Nacional
590 (DCN), Ministerio de Obras Públicas.

591 DCN. 1963. Hoja 6049 (Dabajuro), escala 1:100.000. Caracas: Dirección de Cartografía Nacional
592 (DCN), Ministerio de Obras Públicas.

593 DCN. 1964. Hoja 6847 (Caracas), escala 1:100.000, preliminary ed. Caracas: Dirección de Cartografía
594 Nacional (DCN), Ministerio de Obras Públicas.

595 DCN. 1969. Hoja 7546 (Caripito), escala 1:100.000. Caracas: Dirección de Cartografía Nacional
596 (DCN), Ministerio de Obras Públicas.

597 DCN. 1970. Hoja 6141 (Barinas), escala 1:100.000, 2nd ed. Caracas: Dirección de Cartografía
598 Nacional (DCN), Ministerio de Obras Públicas.

599 DCN. 1971. Hoja 6647 (Ocumare de la Costa), escala 1:100.000, 2nd ed. Caracas: Dirección de
600 Cartografía Nacional (DCN), Ministerio de Obras Públicas.

601 DCN. 1974a. Hoja 5747 (El Laberinto), escala 1:100.000, preliminary ed. Caracas: Dirección de
602 Cartografía Nacional (DCN), Ministerio de Obras Públicas.

603 DCN. 1974b. Hoja 6251 (Pueblo Nuevo), escala 1:100.000, 2nd ed. Caracas: Dirección de
604 Cartografía Nacional (DCN), Ministerio de Obras Públicas.

605 DCN. 1974c. Hoja 6252 (El Vínculo), escala 1:100.000, 2nd ed. Caracas: Dirección de Cartografía
606 Nacional (DCN), Ministerio de Obras Públicas.

607 DCN. 1975a. Hoja 6142 (Barinitas), escala 1:100.000, 2nd ed. Caracas: Dirección de Cartografía
608 Nacional (DCN), Ministerio de Obras Públicas.

609 DCN. 1975b. Hoja 6245 (El Tocuyo), escala 1:100.000. Caracas: Dirección de Cartografía Nacional
610 (DCN), Ministerio de Obras Públicas.

611 DCN. 1976a. Hoja 6042 (Timotes), escala 1:100.000, 2nd ed. Caracas: Dirección de Cartografía
612 Nacional (DCN), Ministerio de Obras Públicas.

613 DCN. 1976b. Hoja 6546 (Campo de Carabobo), escala 1:100.000, 2nd ed. Caracas: Dirección de
614 Cartografía Nacional (DCN), Ministerio de Obras Públicas.

- 615 DCN. 1977. Hoja 5941 (Mérida), escala 1:100.000. Dirección de Cartografía Nacional (DCN),
616 Ministerio de Obras Públicas, Caracas.
- 617 DCN. 1978. Hoja 7645 (Caño Frances), escala 1:100.000. Caracas: Dirección de Cartografía
618 Nacional (DCN), Ministerio de Obras Públicas.
- 619 DCN. 1979a. Hoja 7348 (Macanao sur), escala 1:100.000, 2nd ed. Caracas: Dirección de Cartografía
620 Nacional (DCN), Ministerio de Obras Públicas.
- 621 DCN. 1979b. Hoja 7449 (La Asunción), escala 1:100.000, 2nd ed. Caracas: Dirección de Cartografía
622 Nacional (DCN), Ministerio de Obras Públicas.
- 623 DCN. 1983. Hoja 6547 (Puerto Cabello), escala 1:100.000, 2nd ed. Caracas: Dirección de Cartografía
624 Nacional (DCN), Ministerio de Obras Públicas.
- 625 DCN. 1990. Hoja 7448 (Porlamar), escala 1:100.000, 2rd ed. Caracas: Dirección de Cartografía
626 Nacional (DCN), Ministerio de Obras Públicas.
- 627 Díaz, M. and Granadillo, E. 2005. The significance of episodic rains for reproductive phenology and
628 productivity of trees in semiarid regions of northwestern Venezuela. – *Trees* 19: 336–348.
- 629 Downs, W. G. et al. 1968. Arbovirus studies in Bush Bush Forest, Trinidad, W.I., September 1959–
630 December 1964. I. Description of the study area. – *Am. J. Trop. Med. Hyg.* 17: 224–236.
- 631 Fairchild, G. B. and Handley, C. O. Jr. 1966. Gazetteer of collecting localities in Panama. – In:
632 Wenzel, R. L. and Tipton, V. J. (eds), *Ectoparasites of Panama*. Field Museum of Natural
633 History. Chicago. pp. 9–22.
- 634 Fleming, T. H. 1970. Notes on the rodent faunas of two Panamanian forests. – *J. Mamm.* 51: 473–
635 490.
- 636 Gardner, A. L. ed. 2008. *Mammals of South America*. Vol. 1. Marsupials, xenarthrans, shrews, and
637 bats. Chicago University Press. Chicago.

638 GE (Google Earth). 2010. Google Earth 5.2. Available at [http://earth.google.com/download-](http://earth.google.com/download-earth.html)
639 [earth.html](http://earth.google.com/download-earth.html). Accessed July 20, 2010.

640 Hernández-Camacho, J. 1956. Una subespecie nueva de *Heteromys anomalus* (Mammalia: Rodentia). –
641 *Lozania* 10: 1–15.

642 Hershkovitz, P. 1947. Mammals of northern Colombia, preliminary report no. 1: squirrels
643 (Sciuridae). – *Proc. U. S. Natl. Mus.* 3208: 1–46.

644 Hershkovitz, P. 1960. Mammals of northern Colombia, preliminary report no. 8: arboreal rice rats, a
645 systematic revision of the subgenus *Oecomys*, genus *Oryzomys*. – *Proc. U. S. Natl. Mus.* 110:
646 513–568.

647 IGAC (Instituto Geográfico “Agustín Codazzi”). 1985a. Departamento de Huila, escala 1:400.000.
648 Ministerio de Hacienda y Crédito Público, subdirección cartográfica. Bogotá.

649 IGAC (Instituto Geográfico “Agustín Codazzi”). 1985b. Departamento de Norte de Santander,
650 escala 1:250.000. Ministerio de Hacienda y Crédito Público, subdirección cartográfica.
651 Bogotá.

652 IGAC (Instituto Geográfico “Agustín Codazzi”). 1988. Departamento de La Guajira, escala
653 1:400.000.: Ministerio de Hacienda y Crédito Público, subdirección cartográfica. Bogotá.

654 Mavárez, J. et al. 2002. Genetic differentiation, dispersal and mating system in the schistosome-
655 transmitting freshwater snail *Biomphalaria glabrata*. – *Heredity* 89: 258–265.

656 Musser, G. G. et al. 1998. Systematic studies of oryzomyine rodents (Muridae, Sigmodontinae):
657 diagnoses and distributions of species formerly assigned to *Oryzomys* “*capito*”. – *Bull. Amer.*
658 *Mus. Nat. Hist.* 236: 1–376.

659 NGA (National Geospatial-Intelligence Agency of the United States). (2010) NGA GEOnet Names
660 Server (GNS). Available at <http://earth-info.nga.mil/gns/html/> Accessed 18 August 18,
661 2010.

- 662 Ochoa-G. J. et al. 1988. Inventario de los mamíferos de la Reserva Forestal de Ticoporo y la Serranía
663 de Los Pijiguaos, Venezuela. – Acta Cient. Venez. 39: 269–280.
- 664 O.S. (Ordnance Survey). 1930. Map of Trinidad, scale 1:150,000. Unknown place of publication.
- 665 Paynter, R. A. Jr. 1982. Ornithological gazetteer of Venezuela. Museum of Comparative Zoology,
666 Harvard University. Cambridge, Massachusetts.
- 667 Paynter, R. A. Jr. 1997. Ornithological gazetteer of Colombia, 2nd edn. Museum of Comparative
668 Zoology, Harvard University. Cambridge, Massachusetts.
- 669 Polisar, J. et al. 2003. Jaguars, pumas, their prey base, and cattle ranching: ecological interpretations
670 of a management problem. – Biol. Cons. 109: 297–310.
- 671 SAGCN (Servicio Autónomo de Geografía y Cartografía Nacional). 1990. Hoja 6151-II-NE
672 (Yabuquiva), escala 1:25.000, 2nd edn. Ministerio del Ambiente y de los Recursos Naturales
673 Renovables. Caracas.
- 674 SAGCN (Servicio Autónomo de Geografía y Cartografía Nacional). 1994. Mapa del Estado Yaracuy,
675 3rd edn. Ministerio del Ambiente y de los Recursos Naturales Renovables. Caracas.
- 676 SAGCN (Servicio Autónomo de Geografía y Cartografía Nacional). 1996. Mapa del Estado
677 Monagas, 4th edn. Ministerio del Ambiente y de los Recursos Naturales Renovables.
678 Caracas.
- 679 Sosa, M. and Soriano, P. J. 1996. Resource availability, diet and reproduction in *Glossophaga longirostris*
680 in an arid zone of the Venezuelan Andes. – J. Trop. Ecol. 12: 805–818.
- 681 Voss R. S. 1991. An introduction to the Neotropical muroid rodent genus *Zygodontomys*. – Bull.
682 Amer. Mus. Nat. Hist. 210: 1–113.
- 683

684 **APPENDIX 2.**—Supplemental material with regards to preliminary models.

685

686 **Methods employed to calibrate preliminary models**

687

688 To approximate optimal model complexity, which implies the best approximation to reality with the
689 least degree of overfitting—we tuned model settings. We did so via preliminary models of each
690 species and then making final models using all localities (and the settings selected as optimal during
691 the tuning process). Specifically, we varied both feature classes and regularization multiplier (see
692 below). Because only a few localities for *Marmosa xerophila* were available (likely requiring very
693 simple models; Anderson and Gonzalez 2011), we used the simple combination of feature classes
694 suggested by MAXENT default settings and created preliminary models by varying only the
695 regularization multiplier. In contrast, for *M. robinsoni*, represented by numerous localities, we created
696 preliminary models varying both feature classes and the regularization multiplier (via k -fold cross-
697 partitioning, with $k = 5$, leading to $\sim 80\%$ for calibration and $\sim 20\%$ for evaluation in each iteration).

698 Together, regularization multiplier and feature class affect model complexity. The
699 regularization multiplier controls the strength of the penalties for complex models (the stronger the
700 multiplier, the stronger the penalty for a complex model; Phillips et al. 2006; Warren and Seifert
701 2011). Complex models, unfortunately, are more prone to overfitting (i.e. situations in which a
702 model is more complex than the real relationships between the species' niche and the examined
703 environmental variables; Anderson and Gonzalez 2011, Warren and Seifert, 2011). Feature classes
704 represent the kinds of mathematical responses that the algorithm is allowed to consider. For
705 *Marmosa robinsoni*, we considered combinations of feature classes likely to be reasonable given the
706 number of localities available (see Phillips et al. 2006, Phillips and Dudík 2008, Anderson and
707 Gonzalez 2011): linear, quadratic, and hinge (LQH); linear, quadratic, and product (LQP); linear,

708 quadratic, product, and hinge (LQPH); linear, quadratic, product, and threshold (LQPT); and linear,
709 quadratic, product, hinge, and threshold (LQPHT; the default combination of feature classes for this
710 number of localities). For *M. xerophila*, we used linear and quadratic features (LQ; the default
711 combination of feature classes for this number of localities; see above). For each of these feature-
712 class combinations, we constructed models using regularization multiplier values of 0.5, 1.0, 1.5, 2.0,
713 2.5, 3.0, 3.5, and 4.0, and implemented replicates to identify the settings that led to the highest
714 average performance on held-out data (see below).

715

716 **Methods employed to evaluate preliminary models**

717

718 We employed threshold-independent and threshold-dependent measures to evaluate preliminary-
719 model performance according to two criteria: 1) the degree to which they avoided overfitting and 2)
720 their discriminatory power (Radosavljevic and Anderson 2013, Shcheglovitova and Anderson 2013).
721 Our primary criterion for these evaluations was the least degree of overfitting. Overfit models
722 underestimate species' abiotically suitable areas, with various detrimental effects (Phillips and Dudík
723 2008, Anderson and Raza 2010, Anderson and Gonzalez 2011). We assessed overfitting with both
724 threshold-independent and threshold-dependent measures. For the former, we used AUC_{Diff} of
725 Warren and Seifert (2011), which is based on the area under the curve (AUC) of the receiver
726 operating characteristic (ROC) plot. For any given model, AUC_{Diff} (difference) equals the calibration
727 AUC minus the evaluation AUC ($AUC_{Diff} = AUC_{Train} - AUC_{Test}$ of Warren and Seifert 2011).
728 Because overfitting typically results in high calibration AUCs and low evaluation AUCs, the first
729 optimality criterion implemented here preferred MAXENT settings that yielded the lowest possible
730 AUC_{Diff} . As a second measure to assess this first optimality criterion (low overfitting), we used the
731 threshold-dependent omission rate. An omission rate indicates the proportion of the localities of the

732 species that fall outside of (are omitted from) areas predicted to be suitable by the model (Anderson
733 et al. 2003, Phillips et al. 2006). Overfit models tend to yield high omission rates (Anderson and
734 Gonzalez 2011, Peterson et al. 2011). Because of this, the first optimality criterion preferred those
735 MAXENT settings that yielded the lowest possible omission rates (and those that best approximated
736 the theoretical expectation of the thresholding rule applied). To convert model output to binary
737 predictions and calculate the omission rates, we applied the 10th percentile threshold (i.e. 10
738 percentile training omission threshold of MAXENT; “T10” of Pearson et al. 2007), the value at which
739 the model omits 10% of the calibration localities. Using this rule, we expect approximately 10%
740 omission of evaluation localities.

741 Our secondary optimality criterion for evaluating preliminary models, high discriminatory
742 power, refers to a model’s capacity to distinguish correctly between unsuitable and suitable
743 conditions for the focal species across the full gradient of suitability. This desirable property was
744 gauged with a rank-based threshold-independent measure, the AUC of the ROC plot obtained based
745 on evaluation data. Thus, this criterion preferred MAXENT settings that yielded the highest
746 evaluation AUC.

747 To implement these measures of model performance, we cross-validated preliminary models
748 for each species. For *Marmosa xerophila*, we assessed model performance and significance using ten
749 partitions via an extension of the $n - 1$ jackknife approach proposed by Pearson et al. (2007) for
750 cases in which only a small number of localities are available (here, $n = 10$; Shcheglovitova and
751 Anderson 2013). For *M. robinsoni*, we implemented k -fold cross validation, with $k = 5$ bins (each
752 iteration withheld one group for evaluation; Peterson et al. 2011). These numbers of partitions per
753 species allowed us to produce final models with similar numbers of localities as the respective
754 preliminary models; thus, we expect that settings selected to approximate optimal model complexity

755 based of preliminary-model performance will likely remain reasonable in calibration of the final
756 models.

757 We assessed the statistical significance of a subset of the preliminary models. Specifically, we
758 did so for replicates that corresponded to the settings that yielded optimal performance in the tuning
759 experiments. For each of those models, we converted the continuous output into binary predictions
760 by applying the 10th percentile threshold (as before). For *Marmosa robinsoni*, we then used one-tailed
761 binomial probabilities to determine whether evaluation localities fell into regions of predicted
762 presence more often than expected by chance (Anderson et al. 2002, Phillips *et al.* 2006). For *M.*
763 *xerophila*, we implemented a more-complicated test with the same intent, appropriate for the $n - 1$
764 jackknife applied to a dataset of few localities (Pearson et al. 2007).

765

766 **Results from evaluations of preliminary models**

767 Among the preliminary models of *Marmosa robinsoni*, those that showed the least overfitting and the
768 highest discriminatory power were calibrated with linear, quadratic, and hinge (LQH) feature classes
769 and a regularization multiplier value of 2.5. At this regularization multiplier value, the LQH feature
770 classes yielded both the lowest average AUC_{DIFF} (0.0548) and the lowest omission rate (13%), which
771 was also the omission rate closest to the theoretical expectation (i.e. 10% for the applied 10th
772 percentile threshold rule). With regard to discriminatory power, the LQH feature classes yielded
773 higher evaluation AUC values than other feature classes across all regularization multipliers;
774 however, there was little variation among the evaluation AUC values across regularization
775 multipliers. Each of the five preliminary models calibrated with LQH feature classes and
776 regularization multiplier 2.5 predicted evaluation localities significantly better than random ($P <$
777 0.012). Based on these results, we calibrated the final model of *M. robinsoni* using the LQH feature
778 classes and a regularization multiplier value of 2.5.

779 Tuning experiments for *Marmosa xerophila* led to selection of the regularization multiplier 1.5
780 as optimal (as mentioned earlier, we used default feature classes for this species; i.e. linear and
781 quadratic; LQ). The value 1.5 yielded both the lowest AUCDIFF (0.085) and the lowest average
782 evaluation omission rate (20%). This omission rate is somewhat higher than that theoretically
783 expected (10%) for the threshold rule employed. Taken as a whole, the suite of jackknifed models
784 for this species did not lead to statistical significance ($P = 0.755$), likely due to a very large
785 proportional predicted area (average = 75% of the study region, which afforded very low statistical
786 power). Based on these results, we calibrated the final model of *M. xerophila* using the LQ feature
787 classes and a regularization multiplier value of 1.5.

788

789 **Literature cited in Appendix 2 and not cited in the Reference section of the article**

790

791 Anderson, R. P. et al. 2002. Geographical distributions of spiny pocket mice in South America:
792 insights from predictive models. – *Global Ecol. Biogeogr.* 11: 131–141.

793 Anderson, R. P. et al. 2003. Evaluating predictive models of species' distributions: criteria for
794 selecting optimal models. – *Ecol. Modell.* 162: 211–232.

795

Appendix 3

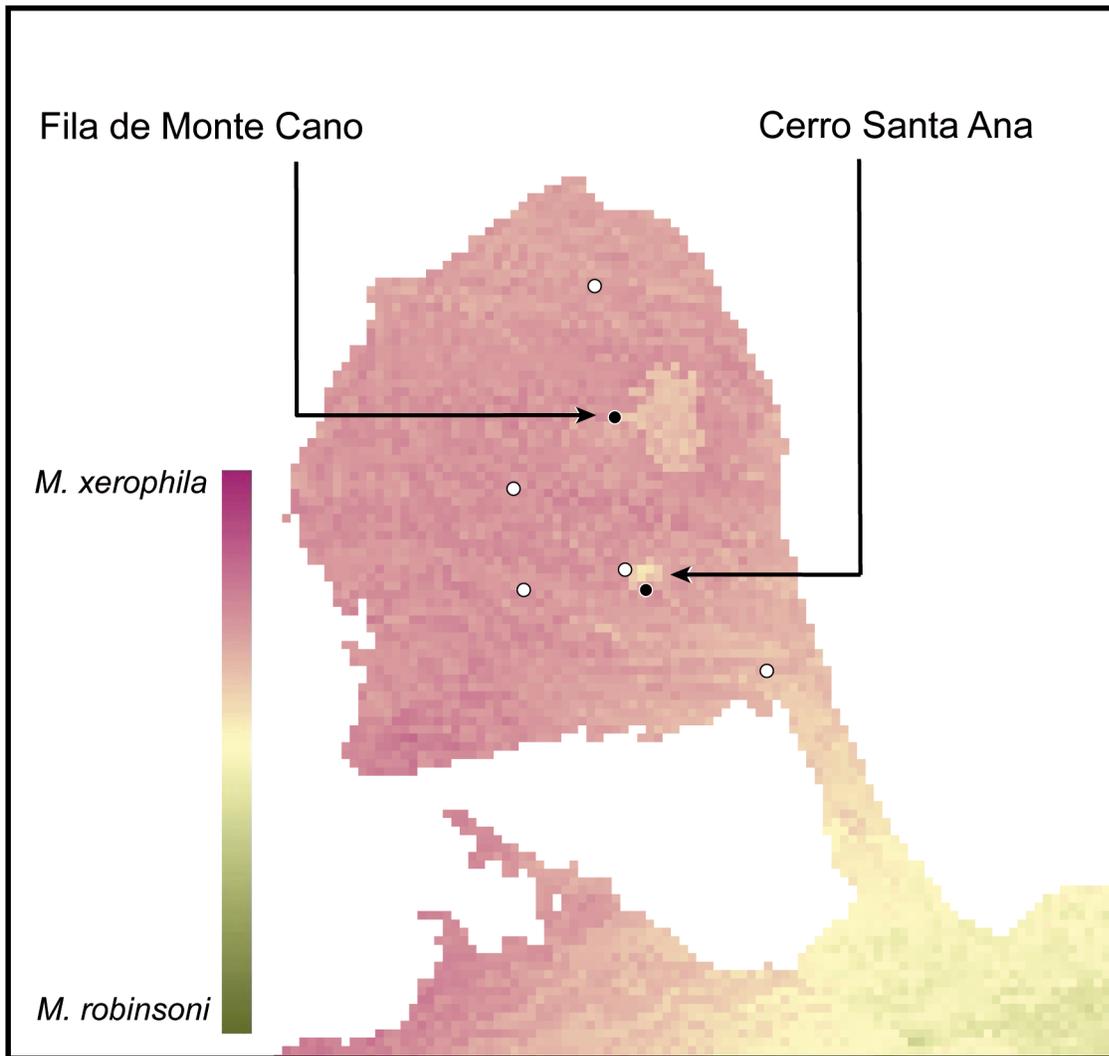


Figure A7. Comparison of predicted environmental suitability for *Marmosa xerophila* and *M. robinsoni* based on the continuous values (logistic output) resulting from final models. Pixels in red represent sites with environmental conditions predicted as more suitable for *Marmosa xerophila* than for *M. robinsoni*, whereas pixels in green represent sites predicted as more suitable for *M. robinsoni* than for *M. xerophila*.