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

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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, Gavrilets 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 Futuya 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 parapary) 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 sympathy – 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 sympathy 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 sympathy 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 sympathy, 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 sympathy 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
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 Paraguaná 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 phyloge netic 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.

**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, Borja 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://biogeo.berkeley.edu/worldclim/worldclim.htm>, at 30° resolution; 0.93 × 0.93 km = 0.86 km² 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 sympathy. 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 sympathy 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 sympathy 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 sympathy 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 binominal 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 sympathy (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 sympathy 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 sympathy 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 sympathy**

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 sympathy 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).
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 Peninsula 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 Peninsula de Paraguana, 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 Peninsula de Paraguana, 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...
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 sympathy 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 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
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

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<tr>
<td>Contraction</td>
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![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.](image)
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 phyleogeographic 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 (Arntz 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 (Wiśniewski et al. 2012, Blois et al. 2013) – should prove insightful to study future species distributions, risks of extinction, and speciation via allopatry (Memott et al. 2007, Hegland et al. 2009, Aguirre et al. 2011, Norberg et al. 2012, Anderson 2013).

References


Kisel, Y. and Barraclough, T. G. 2010. Speciation has a spatial scale that depends on levels of gene flow. – Am. Nat. 175: 316–334.


APPENDIX 1.—Gazetteer and specimens examined. Below we list the localities and specimens of *Marmosa robinsoni* and *M. xerophila* employed in this study. We report data verbatim from specimen tags for cases in which specimens were examined ourselves and follow Rossi et al. (2010) otherwise. Elevation, geographic coordinates, and sources for coordinates are indicated in brackets. Elevational data (if any) are reproduced verbatim from either specimen tags or Rossi et al. (2010) in meters (m). For each entry, boldface type indicates the place name to which geographic coordinates correspond. Literature, maps, and other sources used to georreference localities are indicated within brackets, and the corresponding citations appear in Appendix 2. Estimated georreferencing error is indicated for each entry in kilometers (km). Note that most historical collectors typically collected specimens 1–2 km from their camp, despite providing a single locality description for that site. Hence, in addition to the estimated georeferencing error noted here, specimens likely came from somewhere within a slightly larger radius (in contrast to estimated errors including such “roaming distance,” e.g. Anderson 2003; Anderson and Gutiérrez 2009). Museum catalog numbers for specimens examined (either by us or by Rossi et al. 2010) follow each locality, using the following institutional abbreviations: AMNH, American Museum of Natural History (New York); BMNH, Natural History Museum (London); CVULA, Colección de Vertebrados de la Universidad de los Andes (Mérida); EBRG, Museo de la Estación Biológica de Rancho Grande (Maracay); FMNH, Field Museum of Natural History (Chicago); MHNLS, Museo de Historia Natural La Salle (Caracas); MBUCV, Museo de Biología de la Universidad Central de Venezuela (Caracas); MCZ, Museum of Comparative Zoology, Harvard University (Cambridge); MVZ, Museum of Vertebrate Zoology, University of California (Berkeley); USNM, United States National Museum of Natural History (Washington, DC). Early specimens in the AMNH for which the osteological portion was cataloged in a separate numbering sequence from the skin are indicated as skin number/osteological number. Localities that were not used in analyses because they fell outside the environmental grids (numbers: 29, 37, 99,
150, 151, 186) or because of their large georreferencing error (numbers: 48, 79, 94, 105, 146, 162) are listed here as well.

*Marmosa robinsoni*

COLOMBIA

ATLÁNTICO

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

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

BOLÍVAR

2. **San Juan Nepomuceno** [167 m, 09°57´N, 75°05´W; Paynter 1997], FMNH 69315. Georeference error: ca. 2 km.

CESAR

3. **Río Cesar** [=**El Orinoco**; 158 m, 10°13´N, 73°23´W; Hershkovitz 1960], USNM 280820, 280886–280888; **Río Guaimaral** [=El Guaimaral, 5 km from **El Orinoco**; coordinates correspond to **El Orinoco**, which is located 5 km from El Guaimaral; see Hershkovitz 1960; Anderson 2003], USNM 280817, 280819. Georeference error: ca. 1 km.

4. **Colonia Agrícola de Caracolicito** [400 m, 10°18´N, 74°00´W; Hershkovitz 1947], USNM 280806. Georeference error: ca. 1 km.

5. **El Salado** [430 m, 10°22´N, 73°29´W; Hershkovitz 1947], USNM 280814–280816. Georeference error: ca. 1 km.
6. **Pueblo Bello** [1067 m, 10°24′N, 73°39′W; Hershkovitz 1947], USNM 280807–280813.
   Georeference error: ca. 1 km.

7. **San Sebastián** [1900–2000 m, 10°37′N, 73°34′W; Hershkovitz 1947], FMNH 69320, 69321.
   Georeference error: ca. 1 km.

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**CUNDINAMARCA**

8. **Bogotá** [2590 m, 05°26′N, 74°34′W; Hernández-Camacho, 1956 (but see Anderson, 1999; Anderson 2003) clarified that this locality corresponded to "Volcanes, cerca a la cabecera del corregimiento de Córdoba, Municipio de Caparrapi, Departamento de Cundinamarca; vertiente occidental de la Cordillera Oriental. Colombia. Alt. 250 metros"; not Rossi et al. 2010, who provided coordinates for Bogotá (at an elevation of 2590 m) missing the mention of "Volcanes" on the oldest museum tag tied to the specimen], AMNH 143521. Georeference error: ca. 2 km.

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**HUILA**

9. Valle de Suaza, **Naranjal** [02°01′N, 75°51′W; NGA 2010], USNM 541857–541861, 543120.
   Georeference error: ca. 2 km.

10. **7.5 km E Villavieja** [488 m, 03°14′N, 75°10′W; GE 2010], specimens from this locality were reported by Rossi et al. 2010 under locality "16 km NE Villavieja" (see below). Georeference error: ca. 1 km.

11. **5 km N Villavieja** [488 m, 03°16′N, 75°12′W; IGAC 1985a], specimens from this locality were reported by Rossi et al. 2010 under locality "16 km NE Villavieja" (see below). Georeference error: ca. 1 km.

12. **16 km NE Villavieja** [488 m, 03°21′N, 75°10′W; IGAC 1985a], MVZ 113366, 113367, 113833–113840. Georeference error: ca. 1 km.
LA GUAJIRA

13. Sierra Negra, Villanueva, Valledupar District [274 m, 10°37’N, 72°58’W; Hershkovitz 1960], USNM 280821–280852; Villanueva, Valledupar District, USNM 280853–280875. Georeference error: ca. 1 km.

14. Las Marimondas, Fonseca District [1000 m, 10°52’N, 72°43’W; Hershkovitz 1947], USNM280876–280880, 280882, 280883, 280885. Georeference error: ca. 1 km.

15. San Miguel [1700 m, 10°58’N, 73°29’W; Paynter 1997], FMNH 18506. Georeference error: ca. 1 km.

16. Santa Marta, Pueblo Viejo [610 m, 10°59’N, 73°10’W; IGAC 1988; see Anderson 2003], FMNH 18508. Georeference error: ≤ 5 km.

17. Pueblo Viejo [=El Pueblito; 610 m, 10°59’N, 73°27’W; IGAC 1988; see Anderson 2003], FMNH 18509; BMNH 9.4.15.18–9.4.15.20; MCZ B8117–B8122, B8123, B8125–B8127, B8132, B8143; USNM 85531, 85532. Georeference error: ≤ 5 km.

18. La Concepción [ca. 800 m, 11°03’N, 73°27’W; Paynter 1997; not Rossi et al. 2010], FMNH 18507. Georeference error: ca. 1 km.

MAGDALENA

19. Palomino [ca. 600 m, 11°02’N, 73°39’W; Paynter 1997], USNM 85533. Georeference error: ca. 1 km.

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

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

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

**NORTE DE SANTANDER**

24. **Cucuta**, 10 mi N [=10 miles N Cúcuta]; 215 m, 08°02′N, 72°08′W; IGAC 1985b], FMNH 18692. Georeference error: ca. 1 km.

**TOLIMA**

25. Madalegna River, **Honda** [183 m, 05°12′N, 74°45′W; Paynter 1997], AMNH 34602–34604. Georeference error: ca. 1 km.

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

**GRENADA**

**SAINT GEORGE**

27. Annandale [=**Annandale waterfalls**; 12°05′N, 61°43′W; NGA 2010], BMNH 87.6.30.5. Georeference error: ca. 1 km.

**PANAMA**

**CANAL ZONE**

28. **Fort Kobbe** [08°54′N, 79°36′W; Fairchild and Handley 1966], USNM 298697, 298698, 300329, 300330, 301141, 303049. Georeference error: ca. 1 km.
29. Quarry Heights [08°57′N, 79°34′W; Fairchild and Handley 1966], USNM 303281–303283.

Georeference error: ca. 1 km.

30. 8 km W Balboa, Rodman Naval Ammo [=Ammunition] Depot [=Rodman Naval Station; 08°57′N, 79°37′W; Fleming 1970], USNM 456818, 456822. Georeference error: ca. 1 km.

31. Miraflores [08°59′N, 79°36′W; Fairchild and Handley 1966], USNM 396415. Georeference error: ca. 1 km.

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

33. Colorado Camp. [=Campamento Cerro Colorado; 08°29′N, 81°48′W; GE 2010], USNM 541324. Georeference error: ca. 2 km.

34. 23–25 km NNE San Felix [=Near Escopeta Camp; 08°30′N, 81°47′W; Rossi et al. 2010], USNM 541000, 541002. Georeference error: ca. 4 km.

35. Finca Santa Clara, 14.5 km NW El Volcán [08°51′N, 82°45′W; GE 2010], USNM 520772. Georeference error: ca. 2 km.

36. 2 mi E Río Hato [08°23′N, 80°08′W; GE 2010; also see Fairchild and Handley 1966], USNM 331069. Georeference error: ca. 2 km.

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

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

39. **Río Santa María, Santa Fé** [08°31′N, 81°04′W; Fairchild and Handley 1966], USNM 304696–304709. Georeference error: ca. 1 km.

TRINIDAD & TOBAGO

TOBAGO

40. **Speyside** [11°18′N, 60°32′W; Anderson and Gutiérrez 2009], AMNH 184845, 184846, 184848, 184849. Georeference error: ca. 3 km.

41. **1 km E Charlotteville** [11°19′N, 60°32′W; GE 2010; Rossi et al. 2010 combined this locality with "Near Charlotteville"], AMNH 259973, 259983; USNM 537898, 537899, 538075–538078. Georeference error: ca. 1 km.

TRINIDAD

42. **Brazil village** [10°33′N, 61°17′W; GE 2010], AMNH 208997, 208998. Georeference error: ca. 3 km.


44. **Caparo** [10°27′N, 61°19′W; Anderson and Gutiérrez 2009], AMNH 7426, 7429, 7660/6046–7664/6050. Georeference error: ca. 3 km.
45. Caura [10°43´N, 61°21´W; Anderson and Gutiérrez 2009], AMNH 7665/6051, 7666/6052, 7667/6053–7670/6056, 7672/6058, 7674/6060–7676/6062; USNM 85556; Caura Mts., AMNH 7430. Georeference error: ca. 3 km.

46. Cedros [10°05´N, 61°51´W; O.S. 1930; coordinates correspond to Bonasse, near Cedros Bay], AMNH 234960, 234961; Cedros Ward, Cedros, St. Patrick Co, AMNH 214424. Georeference error: ca. 5 km.


49. Fishing Pond [10°35´N, 61°03´W; Anderson and Gutiérrez 2009], AMNH 173997. Georeference error: ca. 4 km.


51. Sangre Grande [10°35´N, 61°07´W; Anderson and Gutiérrez 2009], AMNH 173984, 173996, 174000, 174007, 174008, 174012, 174162, 188356; El Reposo Rd., Sangre Grande, AMNH 173990; Maingot Estate, 5 miles from Sangre Grande, AMNH 173998. Georeference error: ca. 10 km.

52. Tamana Ward, Cumuto, St. Andrew [10°35´N, 61°12´W; Anderson and Gutiérrez 2009], AMNH 212303–212305. Georeference error: ca. 3 km.
53. **Mamo** [08°28´N, 63°06´W; Gardner 2008], MHNLS 6463. Georeference error: ca. 2 km.

54. Paso “**Los Cocos**” Río Caris S de El Trigre [08°36´N, 64°04´W; Anderson and Gutiérrez 2009], MBUCV 3131–3134; Sabana “**Los Cocos**”, Río Caris, S El Tigre, MBUCV 3135. Georeference error: ca. 2 km.

55. **Morichal Largo** [=Río Morichal Largo], límite de los Estados Anzoátegui y Monogas [08°46´N, 63°13´W; SAGCN 1996], MHNLS 5611, 5612. Georeference error: ca. 5 km.

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

57. **Complejo De Joces, 15 km E Puerto Piritu** [10°05´N, 64°53´W; collector’s label], EBRG 22811, 22812; **Quebrada Hoces 15 km E Puerto Piritu**, EBRG 22231, 22232. Georeference error: < 5 km.

58. **Caño la Guardia, afluente del Río Capanaparo** [90 m, 06°40´N, 67°35´W; collector’s label], MHNLS 7600, 7601, 7984, 7985. Georeference error: < 5 km.

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

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

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

62. **Hato El Frío, 30 km W del Saman de Apure** [60 m, 07°43´N, 68°58´W; collector’s label], MHNLS 8234. Georeference error: < 5 km.
63. **Hato El Frío** [60 m, 07°49′N, 68°54′W; collector's label], MHNLS 7942; USNM 448524.

   Georeference error: < 5 km.

**ARAGUA**

64. **Fundo Paso del Medio, 10 km ENE San Juan de los Morros** [400–458 m, 09°56′N, 67°16′W; collector's label], EBRG 24083–24086. Georeference error: < 5 km.

65. **Hacienda Macapo, Lago de Valencia** [10°08′N, 67°39′W; collector's label], EBRG 22154, 22158, 22159, 22390. Georeference error: < 5 km.

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

   Georeference error: ca. 5 km.

67. **Rancho Grande** [1050–1100 m, 10°21′N, 67°40′W; Anderson and Gutiérrez 2009], USNM 517262–517270; Parque Nacional Henri Pittier, **Rancho Grande**, Guamitas, EBRG 16903.

   Georeference error: ca. 2 km.

68. **2 km NE Ocumare de La Costa** [183 m, 10°28′N, 67°45′W; DCN 1971], USNM 517271–517280. Georeference error: ca. 1 km.

**BARINAS**

69. **Reserva Forestal Caparo, 30 km E del Cantón** [200 m, 07°28′N, 71°00′W; GE 2010], CVULA I-6539. Georeference error: ca. 3 km.

70. **Reserva Forestal Ticoporo Unidad II**, Compartimiento 23 [200 m, 08°07′N, 70°50′W; Ochoa et al. 1988; GE 2010], EBRG 15757, 15758, 15761; **Reserva Forestal Ticoporo Unidad II**, Compartimiento 16, EBRG 10151, 10274; **Reserva Forestal Ticoporo Unidad II**, área intervenida, EBRG 6386; **Reserva Forestal Ticoporo Unidad II**, 8 km ESE Miri, EBRG 15789; **Reserva Forestal Ticoporo Unidad II**, Compartimiento 23 Río Quiu, EBRG

Georeference error: ca. 5 km.

71. La Erika [=La Erica], 20 km SW Barinas [08°29′N, 70°22′W; DCN 1970], CVULA I-073.

Georeference error: ca. 3 km.

72. **El Irel** [90 m, 08°46′N, 70°06′W; GPS coordinates taken by T. Paparoni in 2010], CVULA I-3375. Georeference error: ca. 1 km.

73. **Río Barragán [=Quebrada Barragán]**, Barinitas [440 m, 08°48′N, 70°27′W; coordinates correspond to a place along the river with the indicated elevation; DCN 1975a], CVULA I-0347. Georeference error: ca. 1 km.

74. La Quinta, 5 km SW Altamira [697 m, 08°48′N, 70°32′W; DCN 1976a], USNM 418540.

Georeference error: ca. 1 km.

75. **Altamira de Caceres** [830 m, 08°50′N, 70°30′W; DCN 1976a], CVULA I-0847. Georeference error: ca. 1 km.

76. **Ciudad Bolívar** [ca. 100 m, 08°08′N, 63°33′W; Paynter 1982], AMNH 16132. Georeference error: ca. 1 km.

77. **Pira-Pira [=Pirapira]**; 09°57′N, 68°04′W; Paynter 1982], EBRG 47. Georeference error: ca. 2 km.

78. **El Trompillo** [ca. 500 m, 10°04′N, 67°46′W; Paynter 1982], BMNH 14.9.1.86–14.9.1.97.

Georeference error: ca. 1 km.
79. Valencia [10°11′N, 68°00′W; Paynter 1982], EBRG 125. Georeference error: > 10 km.

80. 6 km SSE Montalban, Sabana Aguirre [562 m, 10°11′N, 68°18′W; DCN 1976b; A. L. Tuttle's field notes (1967); Tuttle's corrected elevation is 562 m, not 1055 m as indicated on specimen label], EBRG 3972. Georeference error: ca. 1 km.

81. Punta Cabito; Lago de Valencia [420 m, 10°12′N, 67°50′W; Mavárez et al. 2002], MHNLS 2979, 2980, 3188–3194, 3295. Georeference error: ca. 1 km.

82. 1 km E Montalban, Sanjon [579–598 m, 10°12′N, 68°20′W; DCN 1976b; A. L. Tuttle's field notes (1967); Tuttle's corrected elevation is 598 m, not 1091 m as previously indicated on specimen label], EBRG 3975; 2.5 km SE Montalban, El Castaño, EBRG 3977; Montalban, Potrerito, EBRG 3973, 3974, 3976, 3978. Georeference error: ca. 1 km.

83. Embalse Río Moron, Campamento Palmichal [10°18′N, 68°14′W; Anderson and Gutiérrez 2009], EBRG 17081. Georeference error: ca. 2 km.

84. Bahía de Patanemo [10°26′N, 67°55′W; Anderson and Gutiérrez 2009], MHNLS 3732. Georeference error: ca. 3 km.

85. San Esteban [ca. 200 m, 10°26′N, 68°01′W; Paynter 1982], AMNH 31532; BMNH 11.5.25.178–11.5.25.183, 11.5.25.184, 11.5.25.185, 11.5.25.187; San Esteban Valley: BMNH 11.5.25.186. Georeference error: ca. 1 km.

86. Caño Alpargatón, Petroquímica de Moron [10°28′N, 68°15′W; DCN 1976a], MBUCV 4078; La Batea, 5 km SO [SW] de Moron, MBUCV 4097, 4101–4104. Georeference error: ca. 3 km.

87. 10 km NO [NW] Urama, Río Yaracuy [125 m, 10°32′N, 68°23′W; DCN 1983; not Rossi et al. 2010], EBRG 3959. Georeference error: ca. 2 km.
88. **El Central**, 10 km NW Urama, Río Yaracuy [25 m, 10°33’N, 68°25’W; Gardner 2008; see also Handley 1976], USNM 372938–372940, 372942–372944, 372947. Georeference error: ca. 1 km.

COJEDES

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

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

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


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

DISTRITO CAPITAL

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

FALCÓN

95. 20 km S and 98 km E Maracaibo (**Hacienda Socopito**) [470–480 m, 10°30’N, 70°44’W; Handley 1976; see also Anderson 2003], USNM 443801; 24 km S and 94 km E Maracaibo (**Hacienda Socopito**), USNM 418531, 418532. Georeference error: ≤ 5 km.
96. **Near Mirimire** [250 m, 11°10′N, 68°44′W; Handley 1976; coordinates correspond to the nearest site to Mirimire visited by collector at indicated elevation], USNM 406953. Georeference error: ca. 8 km.

97. 5 km N and 13 km E Mirimire (cerca **La Pastora**) [122 m, 11°11′N, 68°35′W; Anderson 2003], EBRG 3979. Georeference error: ≤ 5 km.

98. **Parque Nacional Juan Cristóforo Falcón, sector Acurigua** [650 m, 11°17′N, 69°28′W; collector's label], EBRG 23773, 23887, 23888. Georeference error: ca. 2 km.

99. **Campechano cerca Boca Río Hueque, Municipio Píritu** [0 m, 11°27′N, 68°57′W; collector's label], EBRG 22549, 22556, 22558, 22560. Georeference error: < 5 km.

100. **Cerro Santa Ana**, Península de Paraguaná [300–615 m, 11°49′N, 69°57′W; Anderson 2003; SAGCN 1990], EBRG 3698, 3707, 15977, 15982, 15986; 49 km N and 32 km W Coro, **Cerro Santa Ana**, EBRG 3993–3997; Península de Paraguaná, **Cerro Santa Ana**, 4 km N Santa Ana, AMNH 276478, 276479, 276487, 276489, 276496, 276502, 276530, 276531, 276537, 276541, 276543, 276562; EBRG 25346–25351, 25357, 25359, 25367, 25371, 25465, 25496, 25498, 25512, 25514; 15 km SSW Pueblo Nuevo [=49 km and 32 km of Coro], **Cerro Santa Ana**, Península de Paraguaná, USNM 442907; 49 km N and 32 km W Coro **(Cerro Santa Ana)**, USNM 443870–443874, 443877, 443880–443888, 443890–443896. Georeference error: ca. 1 km.

101. **Reserva Biológica Monte Cano**, 5 km de Pueblo Nuevo Península de Paraguaná [200 m, 11°58′N, 69°59′W; GPS coordinates taken by M. Soley-Guardia in 2009], EBRG 23557–23566; Estación Biológica Monte Cano, San José de Cocodite, EBRG 24097–24099; Montecano Pueblo Nuevo Península Paraguaná, EBRG 20677–20679; San José de Cocosite Estación Biológica de Monte Cano Municipio Falcón Península de Paraguaná, EBRG 23585–23591. Georeference error: ca. 1 km.
102. Reserva de Fauna Silvestre Tucurere, **Hacienda Somosagua** [near Boca de Tocuyo],
Municipio Acosta [40 m, 11°03´N, 68°26´W; GE 2010], EBRG 24923. Georeference error: ca. 3 km.

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

**GUÁRICO**

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

105. Paso Mereyal, **Hato La Muerta, Espino** [08°17´N, 65°46´W; www.fallingrain.com].

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

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

9 km SE Calabozo, **Estación Biológica de los Llanos**, USNM 442908, 443906, 443908,
443910. Georeference error: ca. 2 km.
109. **Dos Caminos** (50 km S, San Juan de Los Morros) [09°35’N, 67°18’W; Gardner 2008], CVULA I-0261, I-0117. Georeference error: ca. 2 km.

110. **Hato Las Palmitas** [181 m, 09°36’N, 67°27’W; Handley 1976], EBRG 3980; 34 km S and 12 km O [W] San Juan de Los Morros, **Hato Las Palmitas**, EBRG 3971, 3981–3992; Hato La Palmita [=**Hato Las Palmitas**], San Francisco de Tiznados, MBUCV 1557; 34 km S and 12 km W San Juan de los Morros, **Hato Las Palmitas**, USNM 385053–385056, 418518, 418519, 443794, 443797, 443798, 443800. Georeference error: ca. 5 km.

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

LARA

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

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

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

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

MÉRIDA

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

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

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

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

**MIRANDA**

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

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

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

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

**MONAGAS**

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

126. **Carretera Los Barrancos-Chaguaramas**, km 20 [08°32´N, 62°45´W; SAGCN 1996; coordinates correspond to 20 km N Los Barrancos on the indicated road], MHNLS 4723, 4724, 4726, 4729–4731. Georeference error: ca. 5 km.
127. **Uverito**, 35 km S Temblador Distrito Sotillo [40 m, 08°40´N, 62°37´W; SAGCN 1996], EBRG 16226, 16228, 16229, 16232. Georeference error: ca. 6 km.


129. **Río Ñato**, 4 km N Las Gaviotas, Municipio Aguasay [09°10´N, 63°22´W; collector's label], EBRG 22378. Georeference error: < 5 km.

130. 55 km SSE Maturín, **Hato Mata de Bejuco** [18 m, 09°19´N, 62°56´W; Handley 1976; Rossi et al. 2010 lumped this locality with “**Hato Mata de Bajuco**”], USNM 443915–443917, 442720. Georeference error: ca. < 5 km.

131. **47 km SE Maturín**, Hato Santa Barbara [18 m, 09°22´N, 63°01´W; GE 2010; see also Handley 1976], USNM 385068–385072. Georeference error: ca. 1 km.


133. **Entre Arbolito y Buena Vista, Suroeste de San Antonio de Capayacual** [850 m, 10°04´N, 63°46´W; collector's label], MHNLS 9912, 9914. Georeference error: < 5 km.

134. San Antonio [=**San Antonio de Maturin**; 549 m, 10°07´N, 63°43´W; Paynter 1982], AMNH 69939, 69940. Georeference error: ca. 1 km.

135. **Caripe** [860 m, 10°11´N, 63°30´W; DCN 1969], MBUCV 397–400. Georeference error: ca. 2 km.

136. 5 km NW Caripe, **San Agustín** [1150 m, 10°12´N, 63°32´W; Handley 1976], USNM 406951. Georeference error: ca. 2 km.

137. **Ipuré**, Cumaná [10°22´N, 64°08´W; Anderson and Gutiérrez 2009], BMNH 0.5.1.59. Georeference error: ca. 7 km.
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.
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.

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

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

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

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

159. 30 km NW Valera, Nr. **El Dividive** [90 m, 09°29’N, 70°44’W; Anderson 2003], USNM 371305, 371315, 371316. Georeference error: ≤ 5 km.

160. **Hacienda Valle Verde** [29 m, 09°29’N, 70°59’W; GE 2010; coordinates in Handley 1976 correspond to La Ceiba, which is located ca. 8 km W of Hacienda], USNM 371317; **Hda. Valle Verde** [=46 km WNW Valera; see Handley 1976] vía Puerto La Ceiba, CVULA I-3231. Georeference error: ca. 5 km.

161. 23 km NW Valera, Nr. **Agua Santa** [90 m, 09°32’N, 70°39’W; Anderson 2003], USNM 370048, 370049. Georeference error: ≤ 5 km.

**Vargas**

162. **Canales de Naiguatá**, Parque Nacional El Avila, DF [720–750 m, 10°35’N, 66°44’W; Anderson and Gutiérrez 2009], MHNLS 8577; **Canales de Naiguatá**, DF, MHNLS 7166; Los **Canales de Naiguatá**, Naiguata, DF, MBUCV 2971, 2972. Georeference error: > 10 km.

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

**YARACUY-CARABOBO**

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

**ZULIA**

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

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

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

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

169. **La Soledad, Hacienda Grano de Oro, Campo Boscán, Cuenca Baja del Río Palmar**

[10°16′N, 72°04′W; collector's label], MHNLS 11929. Georeference error: < 5 km.

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

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

172. **Refugio de Fauna Silvestre y Reserva de Pesca Los Olivitos, Municipio Miranda** [0 m, 10°48′N, 71°26′W; collector's label], EBRG 22568. Georeference error: < 5 km.
173. **17 km N and 55 km W Maracaibo (Hacienda El Tigre)** [80 m, 10°48′ N, 72°18′ W; NGA 2010; not Musser et al. 1998 who provided coordinates for Maracaibo], USNM 443807; 18 km N and 56 km W Maracaibo [=Hda. El Tigre], USNM 443802–443804. Georeference error: ca. 2 km.

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

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

**Marmosa xerophila**

**COLOMBIA**

**LA GUAJIRA**

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

**VENEZUELA**

**FALCÓN**

177. **18 km WSW Capatárida**, Capatárida [75 m, 11°02′ N, 70°40′ W; DCN 1963], USNM 442728. Georeference error: ca. 3 km.
178. **Capatárida** [40–75m, 11°10′N, 70°37′W; DCN 1963; A. L. Tuttle's field notes (1968); see also Handley (1976), who reported the same coordinates], EBRG 4004, 4006–4031; USNM 442721–442727, 442729–442731, 442733–442735, 442744, 443918–443925, 443927–443929, 443931, 443936–443938, 443940–443942, 443946, 443947, 443951, 443952, 443955–443957, 443959, 443960, 443963–443972, 443974–443978. Georeference error: ca. 2 km.

179. Serranía de San Luis, **La Chapa**, 15 km N Cabure [350–380 m, 11°17′N, 69°36′W; collectors' label], AMNH 276582 (previously EBRG 25427), 276586 (previously EBRG 25433); EBRG 25432, 25437, 25439. Georeference error: ca. 1 km.


181. 48 km N and 46 km W Coro, **Yabuquiva** [13 m, 11°48′N, 70°04′W; N. E. Peterson field notes, 1968; SAGCN 1990; DCN 1962; =25 km SW Pueblo Nuevo in Handley 1976], EBRG 4035–4045; 25 km SW Pueblo Nuevo, **Yabuquiva**, Península de Paraguaná, USNM 442906; 48 km N and 46 km W Coro (**Yabuquiva**), USNM 443852, 443854–443856, 443862, 443863, 443868–443869. Georeference error: < 5 km.

182. 49 km N and 33 km W Coro (**Moruy**) [80–90m, 11°49′N, 69°58′W; N. E. Peterson field notes, 1968; M. Soley-G. in litt.; not Anderson 2003], EBRG 4032, 4033; USNM 443834–443848, 443851. Georeference error: ca. 2 km.

183. 49 km N and 34 km W Coro (**Moruy**) [55 m, 11°50′N, 69°59′W; Anderson 2003], EBRG 4034. Georeference error: ≤ 5 km.

184. San Pedro, **Jadacaquiva**, Península de Paraguaná [11°54′N, 70°05′W; DCN 1962], EBRG 22111. Georeference error: ca. 3 km.

185. **Guaidabacoa**, 22 km NW Pueblo Nuevo, Paraguaná [60 m, 12°06′N, 70°00′W; Díaz and Granadillo, 2005], CVULA I-3498, I-3499; **Guaidabacoa**, Península de Paraguaná, EBRG
22112, 22115–22117, 22119; Hato Guaidabacoa, Península Paraguaná, EBRG 20671, 22113, 22114, 22118. Georeference error: ca. 2 km.

186. La Voz de Venezuela, Puerto Tumatey [=Punta Tumatey], Península de Paraguaná [12°10´N, 69°56´W; DCN 1974c], EBRG 20668, 20669. Georeference error: ca. 2 km.

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

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


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Methods employed to calibrate preliminary models

To approximate optimal model complexity, which implies the best approximation to reality with the least degree of overfitting—we tuned model settings. We did so via 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 both feature classes and regularization multiplier (see below). Because only a few localities for *Marmosa xerophila* were available (likely requiring very simple models; Anderson and Gonzalez 2011), we used the simple combination of feature classes suggested by MAXENT default settings and created preliminary models by varying only the regularization multiplier. In contrast, for *M. robinsoni*, represented by numerous localities, we created preliminary models varying both feature classes and the regularization multiplier (via \( k \)-fold cross-partitioning, with \( k = 5 \), leading to \(~80\%\) for calibration and \(~20\%\) for evaluation in each iteration).

Together, regularization multiplier and feature class affect model complexity. The regularization multiplier controls the strength of the penalties for complex models (the stronger the multiplier, the stronger the penalty for a complex model; Phillips et al. 2006; Warren and Seifert 2011). Complex models, unfortunately, are more prone to overfitting (i.e. situations in which a model is more complex than the real relationships between the species’ niche and the examined environmental variables; Anderson and Gonzalez 2011, Warren and Seifert, 2011). Feature classes represent the kinds of mathematical responses that the algorithm is allowed to consider. For *Marmosa robinsoni*, we considered combinations of feature classes likely to be reasonable given the number of localities available (see Phillips et al. 2006, Phillips and Dudík 2008, Anderson and Gonzalez 2011): linear, quadratic, and hinge (LQH); linear, quadratic, and product (LQP); linear,
quadratic, product, and hinge (LQPH); linear, quadratic, product, and threshold (LQPT); and linear, quadratic, product, hinge, and threshold (LQPHT; the default combination of feature classes for this number of localities). For *M. xerophila*, we used linear and quadratic features (LQ; the default combination of feature classes for this number of localities; see above). For each of these feature-class combinations, we constructed models using regularization multiplier values of 0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, and 4.0, and implemented replicates to identify the settings that led to the highest average performance on held-out data (see below).

**Methods employed to evaluate preliminary models**

We employed threshold-independent and threshold-dependent measures to evaluate preliminary-model performance according to two criteria: 1) the degree to which they avoided overfitting and 2) their discriminatory power (Radosavljevic and Anderson 2013, Shcheglovitova and Anderson 2013). Our primary criterion for these evaluations was the least degree of overfitting. Overfit models underestimate species’ abiotically suitable areas, with various detrimental effects (Phillips and Dudík 2008, Anderson and Raza 2010, Anderson and Gonzalez 2011). We assessed overfitting with both threshold-independent and threshold-dependent measures. For the former, we used $\text{AUC}_{\text{Diff}}$ of Warren and Seifert (2011), which is based on the area under the curve (AUC) of the receiver operating characteristic (ROC) plot. For any given model, $\text{AUC}_{\text{Diff}}$ (difference) equals the calibration AUC minus the evaluation AUC ($\text{AUC}_{\text{Diff}} = \text{AUC}_{\text{Train}} - \text{AUC}_{\text{Test}}$ of Warren and Seifert 2011). Because overfitting typically results in high calibration AUCs and low evaluation AUCs, the first optimality criterion implemented here preferred MAXENT settings that yielded the lowest possible $\text{AUC}_{\text{Diff}}$. As a second measure to assess this first optimality criterion (low overfitting), we used the threshold-dependent omission rate. An omission rate indicates the proportion of the localities of the
species that fall outside of (are omitted from) areas predicted to be suitable by the model (Anderson et al. 2003, Phillips et al. 2006). Overfit models tend to yield high omission rates (Anderson and Gonzalez 2011, Peterson et al. 2011). Because of this, the first optimality criterion preferred those MAXENT settings that yielded the lowest possible omission rates (and those that best approximated the theoretical expectation of the thresholding rule applied). To convert model output to binary predictions and calculate the omission rates, we applied the 10th percentile threshold (i.e. 10 percentile training omission threshold of MAXENT; “T10” of Pearson et al. 2007), the value at which the model omits 10% of the calibration localities. Using this rule, we expect approximately 10% omission of evaluation localities.

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

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

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

**Results from evaluations of preliminary models**

Among the preliminary models of *Marmosa robinsoni*, those that showed the least overfitting and the highest discriminatory power were calibrated with linear, quadratic, and hinge (LQH) feature classes and a regularization multiplier value of 2.5. At this regularization multiplier value, the LQH feature classes yielded both the lowest average AUC_{diff} (0.0548) and the lowest omission rate (13%), which was also the omission rate closest to the theoretical expectation (i.e. 10% for the applied 10th percentile threshold rule). With regard to discriminatory power, the LQH feature classes yielded higher evaluation AUC values than other feature classes across all regularization multipliers; however, there was little variation among the evaluation AUC values across regularization multipliers. Each of the five preliminary models calibrated with LQH feature classes and regularization multiplier 2.5 predicted evaluation localities significantly better than random \((P < 0.012)\). Based on these results, we calibrated the final model of *M. robinsoni* using the LQH feature classes and a regularization multiplier value of 2.5.
Tuning experiments for *Marmosa xerophila* led to selection of the regularization multiplier 1.5 as optimal (as mentioned earlier, we used default feature classes for this species; i.e. linear and quadratic; LQ). The value 1.5 yielded both the lowest AUCDIFF (0.085) and the lowest average evaluation omission rate (20%). This omission rate is somewhat higher than that theoretically expected (10%) for the threshold rule employed. Taken as a whole, the suite of jackknifed models for this species did not lead to statistical significance (*P* = 0.755), likely due to a very large proportional predicted area (average = 75% of the study region, which afforded very low statistical power). Based on these results, we calibrated the final model of *M. xerophila* using the LQ feature classes and a regularization multiplier value of 1.5.

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


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*.