Research

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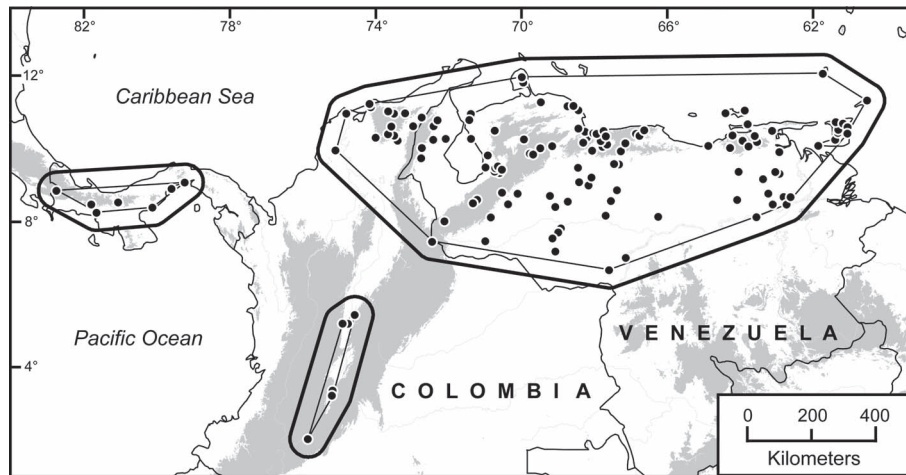
Figure 1. Spatially filtered localities of *Marmosa robinsoni* and study region used to calibrate models of its abiotically suitable areas. For each section of the study region, minimum convex polygons (thin lines) and their corresponding buffer (thick lines) are indicated (Material and methods). Shaded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

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
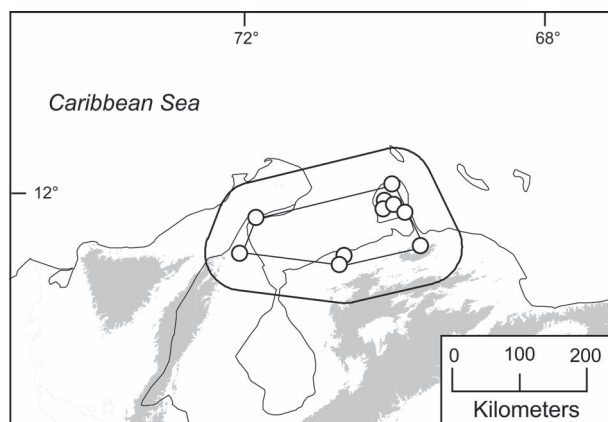

Figure 2. Spatially filtered localities of *Marmosa xerophila* and study region used to calibrate models of its abiotically suitable areas. The minimum convex polygon (thin line) and its corresponding buffer (thick line) are indicated (Material and methods). Shaded areas represent elevations ≥ 500 m.

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 georreferencing 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://biogeo.berkeley.edu/worldclim/worldclim.htm>, at 30″ resolution; 0.93×0.93 km $= 0.86$ 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).
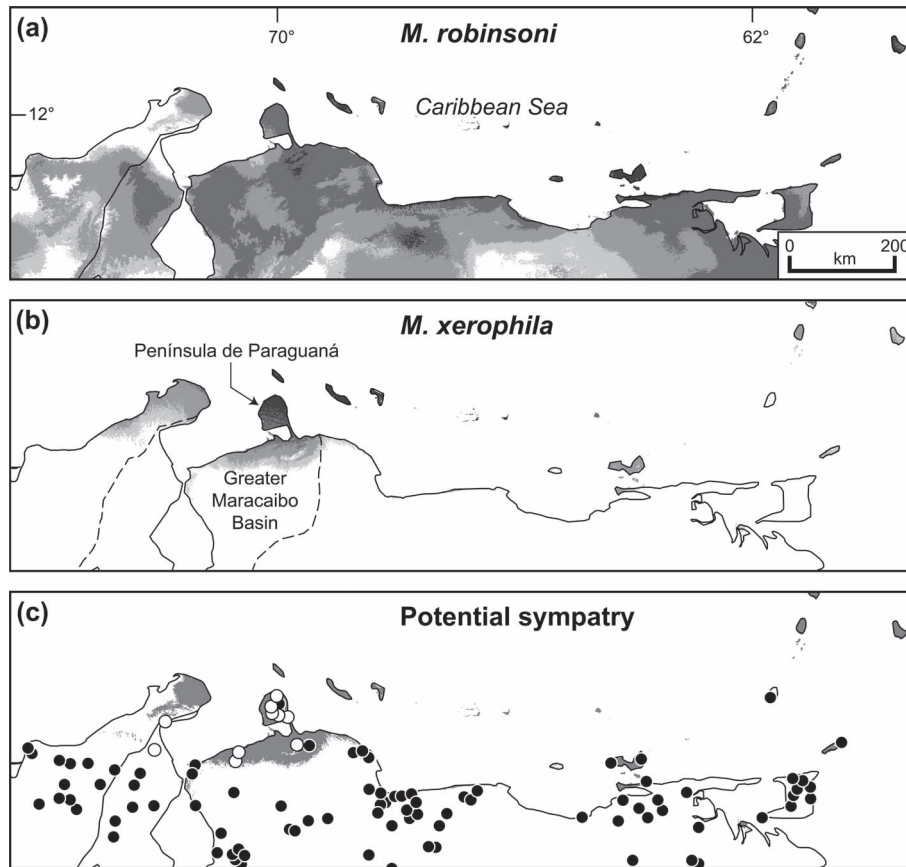
Figure 3. Results of ecological niche models, shown in northcentral South America and adjacent Caribbean islands: (a) final Maxent model of abiotically suitable areas for *Marmosa robinsoni*; (b) final Maxent model of abiotically suitable areas for *M. xerophila*, and (c) areas of potential sympatry 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
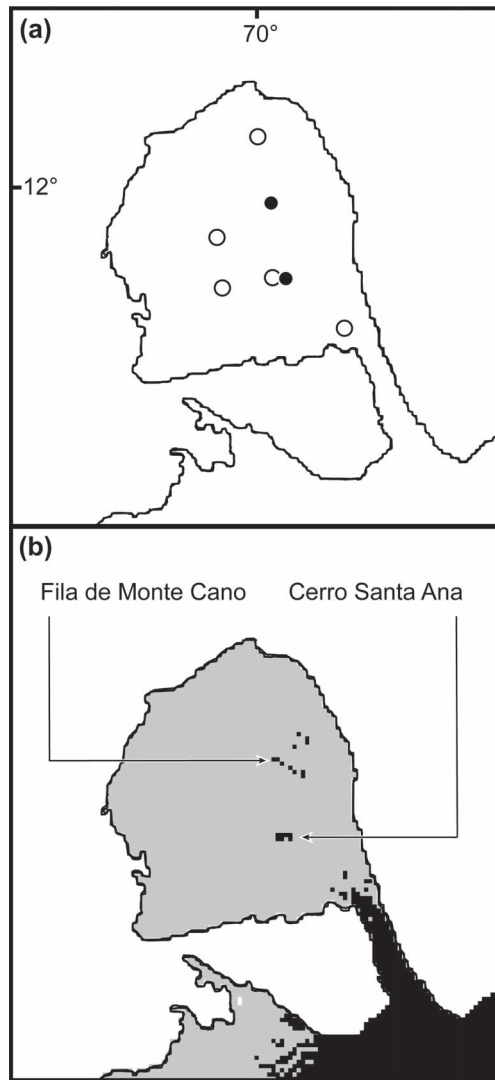
Figure 4. Areas of potential sympatry for *Marmosa robinsoni* and *M. xerophila* in northern Estado Falcón (Venezuela) showing areas more strongly predicted for each species. (a) Occurrence records of focal species. Black circles represent localities of *M. robinsoni*; white circles represent localities 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,
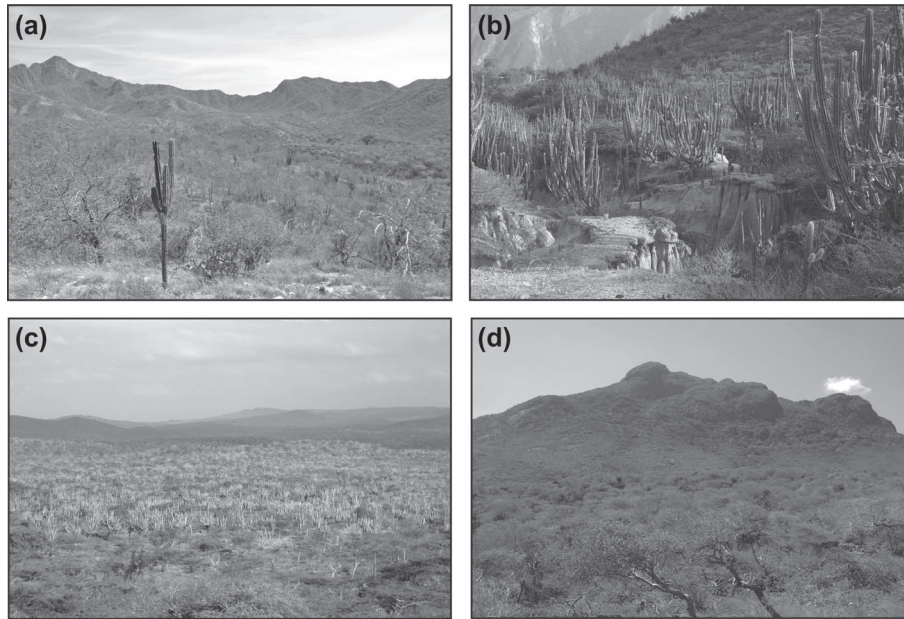
Figure 5. Examples of Venezuelan regions with suitable conditions for both of the focal species but occupied by *Marmosa robinsoni*. The first three represent xeric landscapes in areas far from the documented distribution of *M. xerophila*. The last constitutes a more mesic area along the documented 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). Futhermore, 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 modifed 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
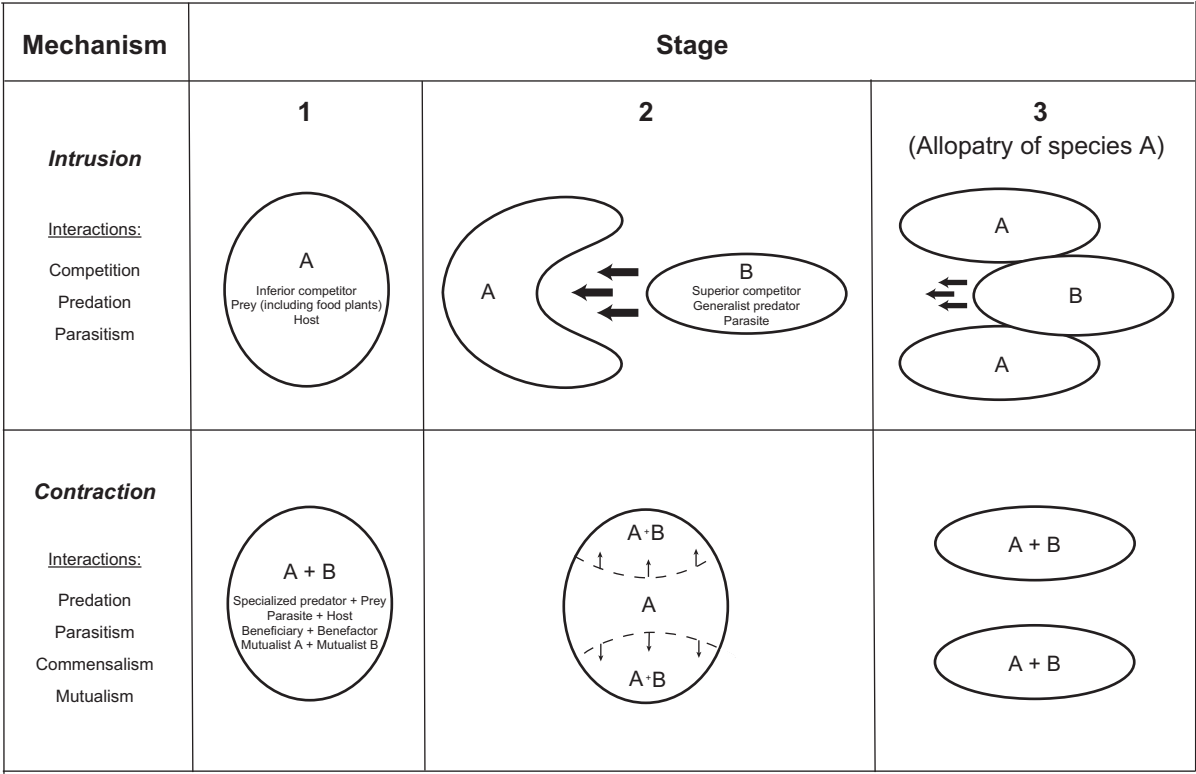

Figure 6. Schematic view of the classes of mechanisms by which biotic interactions can lead to allopatry. Species A experiences division of its original range as a consequence of its interaction with species B, and its resulting distributional areas are allopatric. Range intrusion: the intrusion of species 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 comensalist (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. Transfering 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).

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 Paraguaná – 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 Península 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.ecography.org/readers/appendix>). Appedix 1–3.