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The effect 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**

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ABSTRACT

Various niche-based techniques exist to model a species' potential geographic distribution in a Geographic Information Systems (GIS) framework. These models compare the environmental conditions of localities of a species' occurrence versus those of the overall study region. In addition to uses in areas such as macroecology and conservation biology, this approach has been applied recently to studies of niche evolution and historical biogeography. Definition of the study region is critical for all of these applications but has not been addressed previously. Here, I examine the effect of changes in the extent of the study region on potential distribution models of two rodents (genus *Nephelomys*) in northern Venezuela. Models were produced using Maxent (a computer modeling program that utilizes the maximum-entropy principle), occurrence records from the literature, and 19 bioclimatic variables. First, I modeled each species in a large study region that included the ranges of both species (Method 1; typically employed in most studies to date). Second, I modeled each species in a smaller study region surrounding its respective localities, and then applied the model to the larger region (Method 2). Because the study region of Method 1 is likely to include areas of bioclimatically suitable habitat that are unoccupied by the species due to dispersal limitations and/or biotic interactions, this approach is prone to overfitting to conditions found near the known localities. In contrast, Method 2 is predicted to avoid such problems. I assessed differences in predictions for each species due to changes in the extent of the study region by calculating several measures of geographic interpredictivity between the species (indirect measures of niche overlap). Method 2 reduced problems

characteristic of overfitting. In addition, it led to higher—and likely more realistic—estimates of interpredictivity between the species, which suggests higher niche conservatism. Models of species' potential geographic distributions should be made using a study region that excludes areas of suitable conditions from which the species is known or likely to be absent because of dispersal limitations and/or biotic interactions.

Keywords: background sampling, Maxent, niche overlap, overfitting, presence-only modeling, range, transferability

INTRODUCTION

Recent studies modeling species potential geographic distributions using Geographic Information Systems (GIS) have led to a renaissance in studies of the ecological and evolutionary aspects of distributions (Graham et al., 2004). These modeling approaches use two kinds of data. First, they require localities (occurrence records) of the species' presence, but do not need information regarding localities where the species is absent. Second, they utilize environmental, usually climatic, variables for the study region. Using these input data, the algorithms generate a model of the species' niche requirements in the examined dimensions of ecological space. The niche model is then applied to geographic space to identify areas potentially suitable for the species.

In forming the niche model, most of the algorithms compare the environmental conditions in areas where a species is known to occur versus those of the overall study region, typically by taking a random “background,” or “pseudoabsence,” sample of pixels (grid cells on a raster map) from the study region (Elith et al., 2006; see also Zaniwski et al., 2002). These pixels are used to characterize the environmental conditions available in the study region for comparison with the conditions in pixels where the species is known to inhabit. Thus, definition of the study region is a critical issue, but it has not yet been addressed. Although I focus my study of this issue specifically in the context of niche evolution, resolution of this problem is crucial for all uses of niche-based distributional modeling including conservation biology (e.g., Kremen et al., 2008)—and perhaps especially for the study of invasive species (e.g., Welk et al., 2002), estimation of distributional changes under climatic change (e.g., Araújo et al., 2005), and examination

of niche evolution in a phylogenetic context (e.g., Peterson et al., 1999; Graham et al., 2004; Wiens & Graham, 2005; Kozak & Wiens, 2006). Furthermore, it may help resolve polemic issues regarding model utility and transferability (generality) brought up recently (Randin et al., 2006; Peterson et al., 2007; Phillips, 2008).

Here, I examine the effects that changes in the study region have on niche models and geographic predictions for two closely related species. Using Maxent (Phillips et al., 2006), I model the distributions of two rodents, *Nephelomys caracolus* (Thomas) and *N. meridensis* (Thomas), in northern Venezuela. The genus *Nephelomys* was described recently for the “*albigularis*” species group, which was formerly assigned to the polyphyletic genus *Oryzomys* (Weksler et al., 2006). *Nephelomys caracolus* inhabits the coastal mountains of north-central Venezuela (Cordillera de la Costa), whereas *N. meridensis* is found in the Cordillera de Mérida in northwestern Venezuela (Fig. 1). These species inhabit montane forests from approximately 1050 to 4000 m (Percequillo, 2003). Externally, they are indistinguishable from one another; however, internal morphological and karyological research have shown consistent differences indicating that they are distinct species (Aguilera et al., 1995; Márquez et al., 2000; Percequillo, 2003). Although the current analyses do not require that they be sister species, their probable close phylogenetic relationship makes it likely that they will have similar niches and potential geographic distributions. This likely similarity is not at all required for my analyses; however, such a situation makes these species a convenient model for studying the effect of the study region on species’ predicted distributions and niche overlap.

I use two methods of defining the study region. In the first (Method 1), each species’ potential distribution is modeled in a large study region that includes the ranges

of both species. In the second (Method 2), each species is modeled in a smaller study region immediately surrounding its known localities. The resulting model is then applied (projected) to the larger region (that used for modeling in Method 1), identifying the areas that are suitable for the species according to the model made using the smaller study region. After making the models using each method, I analyze how well the potential distribution of the focal species predicts the localities of the other species (interpredictivity), indicating the level of niche conservatism (lack of niche evolution) present between the species. Based on these results, I make recommendations for selecting an appropriate study region.

MATERIALS AND METHODS

Locality data

Niche-based distributional modeling requires two types of input data: known localities of a species and environmental data for the study region. I obtained localities for the species from a variety of taxonomic and faunal studies (Díaz de Pascual, 1994; Moscarella & Aguilera, 1999; Márquez et al., 2000; Percequillo, 2003; Rivas & Salcedo, 2006). I then georeferenced (assigned latitude and longitude to) each locality using gazetteers, detailed topographic maps, and other sources (see Appendix 1), leading to 14 unique localities (unique latitude–longitude combinations) for *Nephelomys caracolus* and 19 for *N. meridensis*. The process of georeferencing includes an assessment of the uncertainties in geographic coordinates (e.g., missing data, precision of the locality description, map scale, and ambiguity in linear versus road distances). Based on the level of uncertainty, I estimated maximum error in kilometers for the coordinates of each locality. Then, I identified clusters of localities that likely represented the result of sampling bias (e.g., more sampling near major cities or universities, along roads, etc.). To reduce the effect of sampling bias, I obtained the maximum number of localities for each species that were at least 10 km apart (see below). When multiple equally optimal solutions were possible for a given cluster, I retained the combination of localities with the lowest total error. This process yielded 8 spatially filtered localities for *N. caracolus* and 8 for *N. meridensis* (Fig. 1), which were used for all subsequent analyses. Although these filtered localities are a reduced set, they have two important advantages over the original georeferenced localities. First, since they likely reflect less of an environmental bias produced by

uneven sampling by mammalogists, they should yield better estimates of the species' niches. Second, for the same reason, they provide more reasonable data for evaluating how well the models of one species predict known localities of the other (interpredictivity). Given the heterogeneity of the terrain in the known ranges of the species, the cutoff of 10 km likely achieves these goals without unduly decreasing the number of localities available for modeling.

Environmental variables

For the environmental data, I used 19 bioclimatic variables from WorldClim 1.4 (Hijmans et al., 2005; <http://www.worldclim.org>). These bioclimatic variables are derived from monthly temperature and precipitation data to create variables that are more biologically relevant (e.g., annual mean temperature, temperature of the wettest quarter, precipitation seasonality, etc.; see Appendix 2). I used raster grids (data spatially structured into grid cells, or pixels, each containing a value for a given variable) of these bioclimatic variables with a spatial resolution of 30 seconds ($0.93 \text{ km} \times 0.93 \text{ km} = 0.86 \text{ km}^2$ at the equator).

Defining the study region

As mentioned above, I used two methods of defining the study region in my analyses. In Method 1 (Fig. 1A), following the practice typically used in the literature (see below), I modeled the potential distribution of each species in a large study region that included the ranges of both species as well as other adjacent regions of biogeographic interest (extending the study region to the Caribbean coast in the north; $7.5\text{--}13^\circ \text{ N}$ and $65\text{--}72.5^\circ$

W). In Method 2 (Fig. 1B, C), I modeled each species in a smaller study region immediately surrounding its known, spatially filtered, localities (9.5–11° N and 66–69° W for *N. caracolus*; 7.5–10° N and 69–72.5° W for *N. meridensis*). For Method 2, I then applied the respective model to the larger study region (employed for modeling in Method 1).

In delimiting the study regions in this way, I aimed to compare current common practices in the field with a possible alternative. Most researchers delimit a study region including all areas of interest to them when interpreting the model in geography (e.g., Kozak and Wiens 2006; Phillips et al., 2006). While Method 1 follows the spirit of this common approach, Method 2 contrasts by being much smaller in most cases. An alternative intermediate option could be to delimit a study region that immediately encompasses only the areas surrounding *both* species' known occurrences. Here, such a tactic would exclude the northernmost regions from 11–13° N (Fig. 1A). Because the difference between such a study region and the one used for Method 1 in the current study is only a difference of 2° in latitude (much of which falls in the Caribbean Sea), it is likely that using such a study region would yield results similar to those obtained here. To simplify comparisons, I only conducted experiments with two study regions but note that the third option could be assessed in future analyses.

Each method has disadvantages in modeling a species' potential distribution. When using a larger study region (Method 1) to model a species' niche, the model may be prone to overfitting to environmental conditions present in the region where the species is known to occur. Such a model would indicate that suitable regions for the species are restricted to areas near known presences (overfitting due to bias in the

localities used to generate the model). This can happen because the model recognizes spurious environmental differences between the region that a species actually inhabits versus other regions that it could inhabit but does not (e.g., because of a geographic barrier that prevents it from dispersing to those regions). Overfitting leads to artificially lowered transferability (Randin et al., 2006; see also Discussion).

However, when a model is constructed using a smaller study region (Method 2) and then applied to a larger study region, the values for one or more environmental variables in some pixels of the larger study region may not be covered by the niche model (which is trained, in the smaller study region). This can arise because such values do not occur in the study region used for training; hence, they lie outside the range of values for the corresponding variable(s) in the study region used for making that niche model. This arises in many other situations as well, such as when applying a model to another time period (e.g., after climatic change) or region (e.g., prediction of an invasive species). In these cases, some assumption about the potential suitability of those pixels must be made, or no prediction can be generated for them (Phillips et al., 2006).

For example, at one extreme, all pixels holding values for climatic variables outside the range (in environmental space) of those in the model can be assumed to be unsuitable for the species; this almost certainly would lead to overly restrictive estimates of a species' potential distribution. At the other end of the spectrum, such pixels could all be assumed to be maximally suitable, producing an overly extensive estimate of the species' potential distribution. Another possible assumption, intermediate between the previous two, extrapolates the trend of environmental suitability that is modeled in the training region. For example, if the model that is made in the smaller study region

indicates that increasingly wetter environments are progressively more suitable for a species, this assumption would lead to the prediction that environments wetter than those found in the training region would be even better for the species. Extrapolation becomes especially risky the farther that the pixel lies in environmental space from conditions present in the training region, at least for response curves that are increasing when truncated by the environment present in the training region.

Currently, Maxent resolves this issue via a more conservative assumption that is termed ‘clamping’ (similar in some ways to Winsorization in biostatistics; Sokal & Rohlf, 1995). Under clamping, in cases where a pixel has a value for a given variable outside the range covered in the model; that pixel is given the closest value present for that variable in the model. For example, if the model calibrated in the smaller study region indicates that increasingly wetter environments are progressively more suitable for a species, the model would then predict that even wetter environments that are found in the larger study region are equally good for the species (but not better). This is more conservative, and probably more realistic, than extrapolation of the trend modeled in the training region (see above). However, clamping remains an untested assumption in most studies and will still be prone to erroneously extensive predictions for response curves that are high (or increasing) when truncated by the environment present in the training region. To alert the user to such possibilities, Maxent provides a map showing the degree of clamping (if any) that was employed in each pixel when making a prediction into the larger study region. No prediction should be interpreted without assessing the effect that clamping has had on the prediction.

Model building

I modeled the potential distributions of *Nephelomys caracolus* and *N. meridensis* using Maxent version 3.1.0 (Phillips et al., 2006; Phillips & Dudík, 2008). Maxent has performed well, based on quantitative measures of model performance, in recent comparisons with other niche-based distributional modeling techniques (Elith et al., 2006; Hernandez et al., 2006; Wisz et al., 2008). I used 19 bioclimatic variables and 8 localities for each species to make the models. I produced models using both linear and quadratic features and with default levels of regularization (penalty for making a complex model, thereby providing protection against overfitting). Lastly, I selected the logistic output format, which yields continuous values ranging from 0–1 indicating relative environmental suitability for the species (specifically, the probability of suitable environmental conditions, or probability of presence if dispersal limitations or biotic interactions are not relevant; see Phillips and Dudík, 2008). I first made preliminary models to evaluate how well the models predicted localities of the focal species itself (using some of the available spatially filtered localities; see below). The goal of these preliminary models was to ensure that the variables used and model settings employed can indeed produce satisfactory models for each individual species. These models were assessed using threshold-dependent evaluations (see below). I then made final models for each species using all available spatially filtered localities, which were used for all subsequent analyses.

Model evaluation

To evaluate the preliminary models, I used threshold-dependent evaluation as an indicator of how well the model of each species predicted its own localities. Because only 8 localities of each species were available, I implemented the jackknife procedure for model assessment (Pearson et al., 2007). For each species, 8 models were built by removing each locality once in turn. In other words, a different set of 7 (out of 8) localities was used to build the model during each training iteration (with a total of 8 iterations per species). Then, I assessed predictive performance based on the ability of each model to predict the single locality excluded from the training data set. The significance of the set of models for each species was assessed based on p -values following Pearson et al. (2007). A p -value for the jackknife tests ≤ 0.05 indicates that test localities are predicted better than by a random prediction with the same fractional predicted area (fraction of the study area predicted suitable for a species). To divide the continuous prediction into a binary prediction of presence or absence for these tests, I used the minimum training weight (MTW) threshold (= lowest presence threshold of Pearson et al., 2007). This is the minimum weight given to any of the training localities and indicates the least-suitable environmental conditions for which a locality was available in the training data set. I conducted these analyses for models made using the smaller study region, and then for models produced using the larger study region.

Assessing interpredictivity

To compare the two methods of defining the study region, I used the final models to assess interpredictivity between the species' niche models in three ways. First, I used the

model for the focal species to assess the strength of the prediction of localities of the *other* species by comparing the Area Under the Curve (AUC) of a Receiver Operating Characteristic plot (Phillips et al., 2006) between the two methods. The AUC values represent a threshold-independent measure of interpredictivity (independent of any cutoff point dividing a prediction into suitable versus unsuitable areas for a species). Hence, these cross-species AUC values provide an overall assessment of how well the model of each focal species predicted localities of the other. For models made using Method 1, I was able to obtain cross-species AUC values from Maxent by specifying the localities for that species as test localities in the focal species' model. However, this was not possible for models built using Method 2. Therefore, for Method 2, I obtained cross-species AUC using DIVA-GIS 5.2 (Hijmans et al., 2001; <http://www.diva-gis.org>). For each species, I selected 1500 random background pixels from the larger study region, along with the pixels corresponding to the localities of the test species, which together were used to obtain ROC plots and the cross-species AUC values for Method 2.

The second way I assessed interpredictivity was by calculating cross-species omission rates, a threshold-dependent measure that indicates how well the model of the focal species predicts localities of the other species. We applied a threshold to convert the continuous prediction of environmental suitability for the species (logistic values from 0 to 1) into a binary prediction, dividing the study region into areas predicted suitable versus unsuitable for the species. As in assessing the preliminary models, I achieved this by applying the minimum training weight (MTW) threshold. Using this binary prediction, I calculated the cross-species omission rates by determining the percentage of localities of the other species falling outside of (omitted from) areas predicted suitable for the focal

species. I then compared these between the two methods.

Third, I examined the effect that the two methods have on the degree of geographic overlap between the two species' potential distributions. I accomplished this by superimposing the potential distributions of the two species in the larger study region (after applying the MTW threshold rule; see above). Then, the percentage of geographic overlap was estimated by dividing the number of pixels predicted suitable for both species by (1) the total number of pixels with data (e.g., excluding the ocean), (2) the total number of pixels predicted suitable for each species alone, and (3) the total number of pixels predicted suitable for either species.

Predictions

I expected the predicted species' distributional models to be less concentrated in the region surrounding the species' localities in Method 2 (reduced overfitting; likely a problem for Method 1). Therefore, I predicted higher interpredictivity in Method 2, as evaluated by (1) higher cross-species AUC values, (2) lower cross-species omission rates, and (3) higher percentage of geographic overlap.

RESULTS

Preliminary models

Threshold-dependent evaluation via the jackknife procedure revealed that the models adequately predicted each individual species' potential distribution. Pixels with values greater than or equal to the MTW threshold are considered suitable, whereas pixels with values below that threshold are deemed unsuitable. Test omission rates were low ($\leq 25\%$; only 1 of 8 iterations omitted the test locality, except for Method 2 for *N. caracolus* in which 2 of 8 iterations omitted the test locality). Furthermore, the jackknife tests indicated that the models were significantly better than random predictions for both species, with p -values well below 0.05 ($p \leq 1 \times 10^{-6}$). Omission rates and significance values were similar for models made with the two study regions.

Qualitative assessment of final models

Maxent generated models of the potential distribution of each species showing a continuous prediction of relative suitability (Fig. 2A–D). The prediction for *Nephelomys caracolus* revealed highest suitability in the mountain ranges of the north-central coast, the Cordillera de Mérida (northwestern Venezuela), and the Serrenía de San Luis (northwestern coast of Venezuela), separated by gaps of low suitability between these ranges (Fig. 2A, C). In contrast, the areas strongly predicted for *N. meridensis* generally appeared to be restricted to the Cordillera de Mérida (Fig. 2B, D). The models for each species varied depending on the method of defining the study region. Models generated using Method 2 predicted larger areas with high suitability than models generated using

Method 1. Additionally, Method 1 yielded models with the highest suitability generally restricted to areas near the focal species' known localities, whereas Method 2 produced predictions that were less concentrated around the known localities of the focal species.

Clamping was minimal in most of the study region. In the present analyses, areas with a high degree of clamping occurred primarily in lowland regions that are unlikely to be suitable for the species (Fig. 2E, F). These included extremely dry lowland regions in the Península de la Guajira in northeastern Colombia and northwestern Venezuela, and along the Caribbean coast of northwestern Venezuela, both east and west of the mouth of the Lago de Maracaibo. Another area of high clamping occurred in very wet regions at the base of the Cordillera de Mérida, southwest of the Lago de Maracaibo.

Quantitative assessment of interpredictivity

Cross-species AUC values varied between the two methods of defining the study region. The AUC for the localities of *Nephelomys meridensis* in the predicted potential distribution of *N. caracolus* was slightly higher in Method 2 (Table 1). Similarly, the potential distribution of *N. meridensis* predicted the known localities of *N. caracolus* with a slightly higher AUC in Method 2 (Table 1).

Cross-species omission rates were lower in models made using Method 2 compared with Method 1. Models of *Nephelomys caracolus* predicted localities of *N. meridensis* better than models of *N. meridensis* predicted localities of *N. caracolus*. At the MTW threshold, the potential distribution of *N. caracolus* predicted slightly over half of the known localities of *N. meridensis* using Method 1, but achieved an omission rate of zero using Method 2 (Fig. 3A, C; Table 1). In contrast, the potential distribution of *N.*

meridensis predicted only half of the known localities of *N. caracolus* in Method 1, and slightly more in Method 2 (Fig. 3B, D; Table 1; at MTW threshold).

The two species showed substantial yet incomplete geographic overlap, but those estimates varied depending on the method of defining the study region. Method 2 revealed a larger predicted area for each species compared with Method 1 (Fig. 3). Not surprisingly, percentages of geographic overlap between the two species' predicted distributions were consistently higher using Method 2 (Table 2).

DISCUSSION

My results show differences in the predicted potential distributions and in estimates of interpredictivity between the two methods of defining the study region. Method 2 appears to perform better because it reduces overfitting (a problem observed for Method 1).

Clamping (a possible drawback to Method 2) did not seem to be a problem in the models analyzed here. These results suggest that the study region used for modeling a species' potential distribution should not include areas where the species may be absent due to dispersal limitation. This is because background pixels randomly drawn from suitable environments in such regions provide a false negative signal that interferes with successful modeling of the species' environmental requirements. Similarly, I also propose that the study region for modeling should not include areas where biotic interactions with other species (principally competition) are likely to restrict the species' distribution to less than its potential (Anderson et al., 2002), for the same reasons mentioned for dispersal limitation. Clearly, such information will be difficult to estimate in many cases. Future research should aim to develop operational guidelines for selecting an appropriate study region based on these principles.

Recent studies have used niche modeling to investigate evolutionary processes, and studies that follow this line of research should consider definition of the extent of the study region and background selection carefully. Niche conservatism refers to the propensity for species to maintain the same niche over evolutionary time (Peterson et. al., 1999). Building on these concepts, Graham et al. (2004) proposed ways to study speciation by integrating phylogenetic information, distributional overlap of species, and

niche models. Similarly, Kozak and Wiens (2006) suggested that niche conservatism and climatic differences in geographic space could play an important role in speciation events. To conduct valid tests of hypotheses of niche evolution versus niche conservatism, researchers should select an appropriate study region for making niche-based models in order to obtain the best estimates of niche overlap.

Additionally, my results are relevant to other areas of research using niche-based distribution modeling. Any application requiring an estimate of the species' potential geographic distribution should strive to conduct modeling based on an appropriate study region. In particular, selection of an appropriate study region is especially germane for studies of invasive species and of species' distributional changes under climatic change (Welk et al., 2002; Araújo et al., 2005). In both of those applications, model transferability (or generality) is critical (Araújo & Rahbek, 2006; Randin et al., 2006; Peterson et al., 2007; Phillips, 2008). Transferability refers to how adequately a model produced in one situation may be transferred to a different context to provide useful insight in the latter case (e.g., another time period after climatic change; or another region in the prediction of an invasive species). Whereas models produced with an overly large study region likely will show low transferability, models made based on an appropriate study region should show higher transferability. The conceptual advances and principles espoused here also may help resolve some currently controversial issues regarding characterization of the background (the study region) and its association to the region from which the training localities derive (Peterson et al., 2007; Phillips, 2008); specifically, future research should consider the possibility that selecting training records from only some portions of the study region may mimic the natural processes discussed

here (dispersal limitation and biotic interactions) that can cause a species to inhabit less than its potential distribution.

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Appendix 1. Gazetteer of spatially filtered occurrence records used in this study.

Boldface type indicates the place to which geographic coordinates correspond. The source for the record follows the elevation, and the source for the coordinates follows the latitude and longitude.

Nephelomys caracolus: VENEZUELA: ARAGUA: **Rancho Grande**, Estación Biológica de Rancho Grande, 13 km NW Maracay [= 14 km N, 14 km W Maracay, Rancho Grande], 1050–1100 m (Percequillo, 2003), 10°21' N, 67°40' W (Handley 1976); Natural Monument **Pico Codazzi**, Coastal Cordillera, 1700 m (Moscarella & Aguilera 1999), 10°23' N, 67°20' W (Moscarella & Aguilera 1999); CARABOBO: **La Cumbre de Valencia**, 1700 m (Percequillo, 2003), 10°20' N, 68°00' W (Paynter 1982); DISTRITO CAPITAL: **Los Venados**, 4 km NNW Caracas [= 5 mi N Caracas], 1400–1739 m (Percequillo, 2003), 10°32' N, 66°54' W (Handley 1976); DISTRITO CAPITAL/MIRANDA/VARGAS: **Alto Ño León**, 31–36 km WSW Caracas [= 5 km S, 23 km W Caracas, Alto Ño León; Alto Ño León, 20 km W Caracas; Petaquire, 20 km N (W) Caracas], 1665–2050 m (Percequillo, 2003), 10°26' N, 67°10' W (Handley 1976); MIRANDA: **5 km NNW Guarenas** [= Curupao, 19 km E Caracas], 1160 m (Percequillo, 2003), 10°31' N, 66°38' W (Handley 1976); **Quebrada Caurimare**, Fila Santa Rosa, Parque Nacional El Ávila, 1750 m (Rivas & Salcedo, 2006), 10°31' N, 66°47' W (DCN 1964, 1979b; coordinates correspond to Río Caurimare [= Quebrada Caurimare] at indicated elevation); **Hacienda Las Planadas**, aproximadamente 25 km [by road] N de Guatire, 1270 m (Rivas & Salcedo, 2006), 10°32' N, 66°30' W (DCN 1964, 1979a; coordinates correspond to indicated elevation at Hacienda Las Planadas).

Nephelomys meridensis: VENEZUELA: LARA: **Yacambú National Park**, 1645 m (Márquez et al., 2000), 9°42' N, 69°37' W (Anderson, 2003; coordinates correspond to El Blanquito, the principal collection locality in Yacambú National Park); MERIDA: Montes de **Los Nevados**, 2500 m (Percequillo, 2003), 8°28' N, 71°04' W (DCN 1977a; Paynter 1982; see also Phelps 1944); **Montes de Chama**, 2500 m (Percequillo, 2003), 8°31' N, 71°11' W (DCN 1977a; Phelps 1944; not Paynter 1982; coordinates correspond to indicated elevations S La Punta as drawn on map in Phelps [1944]); **La Coromoto**, 4 km E, 6.5 km S Tabay [= La Coromoto, 7 km SE Tabay], 3070–3410 m (Percequillo, 2003), 8°36' N, 71°01' W (DCN 1975, 1977a; Handley 1976); near **Santa Rosa**, 1 km N, 2 km W Mérida [= Santa Rosa (La Hechicera) 1–2 km N Mérida], 1970 m (Percequillo, 2003), 8°37' N, 71°09' W (Handley 1976); **San Eusebio**, SE of La Azulita [= La Carbonera, 12 km SE La Azulita], 2190 m (Percequillo, 2003), 8°39' N, 71°23' W (DCN 1977a; see also Handley 1976); **Montes de La Culata**, 2800–4000 m (Percequillo, 2003) 8°45' N, 71°05' W (DCN 1977b; Paynter 1982; coordinates correspond to indicated elevation above La Culata); TRUJILLO: **Hacienda Misisí**, 14 km E Trujillo, 2215–2365 m (Percequillo, 2003), 9°21' N, 70°18' W (Handley 1976).

Appendix 2. List of the 19 bioclimatic variables from WorldClim 1.4 (Hijmans et al., 2005; <http://www.worldclim.org>) that were used in this study.

1. Annual mean temperature
2. Mean diurnal range (mean of monthly values of maximum temperature minus minimum temperature)
3. Isothermality
4. Temperature seasonality
5. Maximum temperature of the warmest month
6. Minimum temperature of the coldest month
7. Temperature annual range
8. Mean temperature of the wettest quarter
9. Mean temperature of the driest quarter
10. Mean temperature of the warmest quarter
11. Mean temperature of the coldest quarter
12. Annual precipitation
13. Precipitation of the wettest month
14. Precipitation of the driest month
15. Precipitation seasonality
16. Precipitation of the wettest quarter
17. Precipitation of the driest quarter
18. Precipitation of the warmest quarter
19. Precipitation of the coldest quarter

Figure 1. The two methods used to define the study region for modeling the potential distributions of *Nephelomys caracolus* (blue circles, B) and *N. meridensis* (red triangles, C). Models (not shown here) were generated using these spatially filtered localities of each species. Shaded areas represent elevations ≥ 1000 m. *N. caracolus* (blue circles in B) is found in the coastal mountains of north-central Venezuela (Cordillera de la Costa), whereas *N. meridensis* (red triangles in C) occurs in the Cordillera de Mérida in the northwest part of the country (the southwestern portion of this map). These species inhabit montane forests at ca. 1050–4000 m. In Method 1, each species' potential distribution was modeled in a large study region that included the ranges of both species (dashed rectangle, A). In Method 2, each species was modeled in a smaller study region encompassing its known localities (solid rectangles, B for *N. caracolus* and C for *N. meridensis*); then, this model was applied to the larger region used for modeling in Method 1 (dashed rectangle, A), identifying environmental suitability for the species throughout the whole larger region.

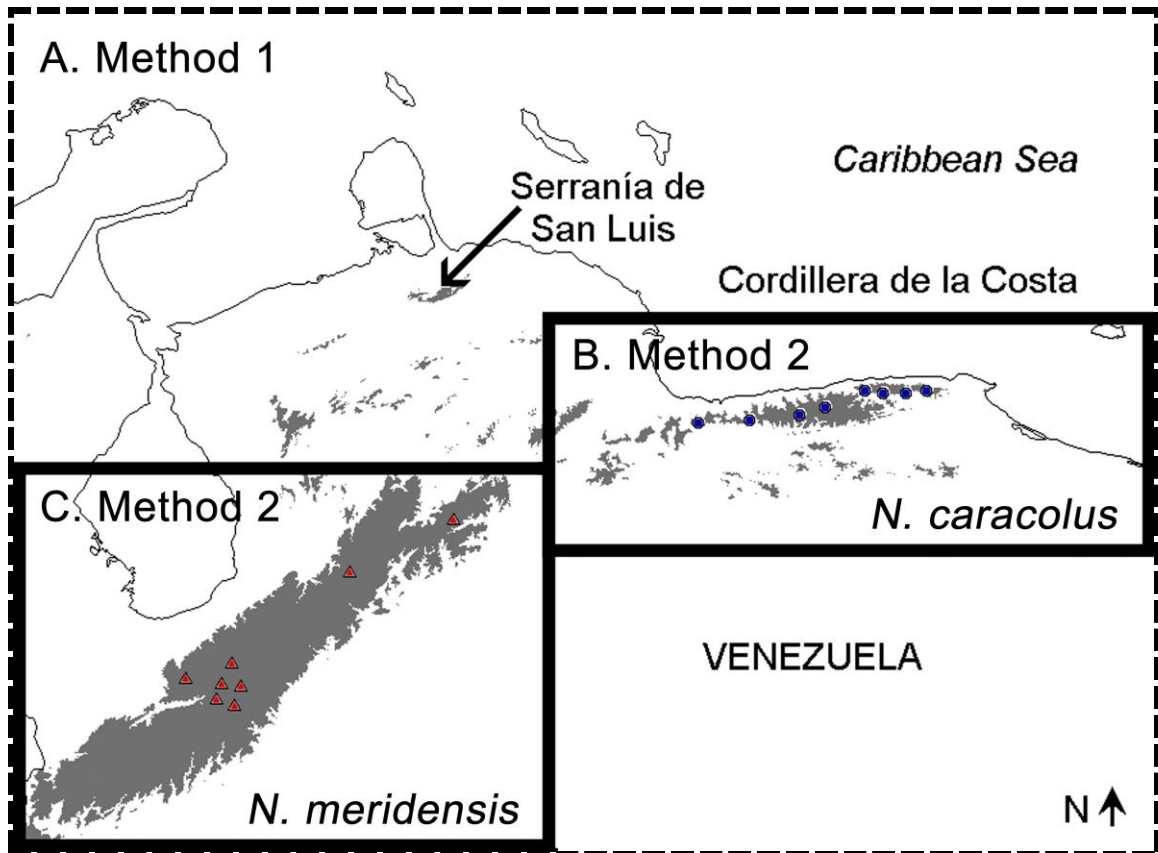


Figure 2. Models of the potential geographic distributions of *Nephelomys caracolus* (left) and *N. meridensis* (right), for each method of defining the study region. The predictions (A–D) show a suitability gradient from low (blue = 0) to high (red = 1) relative environmental suitability. White squares indicate the localities used to make the models. Panels A and B show predictions generated using Method 1 (models made using the large study region), while C and D correspond to the respective predictions for Method 2 (models made using the smaller study region and then projected to the larger one). For Method 2 for each species, E and F reveal the level of clamping, if any, corresponding to each map pixel. Clamping occurs when values of environmental variables fall outside of the range of environmental values in the models (see text). Successively warmer colors show areas where the strength of clamping was greater.

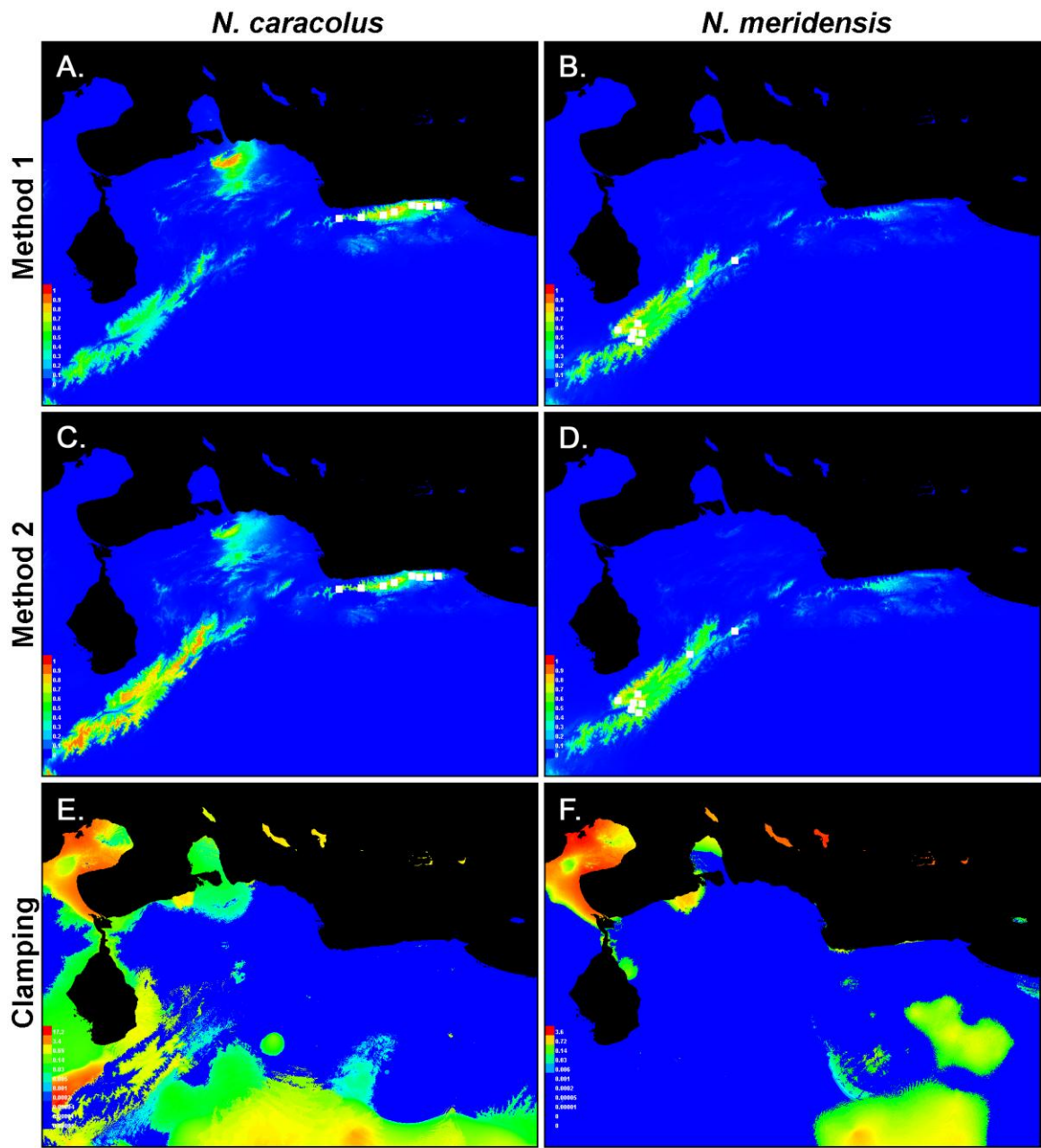


Figure 3. Models of the potential distributions of *Nephelomys caracolus* (A, C) and *N. meridensis* (B, D), for each method of defining the study region, showing binary predictions of the extent of suitable conditions for each species after applying the minimum training weight (MTW) threshold. Each prediction is divided into areas considered suitable (grey) vs. unsuitable (white) for the species. Blue circles and red triangles indicate localities for *N. caracolus* and *N. meridensis*, respectively. Panels A and B indicate predictions made using Method 1 (models made using the large study region), while C and D illustrate the corresponding predictions for Method 2 (models made using the smaller study region and then applied to the larger one). Note the much larger prediction for *N. caracolus* in the Cordillera de Mérida under Method 2 (arrow in C). In contrast, the prediction for *N. meridensis* in the Cordillera de la Costa is only slightly larger under Method 2 (arrow in D).

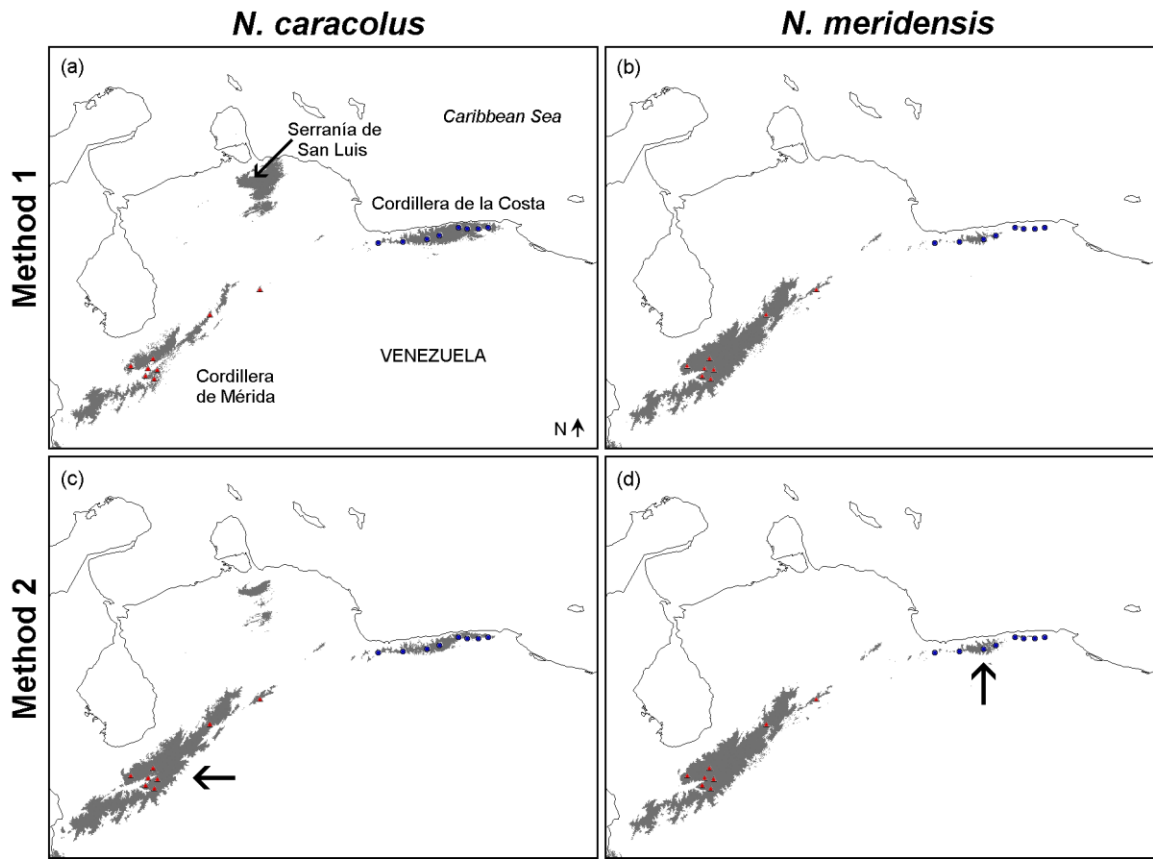


Table 1. Measures of interpredictivity between *Nephelomys caracolus* and *N. meridensis* based on models made with two different methods of defining the study region. In Method 1, each species' potential distribution was modeled in a large study region that included the range of both species (left). In Method 2, each species was modeled in a smaller study region encompassing its known localities, and then applied (projected) to the larger study region (right). Both cross-species omission rates and cross-species AUC values provide measures of how well the model of the focal species predicts localities of the other species. Omission rates constitute a threshold-dependent measure: first, the minimum training weight (MTW) threshold rule is applied to the model of the focal species, yielding a binary prediction; then, the omission rate for localities of the other species is calculated. Complementarily, AUC values represent a threshold-independent measure that assesses the overall ability (across all possible thresholds) of the model for the focal species to predict localities of the other species. Low omission rates and high AUC values indicate high interpredictivity (and low levels of niche evolution). Note that both measures indicate higher interpredictivity for Method 2. The MTW threshold values are provided as additional information regarding the models, but they do not address the issue of interpredictivity. See text for further discussion of omission rates.

	Method 1			Method 2		
	MTW threshold	Cross-species omission rate	Cross- species AUC	MTW threshold	Cross-species omission rate	Cross- species AUC
Model for <i>N. caracolus</i>	0.307	0.375	0.966	0.352	0.000	0.977
Model for <i>N. meridensis</i>	0.178	0.500	0.949	0.178	0.375	0.956

Table 2. Measures of percent geographic overlap of the potential distributions of *Nephelomys caracolus* and *N. meridensis*, for each method of defining the study region. In Method 1, each species' potential distribution was modeled in a large study region that included the range of both species. In Method 2, each species was modeled in a smaller study region encompassing its known localities, and then applied (projected) to the larger study region. All results are for predictions of the species' potential distributions in the larger study region (even though the models for Method 2 were made in the smaller study region), and after converting the continuous prediction to a binary one based on the minimum training weight (MTW) threshold (see text). The percent geographic overlap was calculated in three ways based on overlap of the two species' predictions as a percentage of: (1) the larger study region; (2) the prediction for each respective species alone; and (3) the area predicted for either species. The last measure provides the best single indicator of the amount of geographic overlap between the predictions of the two species.

Percent geographic overlap based on number of pixels in:	Method 1	Method 2
overlap relative to larger study region	1.8	3.4
overlap relative to prediction of <i>N. caracolus</i>	50.1	74.7
overlap relative to prediction of <i>N. meridensis</i>	47.0	84.9
overlap relative to prediction of either species	32.0	65.9