



ORIGINAL
ARTICLE



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

Robert P. Anderson^{1,2*} and Ali Raza¹

¹Department of Biology, City College of the City University of New York, New York, NY, USA, ²Division of Vertebrate Zoology (Mammalogy), American Museum of Natural History, New York, NY, USA

ABSTRACT

Aim Various techniques model a species' niche and potential distribution by comparing the environmental conditions of occurrence localities with those of the overall study region (via a background or pseudoabsence sample). Here, we examine how changes in the extent of the study region (ignored or underappreciated in most studies) affect models of two rodents, *Nephelomys caracolus* and *Nephelomys meridensis*.

Location North-central South America.

Methods We used MAXENT to model the species' potential distributions via two methods of defining the study region. In Method 1 (typical of most studies to date), we calibrated the model in a large study region that included the ranges of both species. In Method 2, we calibrated the model using a smaller study region surrounding the localities of the focal species, and then applied it to the larger region. Because the study region of Method 1 is likely to include areas of suitable conditions that are unoccupied because of dispersal limitations and/or biotic interactions, this approach is prone to overfitting to conditions found near the occupied localities. In contrast, Method 2 should avoid such problems but may require further assumptions ('clamping' in MAXENT) to make predictions for areas with environmental conditions beyond those found in the smaller study region. For each method, we calculated several measures of geographic interpredictivity between predictions for the species (cross-species AUC, cross-species omission rate, and proportional geographic overlap).

Results Compared with Method 1, Method 2 revealed a larger predicted area for each species, less concentrated around known localities (especially for *N. caracolus*). It also led to higher cross-species AUC values, lower cross-species omission rates and higher proportions of geographic overlap. Clamping was minimal and occurred primarily in regions unlikely to be suitable.

Main conclusions Method 2 led to more realistic predictions and higher estimates of niche conservatism. Conclusions reached by many studies depend on the selection of an appropriate study region. Although detailed information regarding dispersal limitations and/or biotic interactions will typically be difficult to obtain, consideration of coarse distributional patterns, topography and vegetational zones often should permit delimitation of a much more reasonable study region than the extremely large ones currently in common use.

Keywords

Background sampling, distributional modelling, MAXENT, *Nephelomys*, niche evolution, niche modelling, overfitting, pseudoabsences, South America, transferability.

*Correspondence: Robert P. Anderson, Department of Biology, City College of the City University of New York, 526 Marshak Science Building, 160 Convent Avenue, New York, NY 10031, USA.
E-mail: anderson@sci.cuny.cuny.edu

INTRODUCTION

The recent use of geographic information systems (GIS) in niche-based modelling has led to a renaissance in research regarding the ecological and evolutionary aspects of species distributions (Wiens & Graham, 2005). Species potential distributions can be modelled directly via mechanistic or physiological experiments. Although this approach is desirable and should lead to the best estimates of a species' fundamental niche and potential distribution, such studies are seldom feasible (Hijmans & Graham, 2006; Kearney, 2006; Morin & Thuiller, 2009). In contrast, GIS-based correlative modelling approaches can be applied to a large number of species, and have recently been widely used to predict species potential distributions (Peterson, 2003; Kozak *et al.*, 2008). Important caveats to this approach exist, however, primarily related to the fact that use of environmental information for occurrence localities from a species' realized niche may lead to underestimates of its fundamental niche and potential distribution. Principally, this is due to biotic interactions and dispersal limitations that do not allow the species to inhabit or even encounter some environmental conditions that may be suitable for it (Anderson *et al.*, 2002b, pp. 4–5; Phillips *et al.*, 2006, p. 232).

Hence, much conceptual and methodological work has been necessary to clarify the degree to which, and under what circumstances, various correlative techniques can estimate a species' potential distribution (rather than its realized distribution; e.g. Anderson & Martínez-Meyer, 2004; Araújo & Guisan, 2006; Soberón, 2007; Morin & Thuiller, 2009). Among other factors, the modelling technique employed and the nature of the data can affect results (Chefaoui & Lobo, 2008; Jiménez-Valverde *et al.*, 2008). In each study using correlative modelling, researchers should take the methodological steps necessary to minimize underestimates as much as possible, as well as state the relevant assumptions clearly (Phillips *et al.*, 2006; Swenson, 2008). For example, modelling a species based on data from differing community contexts, i.e. both with and without a likely competitor, should allow for fuller estimates of its niche and potential distribution (Anderson *et al.*, 2002b). Extending recently developed ideas (Bahn & McGill, 2007; Chefaoui & Lobo, 2008), this study addresses how the extent of the study region may influence results in correlative modelling.

Correlative modelling uses two kinds of data to model a species' environmental requirements and estimate its potential geographic distribution (Pearson & Dawson, 2003; Peterson, 2003; Graham *et al.*, 2004a). First, it requires localities (occurrence records) of the species' presence, but generally does not use information regarding localities where the species is absent (but see techniques that use presence–absence or abundance data, which are often applied for modelling a species' realized distribution; Scott *et al.*, 2002). Second, it utilizes environmental, especially climatic, variables for the study region (typically in the format of a series of raster grids made up of pixels at a resolution relevant for the species and the study at hand). The algorithm employed generates a model (in some cases termed a bioclimatic envelope model) of the

species' niche in the examined dimensions of ecological/environmental space. That niche model is then applied to geographic space to identify areas that are suitable for the species, i.e. its potential distribution.

In forming the niche model, most of these algorithms compare the environmental conditions of localities of a species' occurrence with those available in the overall study region. Typically, this is achieved by taking a sample of pixels from the study region (Elith *et al.*, 2006; see also Zaniwski *et al.*, 2002; note that some techniques, such as BIOCLIM or DOMAIN, only use information from the localities of documented presence; Busby, 1986; Carpenter *et al.*, 1993). In most cases, this is accomplished via a random sample taken either from the entire study region ('background' sample) or from all pixels lacking a presence locality ('pseudoabsence' sample; Graham *et al.*, 2004a; Phillips *et al.*, 2009). Despite this conceptual distinction, such background and pseudoabsence samples will typically be very similar in practice, because in most studies very few pixels hold presence localities, relative to the very large number of pixels in the study region. With either background or pseudoabsence samples, these pixels are used to characterize the environmental conditions available in the study region for comparison with the conditions that the species is known to inhabit. Thus, definition of the study region is a critical issue. Although it has received recent appreciation, especially in the realm of abundance modelling (Bahn & McGill, 2007, p. 735; Chefaoui & Lobo, 2008; Lobo, 2008), it has been ignored or at least not considered explicitly in most recent studies employing background or pseudoabsence sampling (e.g. Kozak & Wiens, 2006; Phillips *et al.*, 2006; Warren *et al.*, 2008).

The choice of correlative modelling technique and of the biological and environmental input data affect the model output, and such decisions should be made based on theoretical principles and depending on the goal of the study, namely, whether an estimate of the species' realized or potential distribution is desired. For example, previous work has suggested that simple presence-only approaches (e.g. BIOCLIM, DOMAIN) may be more effective in estimating a species' potential distribution, whereas at the other end of the spectrum complex presence–absence techniques (e.g. generalized linear models and generalized additive models, when used with true absence data) integrate more information and generally should yield models closer to a species' realized distribution (Jiménez-Valverde *et al.*, 2008). Based on input data, presence–background and presence–pseudoabsence approaches lie intermediate between the two former classes. The models produced by these latter techniques are likely to depend on the input data and on the settings employed (e.g. tuning of model settings; Phillips & Dudík, 2008).

As an example, we address the effect of the study region used for MAXENT, a presence–background technique that has seen much use and development recently (Phillips *et al.*, 2006; Phillips & Dudík, 2008). MAXENT performed well in recent comparative studies aimed at predicting species realized distributions (Elith *et al.*, 2006; Hernandez *et al.*, 2006; Wisz *et al.*, 2008) but also should – in principle and given the appropriate

data – be effective in predicting species potential distributions as well. Although its utility in modelling potential distributions has been questioned (Peterson *et al.*, 2007), the results of that study may derive from violations of stated assumptions regarding input data, specifically regarding the selection of occurrence localities of the species and determination of the region for background sampling (Phillips, 2008). Here, we examine how changes in the extent of the study region – and hence in background sampling – affect models produced by MAXENT.

Although we conduct this study specifically in the context of studies of niche evolution, resolution of the issue of selection of the study region is relevant for all uses of correlative modelling of species potential distributions. Pertinent topics include applications to conservation biology (Kremen *et al.*, 2008), study of invasive species (Welk *et al.*, 2002), estimation of distributional changes under climatic change (Araújo *et al.*, 2005) and examination of niche evolution in a phylogenetic context (Peterson *et al.*, 1999; Graham *et al.*, 2004b; Wiens & Graham, 2005; Kozak & Wiens, 2006; Warren *et al.*, 2008; see also reviews by Kozak *et al.*, 2008; Swenson, 2008). Furthermore, it may help resolve debates regarding model generality and transferability across space and time (Randin *et al.*, 2006; Peterson *et al.*, 2007; Phillips, 2008).

Here, we study two closely related species that show disjunct distributions in adjacent mountain ranges. We model the

distributions of the rodents *Nephelomys caracolus* (Thomas) and *Nephelomys meridensis* (Thomas) in northern Venezuela and adjacent regions of north-eastern Colombia. The genus *Nephelomys* was described recently for the ‘*albigularis*’ species group, which was formerly assigned to the 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 north-western Venezuela (Fig. 1); these species inhabit montane forests from approximately 1050 to 4000 m a.s.l. (Percequillo, 2003). Externally, they are indistinguishable from one another, but studies of karyology and internal morphology have documented consistent differences, indicating that they represent distinct species (Aguilera *et al.*, 1995; Márquez *et al.*, 2000; Percequillo, 2003). Although the current analyses do not require that *N. caracolus* and *N. meridensis* be sister species, their probable close phylogenetic relationship makes it more likely that they will have similar niches and potential geographic distributions (Peterson *et al.*, 1999; Wiens & Graham, 2005). Whereas such a situation is by no means required for these tests, this makes them a convenient study system for examining the effects of background sampling on predicted potential distributions and estimates of niche overlap.

To examine these effects, we use two methods of defining the study region (altering the ‘relative occurrence area’ for the

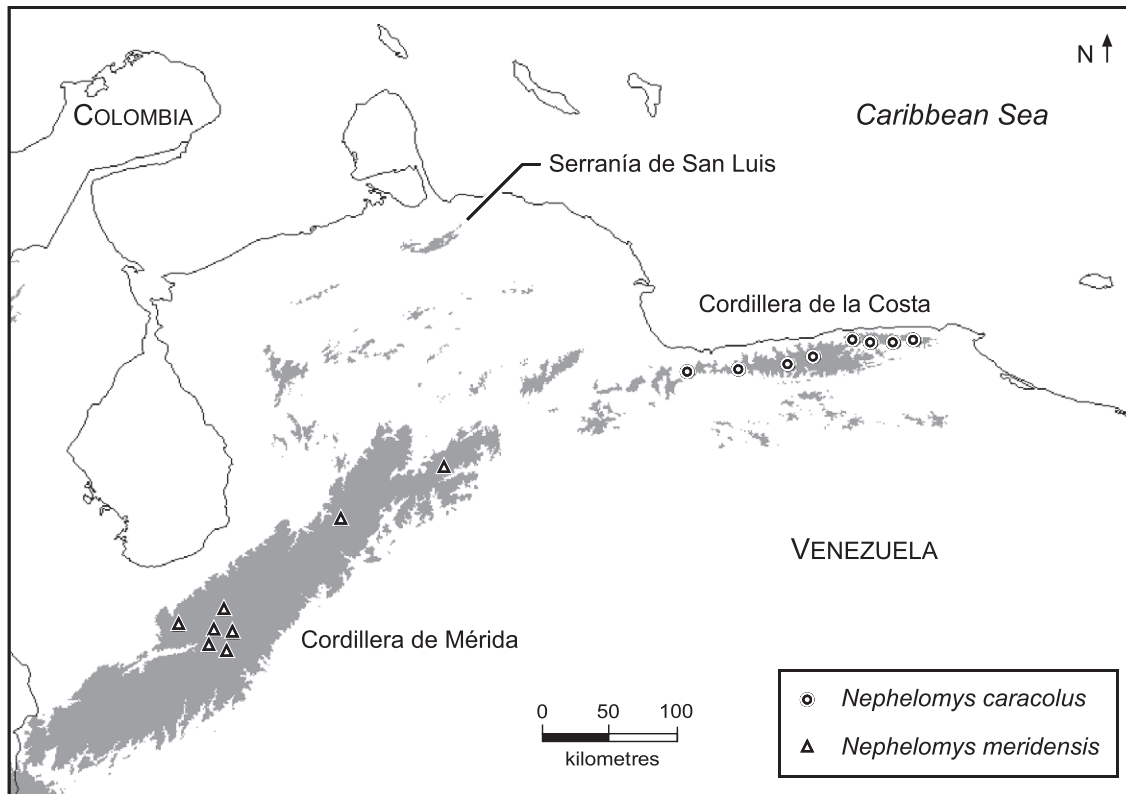


Figure 1 Spatially filtered localities of *Nephelomys caracolus* and *N. meridensis* used in this study. Shaded areas represent elevations ≥ 1000 m. *Nephelomys caracolus* (circles) is found in the coastal mountains of north-central Venezuela (Cordillera de la Costa), whereas *N. meridensis* (triangles) occurs in the Cordillera de Mérida in the north-western part of the country (the south-western portion of this map). These species inhabit montane forests at c. 1050–4000 m a.s.l.

species, *sensu* Lobo *et al.*, 2008; see also Jiménez-Valverde *et al.*, 2008). In the first (Method 1), each species' potential distribution is modelled (= calibrated, or trained) in a large study region that includes the ranges of both species. In the second (Method 2), each species is modelled in a smaller study region immediately surrounding its known localities; the resulting model is then applied (projected) to the larger region (the one used for model calibration in Method 1), identifying the areas matching the species' requirements according to the model calibrated using the smaller study region. Each method holds possible drawbacks (see below). After generating the models using each method, we analyse how well the potential distribution of each species predicted the other species, via various measures of interpredictivity that represent indirect geographic indications of the level of niche conservatism present between the species (more precisely, how close they are to niche equivalency, *sensu* Warren *et al.*, 2008). Based on the results, we make recommendations for selecting an appropriate study region (one that more closely matches a critical assumption of the modelling) by taking advantage of available information regarding likely dispersal limitations for the species and possible negative biotic interactions with other species. Although the detail and quality of data available regarding such factors will invariably remain far less than optimal, consideration of even basic information when selecting the study region for model calibration should lead to more realistic estimates of species potential distributions.

MATERIALS AND METHODS

Locality data

We obtained localities for the species from a variety of taxonomic and faunal studies (Díaz de Pascual, 1994; Moscarella & Aguilera-M., 1999; Márquez *et al.*, 2000; Percequillo, 2003; Rivas & Salcedo, 2006; see also Anderson, 2003a). We then georeferenced each locality (assigned coordinates of latitude and longitude and estimated possible error) using original publications by the collectors, gazetteers, detailed topographic maps and other sources (see Appendix 1), leading to 14 unique localities (unique latitude–longitude combinations) for *N. caracolus* and 19 for *N. meridensis*. When some uncertainty existed regarding the precise location of a particular collection site, coordinates were assigned to a place in the indicated region with the elevation provided by the collector (because environmental variables correlate highly with elevation in these regions).

In order to reduce the effects of sampling bias (e.g. clusters of localities present due to more sampling along roads or near major cities, universities, or research centres; Reddy & Dávalos, 2003; Hortal *et al.*, 2008), we filtered localities of each species to obtain the maximum number of localities that were at least 10 km apart (see below). When multiple equally optimal solutions were possible for a given cluster, we retained the combination of localities with the lowest total possible error. For each species, this process yielded eight spatially filtered

localities (Fig. 1), which were used for all subsequent analyses. Coordinates for most of these filtered localities were accurate to a maximum error of 2–3 km (mostly due to possible displacement by foot from base camp by collectors), and all were accurate to within 5 km. The filtered localities have three important advantages. First, because they are likely to reflect less of an environmental bias caused by uneven sampling by mammalogists, and are less spatially autocorrelated, they should yield better estimates of the species' niches. Second, for the same reasons, they provide more reasonable data for evaluating how well a model calibrated for one species predicts localities of the other (interpredictivity). Given the heterogeneity of the terrain in the known ranges of the species, the cut-off of 10 km (although arbitrary and subjective) probably achieves these goals in this region for these species, without unduly decreasing the number of localities available for modelling (see also Pearson *et al.*, 2007). Third, because the filtered localities were selected to minimize possible error in geographic coordinates as a secondary criterion, they are most likely to fall in the correct pixel of the environmental data (see below).

Environmental variables

Here, we used 19 bioclimatic variables from WorldClim 1.4 (Hijmans *et al.*, 2005; <http://www.worldclim.org/>) for the environmental data. These variables are based on monthly temperature and precipitation data, which were produced from weather-station data using splining techniques (interpolation that takes elevation into account as a covariate). Those authors then derived the bioclimatic variables from the monthly data, yielding variables that are more relevant biologically: annual mean temperature, mean diurnal range (mean of monthly values of maximum temperature minus minimum temperature), isothermality, temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, temperature annual range, mean temperature of the wettest quarter, mean temperature of the driest quarter, mean temperature of the warmest quarter, mean temperature of the coldest quarter, annual precipitation, precipitation of the wettest month, precipitation of the driest month, precipitation seasonality, precipitation of the wettest quarter, precipitation of the driest quarter, precipitation of the warmest quarter and precipitation of the coldest quarter.

These variables are likely to have relevance for the distributions of the study species for several reasons. First of all, rodents are known to have highly heritable physiological tolerances (e.g. French, 1993). In the tropics, variables comprising aspects of temperature can be limiting at both the upper and lower elevational limits for a species. In addition to the direct effects of precipitation on a species' physiological ability to survive, interactions between temperature and precipitation can lead to more complicated patterns of water balance (e.g. Anderson *et al.*, 2002b). For both temperature and precipitation, seasonality is likely to play an important role, because distributions may be limited by the most extreme season (e.g. the driest or warmest), rather than the average

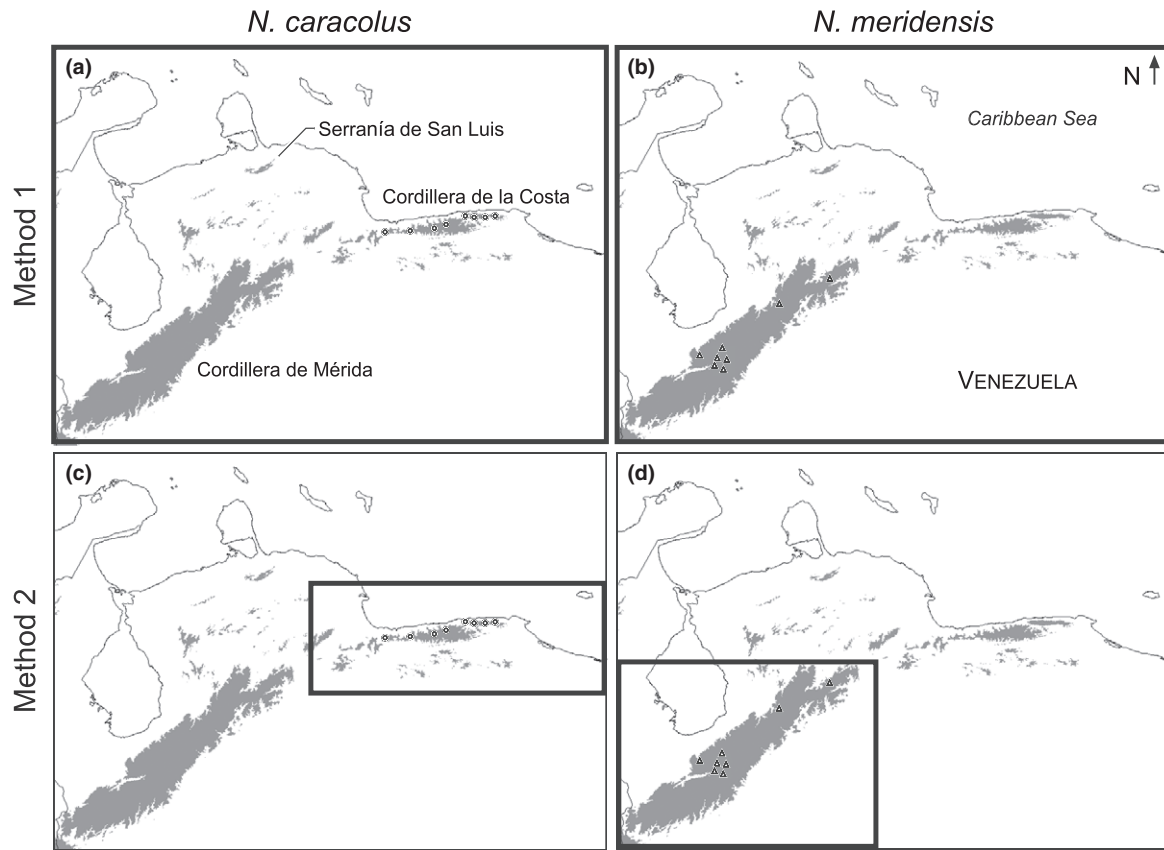


Figure 2 The two methods used to define the study region for calibrating models of the potential distribution of *Nephelomys caracolus* (circles, left) and *N. meridensis* (triangles, right). MAXENT models (not shown here) were calibrated using these spatially filtered localities of each species. Shaded areas represent elevations ≥ 1000 m. In Method 1, each species' potential distribution was calibrated in a large study region that included the ranges of both species (a and b, upper). In Method 2, the model for each species was calibrated in a smaller study region encompassing its known localities (c and d, lower); then, this model was applied to the larger region used for calibration in Method 1, indicating environmental suitability for the species throughout the whole larger region.

value. These kinds of climatic factors seem especially likely to be important for these species, which are found in wet montane areas at intermediate elevations (Percequillo, 2003). In addition, these climatic variables also affect plant distributions (Elith *et al.*, 2006), which can influence the distributions of rodents, both as food sources and material for refuges (e.g., see Rood & Test, 1968).

We used raster grids of the bioclimatic variables with a spatial resolution of $30''$ ($0.93 \text{ km} \times 0.93 \text{ km} = 0.86 \text{ km}^2$ at the equator). Unfortunately, the current version of WorldClim does not provide uncertainty surfaces for the climatic estimates created via splining, and the variables should be interpreted as estimates with unknown (but probably moderate) levels of error. This resolution (although not necessarily the true accuracy) of the climatic variables is slightly finer than the accuracy of some of the occurrence localities, which were georeferenced through much effort using a variety of sources (see above and Appendix 1). However, even if the coordinates assigned to a given locality do not correspond to the correct pixel, they are very likely to fall in an adjacent or nearby one with similar values of the environmental variables.

Defining the study region

As mentioned above, we used two methods to define the study region in our analyses. In Method 1 (Fig. 2a, b), we calibrated the potential distribution of each species in a large study region that included the ranges of both species ($7.5\text{--}13^\circ \text{ N}$ and $65\text{--}72.5^\circ \text{ W}$). In Method 2 (Fig. 2c, d), we calibrated the model for each species in a smaller study region immediately surrounding its known localities ($9.5\text{--}11^\circ \text{ N}$ and $66\text{--}69^\circ \text{ W}$ for *N. caracolus*; $7.5\text{--}10^\circ \text{ N}$ and $69\text{--}72.5^\circ \text{ W}$ for *N. meridensis*). For Method 2, we then applied (projected) the respective model to the larger study region (that employed for calibration in Method 1).

Each method has disadvantages in modelling 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 (an overfitting to bias present in the localities used to calibrate the model, a 'calibration data set', see below). This can happen because the algorithm recognizes spurious environmental differences between the region that a species actually inhabits versus other regions that it could inhabit but does not. Such distributional

patterns may occur because of a geographic barrier that prevents the species from dispersing to those regions, or because of a difference in the biotic interactions in the latter regions, for example, the presence of a superior competitor. Collectively, we refer to such situations as non-equilibrium distributions. For a given species, consider two regions with suitable environmental conditions (potential distribution) for the species: one that the species inhabits, and another to which it has not dispersed. If values for a particular environmental variable differ between the two regions of potential distribution, the model will (incorrectly) integrate that variable into the model and predict the latter region as less suitable for the species, even though the variable is not important in reality. Hence, this constitutes overfitting not to noise but rather to a *bias* present in the calibration data set, namely that the occurrence localities are not a random sample from the entity being modelled, here the species' potential distribution [an explicit assumption of MAXENT (Phillips *et al.*, 2006) and an implicit assumption of many if not all other presence–background modelling techniques]. Overfitting leads to artificially lowered transferability of a model across space or time and should be avoided for applications that require the ability to predict independent data (Araújo & Rahbek, 2006; Randin *et al.*, 2006).

In contrast, when calibrating a model using a smaller study region (Method 2) and then applying it 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 model. Typically, this occurs because such values do not exist in the study region used for calibration; hence, they lie outside the range of values for the corresponding variable(s) in the model. This situation, often referred to as a 'truncated response curve', commonly occurs in other situations, such as when applying a model to another time period (e.g. after climatic change) or region (e.g. prediction of an invasive species; Williams & Jackson, 2007). In such cases, some assumption must be made, or no prediction can be produced for those pixels (Phillips *et al.*, 2006). For example, at one extreme, all pixels holding conditions 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 modelled in the calibration 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 even wetter environments (than those found in the calibration region) would be even better for the species. Whereas it may be more reasonable than either of the two extremes presented above, extrapolation becomes especially risky the farther that the pixel lies in environmental space from conditions present in the calibra-

tion region, at least for response curves that are increasing when truncated by the environment present in the calibration 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 modelled in the calibration 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 calibration 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 calibration (training)

We modelled the potential distributions of *N. caracolus* and *N. meridensis* using MAXENT version 3.1.0 (Phillips *et al.*, 2006; Phillips & Dudík, 2008). MAXENT is a presence–background modelling technique that has performed well in recent comparisons (Elith *et al.*, 2006; Hernandez *et al.*, 2006; Wisz *et al.*, 2008). We used localities for each species and 19 bioclimatic variables (see above) to make the models. Models were calibrated using both linear and quadratic features and with default levels of regularization (a penalty for making a complex model, therefore providing protection against overfitting, especially to noise present in the calibration data set). Lastly, we selected the logistic output format, which yields continuous values ranging from 0 to 1 that indicate relative environmental suitability for the species (specifically, the probability of suitable environmental conditions, or the probability of presence if dispersal limitations and distributional restrictions due to biotic interactions are not relevant; see Phillips & Dudík, 2008). First, we made preliminary models (using some of the available spatially filtered localities via a jackknife procedure; see below) to evaluate how well the models predicted localities of the focal species itself. Then, we made final models for each species using all available spatially filtered localities. We made both preliminary and final models using each of the methods of defining the study region. For hypothesis testing, we used the models calibrated via the jackknife procedure, as these suites of models provide estimates of both mean and variance for the quantities being measured (see below).

Model evaluation (testing)

To evaluate the preliminary models, we used threshold-dependent tests as an indicator of how well the model of each species predicted its own localities. Because only eight localities of each species were available, we implemented the jackknife procedure for model assessment (Pearson *et al.*, 2007). For each species, seven models were built by removing each locality once in turn. In other words, a different set of seven (out of eight) localities was used for calibrating the model for each run (for a total of eight runs per species). Then, we assessed predictive performance based on the ability of each model to predict the single locality excluded from the given calibration 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 of ≤ 0.05 indicates that evaluation (or testing) localities are predicted better than by a random prediction with the same proportional predicted area (the proportion 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, we used the lowest presence threshold (LPT) of Pearson *et al.* (2007) (= minimum training presence threshold of MAXENT software). This is the lowest value of the prediction for any of the pixels that correspond to the localities used in calibrating the model; hence, it indicates the least-suitable environmental conditions for which a locality was available in the calibration data set. Under this thresholding rule, pixels with values equal to or higher than the lowest presence threshold are considered suitable, whereas pixels with values below it are not. We conducted these analyses for models calibrated using the larger study region, and then for models made using the smaller study region.

Assessing interpredictivity

Using both the final models as well as the suites of models produced using jackknifed locality data sets (see above), we assessed interpredictivity between the species' niche models. These tests include both threshold-independent and threshold-dependent approaches and provide comparisons between the two methods of defining the study region used to calibrate the models. Because they are based on data from the realized niche rather than on experiments (see the Introduction), the models used for these tests assume that the occurrence data reflect the species' full niche tolerances, requiring the following caveats and discussion of how likely this assumption may be. Because available distributional data indicate that the two species' ranges do not come into contact, any pattern of environmental partitioning in their realized niches is likely to derive from distinct preferences rather than shared preferences and differential competitive ability (Wisheu, 1998; Anderson *et al.*, 2002b; Swenson, 2008). However, differences in (1) the presence (or abundance) of other, unidentified, interacting species between the two regions of the species' respective ranges, or (2) the available environments in the two regions, may violate the assumption. Furthermore, the species may have diverged in

many other niche dimensions not examined; the present tests can only address any possible differences related to the bioclimatic variables considered here. With these qualifications, we conduct the following tests, which are aimed at identifying any artefactual differences that derive from discrepancies between the two methods of defining the study region.

We assessed interpredictivity in three ways. First, we assessed the ability of the model of the focal species to predict localities of the other species by comparing the area under the curve (AUC) of a receiver operating characteristic (ROC) plot made with the localities of the other species (Phillips *et al.*, 2006). AUC values represent a threshold-independent measure of predictivity. Hence, these cross-species AUC values provide an overall assessment of how well the models of each species predict localities of the other species. Because the MAXENT 3.1.0 user interface does not allow the calculation of AUC values for a projection study region (i.e. as in Method 2), we calculated all AUC values using a command-line tool available in a more recent release (MAXENT version 3.2.19).

The second way we assessed interpredictivity was by calculating cross-species omission rates, a threshold-dependent measure that indicates how well the models of each species predict localities of the other species. We achieved this by applying 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 as suitable versus unsuitable for the species. As in the assessments of the preliminary models, we achieved this by applying the LPT rule of Pearson *et al.* (2007). Using this binary prediction, we then calculated the cross-species omission rates by determining the proportion of localities of the other species falling outside of (omitted from) areas predicted suitable for the focal species.

Third, we examined the effect that the two methods of defining the study region had on the degree of geographic overlap between the two species' potential distributions. We accomplished this by superimposing the potential distributions of the two species in the larger study region (here again, after applying the LPT rule; see above). Then, the proportion of geographic overlap was estimated by dividing the number of pixels predicted suitable for both species by either (1) the total number of pixels with data (e.g. excluding the ocean), or (2) the total number of pixels predicted suitable for each species alone, or (3) the total number of pixels predicted suitable for either species.

Statistical tests comparing Methods 1 and 2

We conducted a series of statistical tests of our predictions of differences between the results of the two methods of defining the study region for model calibration. In Method 2, we expected the models to show larger areas of suitable conditions, less concentrated in the region surrounding the species' localities. Therefore, we also predicted higher interpredictivity in Method 2, as evaluated by: (1) higher cross-species AUC values, (2) lower cross-species omission rates, and (3) higher

proportion of geographic overlap (which we tested using the proportion of overlap relative to the areas predicted for either species). In addition to inspecting these values for the final models produced with all spatially filtered localities for each species, we conducted one-tailed paired *t*-tests based on the models made with the jackknifed locality data sets (these were also used to assess the significance of the models in predicting localities of the focal species itself, see above). We implemented one-tailed tests because the predictions and null hypotheses were directional (i.e. predicted higher AUC, lower omission rate, and higher geographic overlap in Method 2). Paired *t*-tests were appropriate because the localities used for calibration in each jackknife iteration for Method 1 were the same as those in the corresponding iteration for Method 2. Because the jackknife iterations are not independent of one another, estimated variance among iterations must be corrected. With a delete-1 jackknife (used here), variance is equal to the sum of squares multiplied by $(n-1)/n$ (rather than divided by $n-1$, as in normal calculation of variance; Efron & Tibshirani, 1993; see also Shao & Wu, 1989). We conducted these *t*-tests following Zar (1999, pp. 161–164) using formulae in a spreadsheet, and found the exact probability for each *t* value (test statistic) using the cumulative distribution function in MINITAB (2003), release 14.1. Because proportions and rates are seldom distributed normally, we performed arcsine transformations of the data ($\arcsin \sqrt{p}$, where *p* is the proportion or rate) before conducting the *t*-tests whenever relevant (all tests but those for AUC; Zar, 1999, pp. 278–280). To determine significance, we applied $\alpha = 0.05$ for all tests.

RESULTS

Preliminary models

Threshold-dependent evaluation (via the jackknife procedure) revealed informative and significant predictions for each species' potential distribution. With use of the LPT rule, pixels with values equal to and above the threshold are considered suitable for the species, whereas pixels with values below that are deemed unsuitable. Omission rates for evaluation (testing) localities were low ($\leq 25\%$). For three of the four jackknife rounds, only one of eight iterations omitted the evaluation locality, yielding average omission rates of 0.125; for the fourth (Method 2 for *N. caracolus*), two of eight iterations omitted the evaluation locality, producing an average omission rate of 0.25. Furthermore, the jackknife tests indicated that the models were significantly better than random predictions for both species and both methods of defining the study region, with *P*-values well below 0.05 ($P \leq 1 \times 10^{-6}$).

Qualitative assessment of final models

Using all spatially filtered localities, MAXENT generated sensible and intuitive models of the potential distribution of each species, showing a continuous prediction of relative suitability (Fig. 3a–d). The prediction for *N. caracolus* revealed highest

suitability in the mountain ranges of the north-central coast (principally the Cordillera de la Costa), the Cordillera de Mérida (north-western Venezuela) and the Serranía de San Luis (north-western coast of Venezuela), separated by gaps of low suitability between these ranges (Fig. 3a, c). In contrast, the areas most strongly predicted for *N. meridensis* were restricted to the Cordillera de Mérida, with a prediction of only moderate suitability for the species in the Cordillera de la Costa and very low suitability for most other areas (including the Serranía de San Luis; Fig. 3b, d). The models for each species varied depending on the method of defining the study region. Larger areas were predicted with high suitability by models generated using Method 2 compared with Method 1, especially for *N. caracolus*. Additionally, Method 1 yielded models with the highest suitability generally restricted to areas near the known localities of the focal species, whereas Method 2 produced predictions that were less concentrated in such areas (again, in particular for *N. caracolus*).

Clamping (in Method 2) 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 very unlikely to be suitable for the species (Fig. 3e, f). These included extremely dry lowland regions in the Península de la Guajira in north-eastern Colombia and north-western Venezuela and along the Caribbean coast of north-western 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 south-west of the Lago de Maracaibo.

Quantitative assessments of interpredictivity

Measures of interpredictivity varied between the two methods of defining the study region. First of all, Method 2 led to higher cross-species AUC values than Method 1. The AUC for the localities of *N. meridensis* in the predicted potential distribution of *N. caracolus* was somewhat higher in Method 2 (Table 1). Likewise, the potential distribution of *N. meridensis* predicted the known localities of *N. caracolus* with a slightly higher AUC in Method 2 (Table 1). This difference was significant in the suite of jackknifed models calibrated using localities of *N. caracolus* ($t = 3.788$; $P = 0.003$; one-tailed test) but not in that made using localities of *N. meridensis* ($t = 1.146$; $P = 0.144$; one-tailed test).

Similarly, cross-species omission rates were lower in Method 2 compared with Method 1. Models of *N. caracolus* predicted localities of *N. meridensis* better than models of *N. meridensis* predicted localities of *N. caracolus*. At the LPT, the potential distribution of *N. caracolus* omitted three out of the eight localities of *N. meridensis* for Method 1, but achieved an omission rate of zero for Method 2 (Fig. 4a, c; Table 1). In contrast, the potential distribution of *N. meridensis* failed to predict half of the known localities of *N. caracolus* in Method 1, but performed slightly better (omitting three out of eight) in Method 2 (Fig. 4b, d; Table 1; at LPT). As in the analyses of cross-species AUC, the observed difference in cross-species

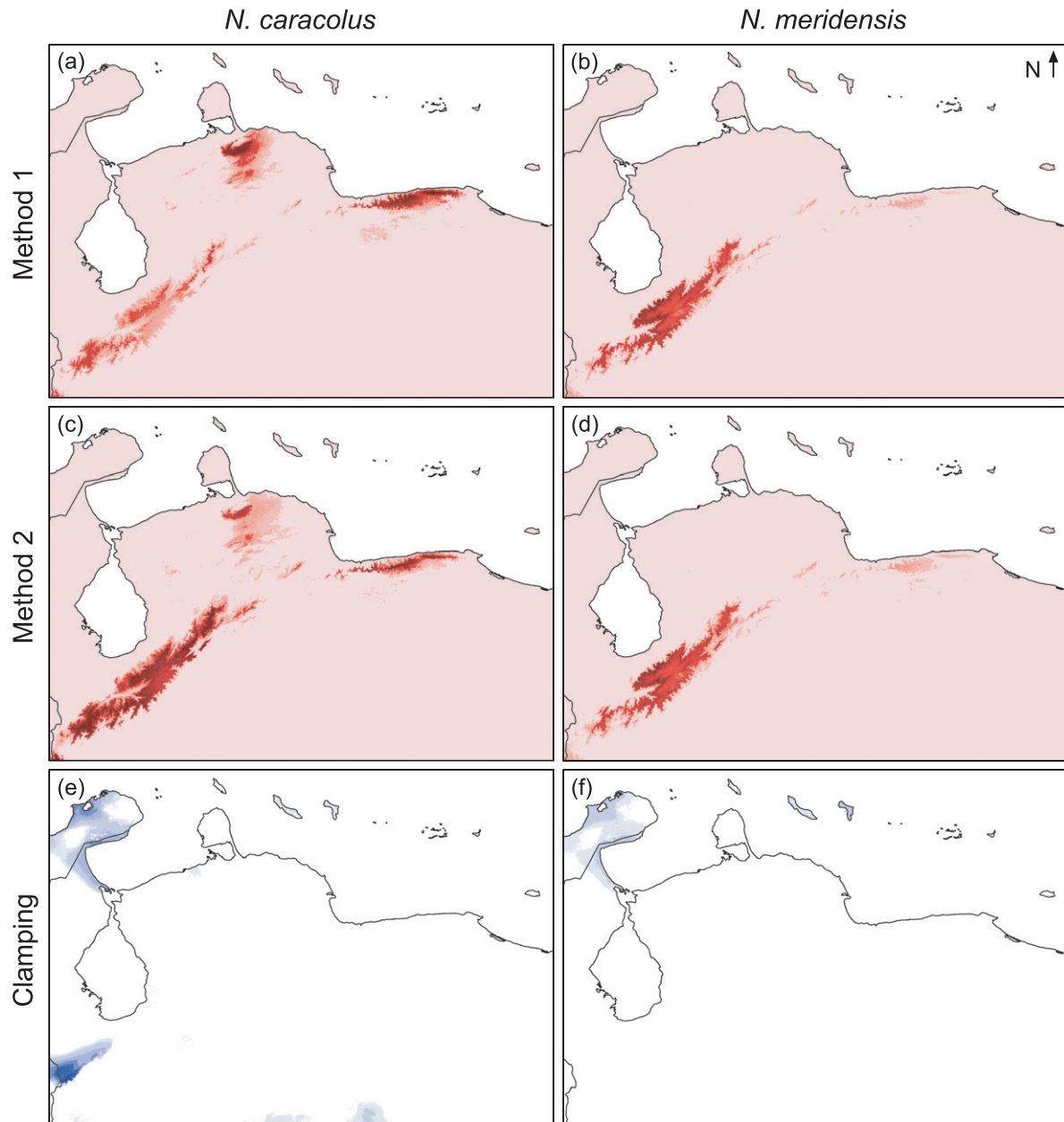


Figure 3 MAXENT models of the potential geographic distributions of *Nephelomys caracolus* (left) and *N. meridensis* (right), for each method of defining the study region. The predictions (a)–(d) show a suitability gradient from low (pale red) to high (dark red) relative environmental suitability (logistic output; probability from 0 to 1). Panels (a) and (b) show predictions generated using Method 1 (models calibrated using the large study region), while panels (c) and (d) correspond to the respective predictions for Method 2 (models calibrated using the smaller study region and then applied to the larger one). For Method 2, for each species, panels (e) and (f) reveal the level of clamping, if any, corresponding to each map pixel. Clamping occurs when values of environmental variables fall outside the range of environmental values in the models (see text); here, successively darker blues show increasing levels of clamping (white indicates values less than 1). See Figs 1 and 2 for the position of localities of each species.

omission rate was significant in the suite of jackknifed models of the potential distribution of *N. caracolus* ($t = 3.010$; $P = 0.010$; one-tailed test) but not in that of *N. meridensis* ($t = 1.259$; $P = 0.124$; one-tailed test).

Finally, the two species showed substantial yet incomplete geographic overlap, but the estimates varied depending on the method of defining the study region. Compared with Method

1, Method 2 revealed a larger predicted area for each species (Fig. 4). Not surprisingly, proportions of geographic overlap between the predicted potential distributions of the two species were consistently higher using Method 2 (Table 2). The difference in the overlap relative to the prediction of either species was significant between the two suites of jackknifed models ($t = 2.769$; $P = 0.014$; one-tailed test).

Table 1 Measures of interpredictivity between *Nephelemys caracolis* and *N. meridensis* based on MAXENT models made using two methods of defining the study region. In Method 1, each species' potential distribution was calibrated in a large study region that included the ranges of both species (left). In Method 2, each species was calibrated 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 lowest presence threshold (LPT) 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 high levels of niche conservatism). Both measures demonstrate higher interpredictivity for Method 2, but the differences were significant only for *N. caracolis* (see text). The LPT values are provided as additional information regarding the models, but they do not address the issue of interpredictivity.

	Method 1			Method 2		
	LPT (threshold)	Cross-species omission rate	Cross-species AUC	LPT (threshold)	Cross-species omission rate	Cross-species AUC
Model for <i>N. caracolis</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

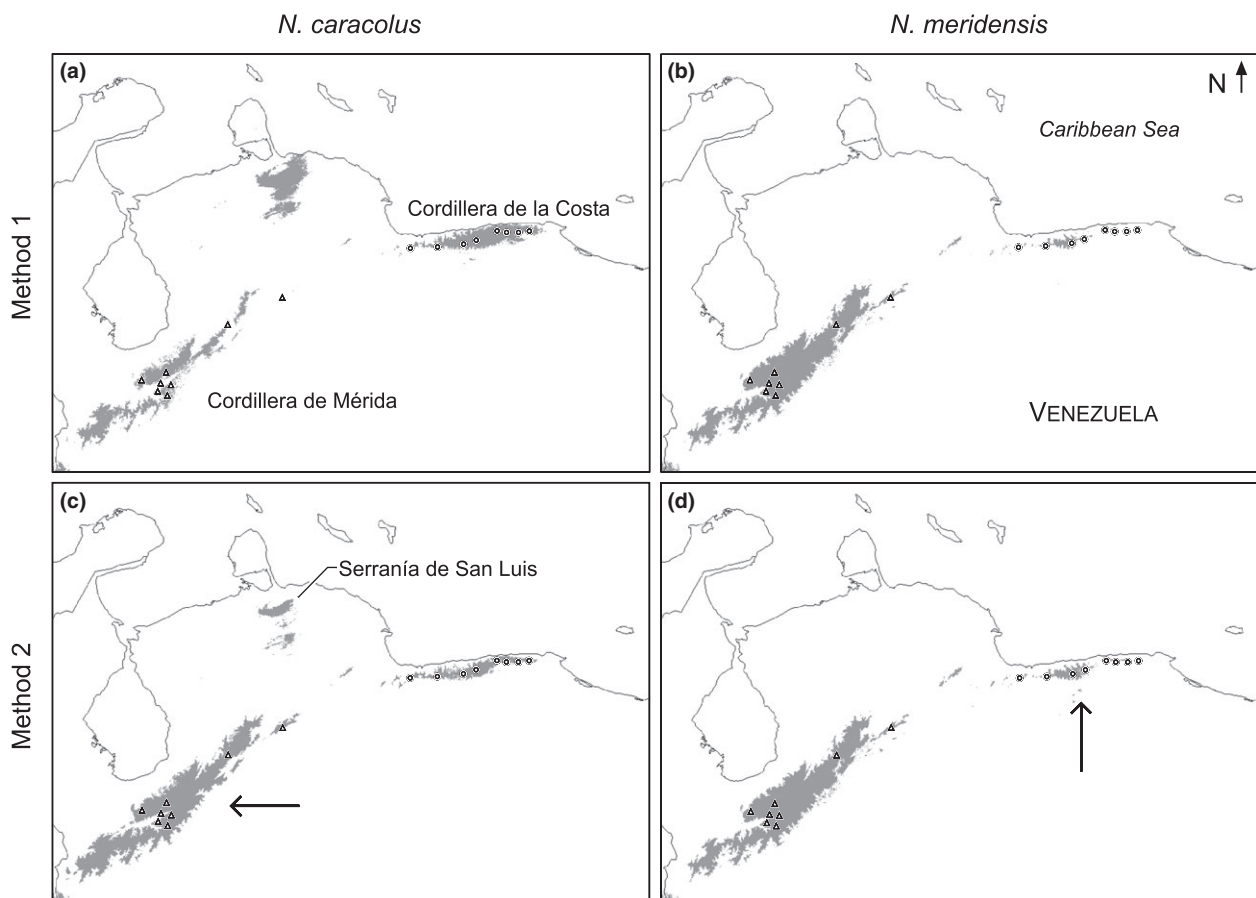


Figure 4 MAXENT models of the potential distributions of *Nephelemys caracolis* (left) and *N. meridensis* (right), for each method of defining the study region, showing binary predictions of the extent of suitable conditions for each species after applying the lowest presence threshold (LPT). Each prediction is divided into areas considered suitable (grey) versus unsuitable (white) for the species. Circles and triangles indicate localities for *N. caracolis* and *N. meridensis*, respectively. Panels (a) and (b) indicate predictions made using Method 1 (models calibrated using the large study region), while panels (c) and (d) illustrate the corresponding predictions for Method 2 (models calibrated using the smaller study region and then applied to the larger one). Note the much larger prediction for *N. caracolis* 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 2 Measures of proportional geographic overlap of the potential distributions of *Nepholomys caracolus* and *N. meridensis* calibrated using all spatially filtered localities, for each method of defining the study region. In Method 1, each species' potential distribution was calibrated in a large study region that included the ranges of both species. In Method 2, a model for each species was calibrated 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 calibrated in the smaller study region), and after converting the continuous prediction to a binary one based on the lowest presence threshold (LPT; see text). The proportional geographic overlap was calculated in three ways based on overlap of the two species' potential distributions as a proportion of: (1) the number of pixels with data in the larger study region; (2) the number of pixels in the prediction for each respective species alone; and (3) the number of pixels 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, and its difference was significant between the two methods of defining the study region (see text).

Proportional geographic overlap based on number of pixels in	Method 1	Method 2
Overlap relative to larger study region	0.018	0.034
Overlap relative to prediction of <i>N. caracolus</i>	0.501	0.747
Overlap relative to prediction of <i>N. meridensis</i>	0.470	0.849
Overlap relative to prediction of either species	0.320	0.659

DISCUSSION

Interpretation of the current results

Our results show that the two methods of defining the study region led to differences in the modelled potential distributions and in estimates of interpredictivity. Furthermore, the directionalities of these differences coincide with the predictions made beforehand (Tables 1 and 2). Specifically, we predicted that Method 2 would avoid problems of overfitting to bias, but that Method 1 would be prone to it (due to non-equilibrium distributions, or areas of suitable conditions that a species does not inhabit because of dispersal limitations or biotic interactions). Hence, Method 2 appears to perform better than Method 1. Indeed, qualitative assessments of the predictions indicate that Method 2 led to more realistic models of the species' potential distributions (based on our knowledge of their natural history and of the climatic and vegetational patterns of the region). Nevertheless, we note that even the predictions made by Method 2 appear implausible in some regions. Specifically, the model for *N. caracolus* showed a surprisingly strong prediction in the lowlands just to the south of the Serranía de San Luis, whereas the model for *N. meridensis* failed to predict the species in mesic highland areas in that range. Finally, issues associated with clamping (a possible drawback to Method 2) do not seem to be problematic in these analyses.

Interestingly, Method 2 led to stronger differences in measures of interpredictivity (always significant) for models of the potential distribution of *N. caracolus* than for those of *N. meridensis*. Whereas the change in the size of the study region between the two methods was dramatic for *N. caracolus* (for which the study region in Method 1 included large areas of likely suitable habitats in the Cordillera de Mérida that are occupied by *N. meridensis*), it was not so substantial for *N. meridensis* (for which the study region in Method 1 included only relatively small areas of likely suitable habitats in the Cordillera de la Costa that are inhabited by *N. caracolus*). These observations make intuitive sense and suggest that models will be more

strongly affected by larger deviations from the assumption of equilibrium distributions in the study region used for calibration (see relative occurrence area of Lobo *et al.*, 2008).

The results suggest that the study region for model calibration should not include areas where the species is absent because of dispersal limitations or biotic interactions (especially competition). This is because background pixels drawn from suitable environments in such regions provide a false negative signal that interferes with successful modelling of a species' environmental requirements. This is not surprising, given that MAXENT assumes that the occurrence localities used for calibration represent a random sample from the statistical distribution being modelled (here, the species' potential distribution in the study region used for calibration; Phillips *et al.*, 2006). Even though background data do not directly inform the model regarding the environmental conditions inhabited by the species, they play a key role in forming a MAXENT model. These principles for selecting an appropriate study region for modelling a species' potential distribution are relevant for all correlative modelling techniques that use background, pseudoabsence or absence data (see Bahn & McGill, 2007; Chefaoui & Lobo, 2008). Based on these principles, future research should aim to develop operational guidelines for selecting a study region that meets this assumption (that the occurrence localities constitute a random sample of the species' potential distribution) as closely as possible. Such guidelines will depend on the taxon being studied and should take into account multiple factors, such as the species' dispersal ability, the topographic complexity of the region in question and the distributional patterns of congeneric (or other closely related) species, especially when congeners show parapatric distributions suggestive of competitive interactions (Koplin & Hoffmann, 1968; Bullock *et al.*, 2000; Anderson *et al.*, 2002b).

Clearly, detailed information regarding dispersal limitations and negative biotic interactors will be difficult to estimate at the beginning of the study – in fact, the point of modelling is often to elucidate such factors (Anderson *et al.*, 2002a,b) – but in many cases, even cursory examination of relevant distributional

patterns can lead to much more reasonable study regions for model calibration than those that have been used in several recent studies (Kozak & Wiens, 2006; Phillips *et al.*, 2006; Warren *et al.*, 2008). For example, despite extensive sampling for small non-volant mammals in northern Venezuela (e.g. Handley, 1976), the two species in this study are not known below 1000 m, and a pronounced lowland depression (the Depresión de Yaracuy; SAGCN, 1995) reaching only *c.* 500 m exists between the respective mountain ranges that they occupy. The species inhabit broadly similar habitats, and no other member of the genus is known definitively from either of these mountain ranges (Percequillo, 2003; but see Aguilera *et al.*, 1995; Márquez *et al.*, 2000). Even this general information allowed us to define simple, smaller rectangular study regions where the relevant assumptions were much less likely to be violated (or at least not violated nearly as strongly). In comparison with the large study regions of Method 1, these study regions led to dramatically different, and arguably more realistic, estimates of the species' potential distributions and, hence, of interpredictivity. This situation should be common with many taxa and in many regions. We anticipate that, frequently, other geometric shapes will prove useful (rotated rectangles, buffered minimum convex polygons, etc.). In addition, researchers may develop an iterative process to model calibration, whereby refined study regions for background or pseudoabsence sampling can be selected using the results of a first round of modelling based on simple, but reasonable, study regions. For example, in a future round of modelling for *N. caracolus*, a more refined study region (smaller than that used in Method 2 here) could include only areas of the Cordillera de la Costa that comprise the Serranía del Litoral along the coast (and not the Serranía del Interior to the south or the Sierra de Aroa to the west – two nearby but disjunct ranges that lack records of the species; see Anderson & Gutiérrez, 2009).

Relevance for the field

The current results are relevant to many areas of research using niche-based distributional modelling. Any application requiring an estimate of a species' potential geographic distribution should strive to calibrate models in an appropriate study region chosen based on the principles outlined here. In particular, this is especially germane for studies of invasive species and of changes in species distribution 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 well a model made in one situation may be transferred to a different context (e.g. another time period after climatic change; or another region for an invasive species). Models produced with an overly large study region are likely to show low transferability. Even studies that aim to estimate a species' realized distribution by modelling its potential distribution and then processing the prediction to take into account the possible effects of competition, dispersal limitations, human-induced changes

and sampling adequacy should follow these recommendations (e.g. Anderson *et al.*, 2002a,b; Anderson, 2003a; Anderson & Martínez-Meyer, 2004).

Studies using niche-based distributional modelling to investigate evolutionary processes should also bear in mind the conclusions of the present study. Niche conservatism refers to the propensity for species to maintain the same niche characteristics over evolutionary time (Peterson *et al.*, 1999), ranging from niche similarity (more similar than expected at random) to full niche equivalency or identity (see Warren *et al.*, 2008). For example, Graham *et al.* (2004b) proposed ways to study speciation by integrating phylogenetic information, distributional overlap of species and niche models. More recently, Kozak & Wiens (2006) showed that niche conservatism and climatic differences in geographic space can 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 models, in order to obtain the best estimates of niche overlap. In light of the current findings, the data from several seminal studies published recently should be reanalysed with more appropriate study regions for model calibration, to determine whether the biological conclusions still hold. Because most papers addressing niche evolution and niche conservatism have used large study regions, we predict that reanalyses will tend to shift interpretations towards conclusions of higher levels of niche conservatism.

Finally, the conceptual issues and principles espoused here should also help resolve some currently controversial issues regarding characterization of the background (the study region used for model calibration) and its association with the region from which the calibration localities derive (Peterson *et al.*, 2007; Phillips, 2008). Specifically, artificially selecting calibration localities from only some portions of the study region used for background sampling may mimic the natural processes discussed here (dispersal limitations and biotic interactions) that can cause a species to inhabit less than its potential distribution. Strictly speaking, this represents a violation of the assumption that the occurrence records represent an unbiased sample from the distribution being modelled (here, the potential distribution; see Phillips *et al.*, 2006). However, if a model performs well despite such violations, it is likely to be more robust to the deleterious effects of sampling bias by biologists (but see Phillips *et al.*, 2009 for an alternative approach). This argument rests on the assumption that the level of bias inserted artificially by the investigator is similar to that of past biological sampling; unfortunately, however, this may be impossible to assess in many cases. Clearly, these corollary issues require further theoretical attention and empirical evaluation. Despite the need for continued research, we conclude that the present results demonstrate: (1) the critical role of definition of the study region, and (2) that when certain principles are taken into account, a presence-background modelling technique can produce more realistic predictions of a species' potential

distribution than those generated using the overly extensive study regions currently in common use. We hope that this study brings attention to the issue of study region selection and encourages further investigation regarding this step of the modelling process.

ACKNOWLEDGEMENTS

The current research was possible via funding from the US National Science Foundation (NSF DEB-0717357, to R.P.A.), American Society of Mammalogists (ASM Undergraduate Student Research Award, to A.R.), City College Academy for Professional Preparation (CCAPP, support to A.R.), and Office of the Dean of Science and Office of the Provost (City College of the City University of New York). We thank Eliécer E. Gutiérrez for assistance in data collection, Mariya Shcheglovitova and Dan L. Warren for insights regarding estimates of variance using the jackknife, and Aleksandar Radosavljevic for guidance running MAXENT from the command line and visualizing the predictions. Amy Berkov, Jorge M. Lobo, the New York Species Distribution Modeling Discussion Group, and two anonymous referees provided helpful comments and suggestions.

REFERENCES

- Aguilera, M., Pérez-Zapata, A. & Martino, A. (1995) Cytogenetics and karyosystematics of *Oryzomys albigularis* (Rodentia, Cricetidae) from Venezuela. *Cytogenetics and Cell Genetics*, **69**, 44–49.
- Anderson, R.P. (2003a) Real vs. artefactual absences in species distributions: tests for *Oryzomys albigularis* (Rodentia: Muridae) in Venezuela. *Journal of Biogeography*, **30**, 591–605.
- Anderson, R.P. (2003b) Taxonomy, distribution, and natural history of the genus *Heteromys* (Rodentia: Heteromyidae) in western Venezuela, with the description of a dwarf species from the Península de Paraguaná. *American Museum Novitates*, **3396**, 1–43.
- Anderson, R.P. & Gutiérrez, E.E. (2009) Taxonomy, distribution, and natural history of the genus *Heteromys* (Rodentia: Heteromyidae) in central and eastern Venezuela, with the description of a new species from the Cordillera de la Costa. *Systematic mammalogy: contributions in honor of Guy G. Musser* (ed. by R.S. Voss and M.D. Carleton). *Bulletin of the American Museum of Natural History*, **331**, 33–93.
- Anderson, R.P. & Martínez-Meyer, E. (2004) Modeling species' geographic distributions for preliminary conservation assessments: an implementation with the spiny pocket mice (*Heteromys*) of Ecuador. *Biological Conservation*, **116**, 167–179.
- Anderson, R.P., Gómez-Laverde, M. & Peterson, A.T. (2002a) Geographical distributions of spiny pocket mice in South America: insights from predictive models. *Global Ecology and Biogeography*, **11**, 131–141.
- Anderson, R.P., Peterson, A.T. & Gómez-Laverde, M. (2002b) Using niche-based GIS modeling to test geographic predictions of competitive exclusion and competitive release in South American pocket mice. *Oikos*, **98**, 3–16.
- Araújo, M.B. & Guisan, A. (2006) Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, **33**, 1677–1688.
- Araújo, M.B. & Rahbek, C. (2006) How does climate change affect biodiversity? *Science*, **313**, 1396–1397.
- Araújo, M.B., Pearson, R.G., Thuiller, W. & Erhard, M. (2005) Validation of species–climate impact models under climate change. *Global Change Biology*, **11**, 1504–1513.
- Bahn, V. & McGill, B.J. (2007) Can niche-based distribution models outperform spatial interpolation? *Global Ecology and Biogeography*, **16**, 733–742.
- Bullock, J.M., Edwards, R.J., Carey, P.D. & Rose, R.J. (2000) Geographical separation of two *Ulex* species at three spatial scales: does competition limit species' ranges? *Ecography*, **23**, 257–271.
- Busby, J.R. (1986) A biogeoclimatic analysis of *Nothofagus cunninghamii* (Hook.) Oerst. in southeastern Australia. *Australian Journal of Ecology*, **11**, 1–7.
- Carpenter, G., Gillison, A.N. & Winter, J. (1993) DOMAIN: a flexible modelling procedure for mapping potential distributions of plants and animals. *Biodiversity and Conservation*, **2**, 667–680.
- Chefaoui, R.M. & Lobo, J.M. (2008) Assessing the effects of pseudo-absences on predictive distribution model performance. *Ecological Modelling*, **210**, 478–486.
- DCN (1964) *Hoja 6847 (Caracas)*, escala 1:100.000. Dirección de Cartografía Nacional, Ministerio de Obras Públicas, Caracas.
- DCN (1975) *Hoja 5941-I-NE (Tabay)*, escala 1:25.000. Dirección de Cartografía Nacional, Ministerio de Obras Públicas, Caracas.
- DCN (1977a) *Hoja 5941 (Mérida)*, escala 1:100.000. Dirección de Cartografía Nacional, Ministerio del Ambiente y de los Recursos Naturales Renovables, Caracas.
- DCN (1977b) *Hoja 5942 (La Azulita)*, escala 1:100.000. Dirección de Cartografía Nacional, Ministerio del Ambiente y de los Recursos Naturales Renovables, Caracas.
- DCN (1979a) *Hoja 6847-I-SE (Perque)*, escala 1:25.000. Dirección de Cartografía Nacional, Ministerio del Ambiente y de los Recursos Naturales Renovables, Caracas.
- DCN (1979b) *Hoja 6847-IV-SE (Los Chorros)*, escala 1:25.000. Dirección de Cartografía Nacional, Ministerio del Ambiente y de los Recursos Naturales Renovables, Caracas.
- Díaz de Pascual, A. (1994) The rodent community of the Venezuelan cloud forest, Mérida. *Polish Ecological Studies*, **20**, 155–161.
- Efron, B. & Tibshirani, R.J. (1993) *An introduction to the bootstrap*. Chapman and Hall, New York.
- Elith, J., Graham, C.H., Anderson, R.P. *et al.* (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129–151.

- French, A.R. (1993) Physiological ecology of the Heteromyidae: economics of energy and water utilization. *Biology of the Heteromyidae* (ed. by H.H. Genoways and J.H. Brown). *Special Publications, American Society of Mammalogists*, **10**, 509–538.
- Graham, C.H., Ferrier, S., Huettman, F., Moritz, C. & Peterson, A.T. (2004a) New developments in museum-based informatics and application in biodiversity analysis. *Trends in Ecology and Evolution*, **19**, 497–503.
- Graham, C.H., Ron, S.R., Santos, J.C., Schneider, C.J. & Moritz, C. (2004b) Integrating phylogenetics and environmental niche models to explore speciation mechanisms in dendrobatid frogs. *Evolution*, **58**, 1781–1793.
- Handley, C.O., Jr (1976) Mammals of the Smithsonian Venezuelan Project. *Brigham Young University Science Bulletin, Biological Series*, **20**(5), 1–91.
- Hernandez, P.A., Graham, C.H., Master, L.L. & Albert, D.L. (2006) The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography*, **29**, 773–785.
- Hijmans, R.J. & Graham, C.H. (2006) The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology*, **12**, 1–10.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.
- Hortal, J., Jiménez-Valverde, A., Gómez, J.F., Lobo, J.M. & Baselga, A. (2008) Historical bias in biodiversity inventories affects the observed environmental niche of the species. *Oikos*, **117**, 847–858.
- Jiménez-Valverde, A., Lobo, J.M. & Hortal, J. (2008) Not as good as they seem: the importance of concepts in species distribution modelling. *Diversity and Distributions*, **14**, 885–890.
- Kearney, M. (2006) Habitat, environment and niche: what are we modelling? *Oikos*, **115**, 186–191.
- Koplin, J.R. & Hoffmann, R.S. (1968) Habitat overlap and competitive exclusion in voles (*Microtus*). *The American Midland Naturalist*, **80**, 494–507.
- Kozak, K.H. & Wiens, J.J. (2006) Does niche conservatism promote speciation? A case study in North American salamanders. *Evolution*, **60**, 2604–2621.
- Kozak, K.H., Graham, C.H. & Wiens, J.J. (2008) Integrating GIS-based environmental data into evolutionary biology. *Trends in Ecology and Evolution*, **23**, 141–148.
- Kremen, C., Cameron, A., Moilanen, A. *et al.* (2008) Aligning conservation priorities across taxa in Madagascar with high-resolution planning tools. *Science*, **320**, 222–226.
- Lobo, J.M. (2008) More complex distribution models or more representative data? *Biodiversity Informatics*, **5**, 14–19.
- Lobo, J.M., Jiménez-Valverde, A. & Real, R. (2008) AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography*, **17**, 145–151.
- Márquez, E.J., Aguilera-M., M. & Corti, M. (2000) Morphometric and chromosomal variation in populations of *Oryzomys albigularis* (Muridae: Sigmodontinae) from Venezuela: multivariate aspects. *Zeitschrift für Säugetierkunde*, **65**, 84–99.
- Minitab (2003) *Minitab, release 14.1*. Minitab, Inc., State College, PA.
- Morin, X. & Thuiller, W. (2009) Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Ecology*, **90**, 1301–1313.
- Moscarella, R.A. & Aguilera-M., M. (1999) Growth and reproduction of *Oryzomys albigularis* (Muridae: Sigmodontinae) under laboratory conditions. *Mammalia*, **63**, 349–362.
- Paynter, R.A., Jr (1982) *Ornithological gazetteer of Venezuela*. Museum of Comparative Zoology, Harvard University, Cambridge, MA.
- Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.
- Pearson, R.G., Raxworthy, C.J., Nakamura, M. & Peterson, A.T. (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography*, **34**, 102–117.
- Percequillo, A.R. (2003) *Sistemática de Oryzomys Baird, 1858: definição dos grupos de espécie e revisão taxonômica do grupo albigularis (Rodentia, Sigmodontinae)*. PhD Thesis, Universidade de São Paulo, Brazil.
- Peterson, A.T. (2003) Predicting the geography of species' invasions via ecological niche modeling. *Quarterly Review of Biology*, **78**, 419–433.
- Peterson, A.T., Papeş, M. & Eaton, M. (2007) Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. *Ecography*, **30**, 550–560.
- Peterson, A.T., Soberón, J. & Sánchez-Cordero, V. (1999) Conservatism of ecological niches in evolutionary time. *Science*, **285**, 1265–1267.
- Phelps, W.H. (1944) Resúmen de las colecciones ornitológicas hechas en Venezuela. *Boletín de la Sociedad Venezolana de Ciencias Naturales*, **61**, 325–444.
- 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. & Dudík, M. (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, **31**, 161–175.
- Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231–259.
- Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J. & Ferrier, S. (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications*, **19**, 181–197.
- Randin, C.F., Dirnböck, T., Dullinger, S., Zimmermann, N.E., Zappa, M. & Guisan, A. (2006) Are niche-based species

- distribution models transferable in space? *Journal of Biogeography*, **33**, 1689–1703.
- Reddy, S. & Dávalos, L.M. (2003) Geographical sampling bias and its implications for conservation priorities in Africa. *Journal of Biogeography*, **30**, 1719–1727.
- Rivas, B.A. & Salcedo, M.A. (2006) Lista actualizada de los mamíferos del Parque Nacional El Ávila, Venezuela. *Memorias de la Fundación La Salle de Ciencias Naturales*, **164**, 29–56.
- Rood, J.P. & Test, F.H. (1968) Ecology of the spiny rat, *Heteromys anomalus*, at Rancho Grande, Venezuela. *American Midland Naturalist*, **79**, 89–102.
- SAGCN (1995) *Mapa físico de la República de Venezuela*, escala 1:2.000.000. Servicio Autónomo de Geografía y Cartografía Nacional, Ministerio del Ambiente y de los Recursos Naturales Renovables, Caracas.
- Scott, J.M., Heglund, P.J., Morrison, M.L., Haufler, J.B., Raphael, M.G., Wall, W.A. & Samson, F.B. (eds) (2002) *Predicting species occurrences: issues of accuracy and scale*. Island Press, Washington, DC.
- Shao, J. & Wu, C.F.J. (1989) A general theory for jackknife variance estimation. *Annals of Statistics*, **17**, 1176–1197.
- Soberón, J. (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, **10**, 1115–1123.
- Sokal, R.R. & Rohlf, F.J. (1995) *Biometry: the principles and practice of statistics in biological research*, 3rd edn. W. H. Freeman, New York.
- Swenson, N.G. (2008) The past and future influence of geographic information systems on hybrid zone, phylogeographic and speciation research. *Journal of Evolutionary Biology*, **21**, 421–434.
- Warren, D.L., Glor, R.E. & Turelli, M. (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution*, **62**, 2868–2883.
- Weksler, M., Percequillo, A.R. & Voss, R.S. (2006) Ten new genera of oryzomyine rodents (Cricetidae: Sigmodontinae). *American Museum Novitates*, **3537**, 1–29.
- Welk, E., Schubert, K. & Hoffmann, M.H. (2002) Present and potential distribution of invasive garlic mustard (*Alliaria petiolata*) in North America. *Diversity and Distributions*, **8**, 219–233.
- Wiens, J.J. & Graham, C.H. (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology and Systematics*, **36**, 519–539.
- Williams, J.W. & Jackson, S.T. (2007) Novel climates, non-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, **5**, 475–482.
- Wisheu, I.C. (1998) How organisms partition habitats: different types of community organization can produce identical patterns. *Oikos*, **83**, 246–258.
- Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H. & Guisan, A. (2008) Effects of sample size on the performance of species distribution models. *Diversity and Distributions*, **14**, 763–773.
- Zaniewski, A.E., Lehmann, A. & Overton, J.M. (2002) Predicting species spatial distributions using presence-only data: a case study of native New Zealand ferns. *Ecological Modelling*, **157**, 261–280.
- Zar, J.H. (1999) *Biostatistical analysis*, 4th edn. Prentice Hall, Upper Saddle River, NJ.

BIOSKETCHES

Robert Anderson, an Associate Professor at the City College of the City University of New York, conducts biogeographical studies at the interface between ecology and evolution. His current research programme focuses on the development of GIS-based methods of modelling species geographic distributions using occurrence records and environmental data. In addition to these techniques of general application to biogeography and conservation, his taxonomic and geographic speciality is Neotropical mammals.

Ali Raza began his research in ecological modelling as an undergraduate at the City College of the City University of New York. Initially, he worked on an independent research project modelling the geographic distributions of climbing mice of the genus *Rhipidomys* in northern South America. His subsequent research has resulted in the present methodological study. Currently, he is pursuing a Master's degree in biology.

Editor: Jon Sadler

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-M., 1999), 10°23' N, 67°20' W (Moscarella & Aguilera-M., 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, 2003b; coordinates correspond to El Blanquito, the principal collection locality in Yacambú National Park); MÉRIDA: 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 elevation 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).