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Modeling species' geographic distributions for preliminary conservation assessments: an implementation with the spiny pocket mice (*Heteromys*) of Ecuador

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Abstract

GIS-based modeling of a species' environmental requirements using known occurrence records can provide estimates of its distribution for conservation assessments when other data are lacking. We used collection records, environmental variables, maps of land cover and protected areas, and the Genetic Algorithm for Rule-Set Prediction (GARP) to estimate the historical, current, and protected ranges of the spiny pocket mice present in Ecuador (*Heteromys australis* and *H. teleus*). The results suggest that ca. 52–63% of the distributional areas of *H. australis* in the country are intact, but suitable habitat in protected areas represents only approximately 11–13% of the species' historical range there. The distribution of *H. teleus* has been much more reduced, with only ca. 13–19% of its historical distribution still forested and an estimated 2–3% intact and falling in protected areas. Our work highlights critical areas for future fieldwork and demonstrates an integrated approach to estimating a species' current distribution for preliminary conservation assessments.

Keywords: Conservation; Deforestation; Distribution; GIS; Range

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1. Introduction

1.1. The geographic distribution

Species' geographic distributions represent the foundation for subsequent levels of biogeographic research (Udvardy, 1969; MacArthur, 1972). In addition, current geographic ranges are critical to conservation assessments, which often make evaluations based on restricted or shrinking distributions when more data-rich studies are lacking (Mace and Lande, 1991; Mace and Stuart, 1994). However, even the *distributions* of many taxa are extremely poorly known, especially in tropical areas (Raven and Wilson, 1992; Voss and Emmons, 1996). This lack of basic information often hinders conservation assessments, even for relatively well-studied groups. For example, of the 369 species of mammals estimated to inhabit Ecuador (Tirira-S., 1999), only 71 were evaluated in the *Libro Rojo de los Mamíferos del Ecuador* following IUCN criteria (Tirira-S., 2001).

Occurrence records, generally in the form of museum or herbarium specimens, constitute the primary documentation of a species' geographic distribution. Because true absence data are lacking for most species (Funk et al., 1999; Ponder et al., 2001; Stockwell and Peterson, 2002a), drawbacks exist to the most common portrayals of geographic ranges in field guides and taxonomic revisions (Rapoport, 1982; Ceballos and Ehrlich, 2002). Dot maps (documented localities plotted on a map) depict a species' range very conservatively, leaving the reader to draw conclusions regarding the true distribution (Skov, 2000). At the other end of the spectrum,

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shaded outline maps attempt to extrapolate a species' range among and beyond known localities, but do not specify the resolution of the underlying data and are highly dependent on subjective knowledge of the group and study region (e.g., Reid, 1997; Emmons, 1997; Eisenberg and Redford, 1999). Generally, they vastly overestimate the species' distribution (see distinction between ''extent of occurrence'' and ''area of occupancy'' in Mace and Stuart, 1994). Fortunately, new distributional modeling techniques provide an improvement over the broad-stroke maps typical of field guides and other faunal and floral treatments.

1.2. Distributional modeling

Recently, several approaches to predictive modeling of species' geographic distributions have been developed in a geographic information system (GIS) environment. Such modeling tools have been applied to problems in biogeography, conservation, evolutionary ecology, and invasive-species management (e.g., Nicholls, 1989; Walker and Cocks, 1991; Sindel and Michael, 1992; Carpenter et al., 1993; Yom-Tov and Kadmon, 1998; Jarvis and Robertson, 1999; Peterson et al., 1999; James and McCulloch, 2002). Among these techniques, the Genetic Algorithm for Rule-Set Prediction (GARP) has shown particular utility and promise under a wide variety of conditions and is especially suited to use with presence-only occurrence data (e.g., Peterson et al., 1999, 2002a, b, c; Elith, 2000; Joseph and Stockwell, 2002; Anderson, 2003a; Anderson et al., 2003; Peterson and Kluza, 2003; and references therein). GARP is a machine-learning tool that uses environmental data and localities of a species' occurrence to produce a model of its requirements in those environmental/ecological dimensions (Stockwell and Noble, 1992; Stockwell and Peters, 1999). This complex rule-set model is then projected into geographic space to create a map of the species' potential distribution.

Although encompassing only a few of the possible niche dimensions (sensu Hutchinson, 1957), currently available GIS layers (digital maps, or coverages) provide environmental data for many major physical variables that commonly influence species' macrodistributions (Grinnell, 1917a, b; Root, 1988; Brown and Lomolino, 1998: 72). A GARP model thus indicates areas potentially habitable for the species. However, few species actually occupy all areas of potential distribution. For example, some such regions may be occupied by closely related species, or may represent suitable areas to which the species has failed to disperse or in which it has gone locally extinct (Peterson et al., 1999; Anderson et al., 2002a, b). After such historical restrictions and biotic interactions have been taken into account, the resulting trimmed GARP model then approximates the species' historical distribution.

Destruction of natural habitats has drastically affected many species' distributions, often reducing their historical ranges to a set of small, fragmented populations (Brooks et al., 2002; Channell and Lomolino, 2000). Such habitat alteration is predicted to lead to substantial extinction in the near future (Pimm and Askins, 1995; Brooks et al., 1999). For an obligate forest species, areas of remaining forest within the modeled historical distribution can be extracted to give an estimate of its current range (Chen and Peterson, 2000). Furthermore, the intersection of a species' current range with a digital map of national parks and other protected areas indicates its protected distribution (see Lizcano et al., 2002 for use with a simple vegetation-surrogate model). Here, we integrate these approaches to provide preliminary conservation assessments for the two species of spiny pocket mice (*Heteromys*) present in Ecuador, including a recently discovered species of special concern (Anderson and Jarrı́n-V., 2002).

2. Methods

2.1. Study species

Spiny pocket mice (Rodentia: Heteromyidae: Heteromyinae) range from Texas (USA) to Ecuador (Patton, 1993; Williams et al., 1993). *Heteromys* is the only heteromyid genus present in South America, where two species have widespread distributions and three others marginal ones (Anderson, 1999, 2003b; Anderson and Soriano, 1999; Anderson and Jarrı́n-V., 2002). *Heteromys anomalus* ranges across the Caribbean coast of Colombia and Venezuela and is also found in Trinidad and Tobago. Complementarily, *H. australis* is distributed from western Venezuela and eastern Panama through suitable areas in Colombia to northwestern Ecuador. Additionally, a member of the *H. desmarestianus* species complex inhabits extreme northwestern Colombia in the Serranı́a del Darién (Anderson, 1999), and *H. oasicus* is found only on the Penı́nsula de Paraguaná in northwestern Venezuela (Anderson, 2003). Finally, *H. teleus* is endemic to central-western Ecuador (Anderson and Jarrı́n-V., 2002).

Although both species of spiny pocket mice present in Ecuador (*Heteromys australis* and *H. teleus*) are restricted to evergreen forests, the environmental characteristics of their respective collection localities differ somewhat. Occurrence sites and coarse climatic data suggest that differences between the areas that the two species inhabit correspond to the strong precipitation gradient from north to south in western Ecuador (Albuja-V. et al., 1980; Anderson and Jarrı́n-V., 2002). Within the country, *H. australis* is restricted to wet, unseasonal areas of the Chocó and adjacent western slopes of the Andes in extreme northwestern Ecuador, from ca. sea level to 1400 m (Fig. 1; Anderson and Jarrín-V., 2002). In contrast, *H. teleus* is found only in central-western Ecuador, in areas supporting evergreen forests that receive less precipitation in a more seasonal regime (Sierra et al., 1999a, b; IGM, 1995a, b). In addition to lowland habitats, *H. teleus* is also found on the western slopes of the Andes and in the isolated Cordillera de Chongón-Colonche (southern extension of the Cordillera de la Costa). Whereas the surrounding lowlands support only deciduous forests and various xeric, nonforested vegetation types, the summits and high western slopes of Chongón-Colonche are nourished by mist and fog coming off the Pacific, creating isolated patches of evergreen forest (Foster, 1992; Best and Kessler, 1995). Its known elevational range extends from 50 to 2000 m (Anderson and Jarrín-V., 2002).

Both *Heteromys australis* and *H. teleus* have been captured in disturbed as well as primary forests

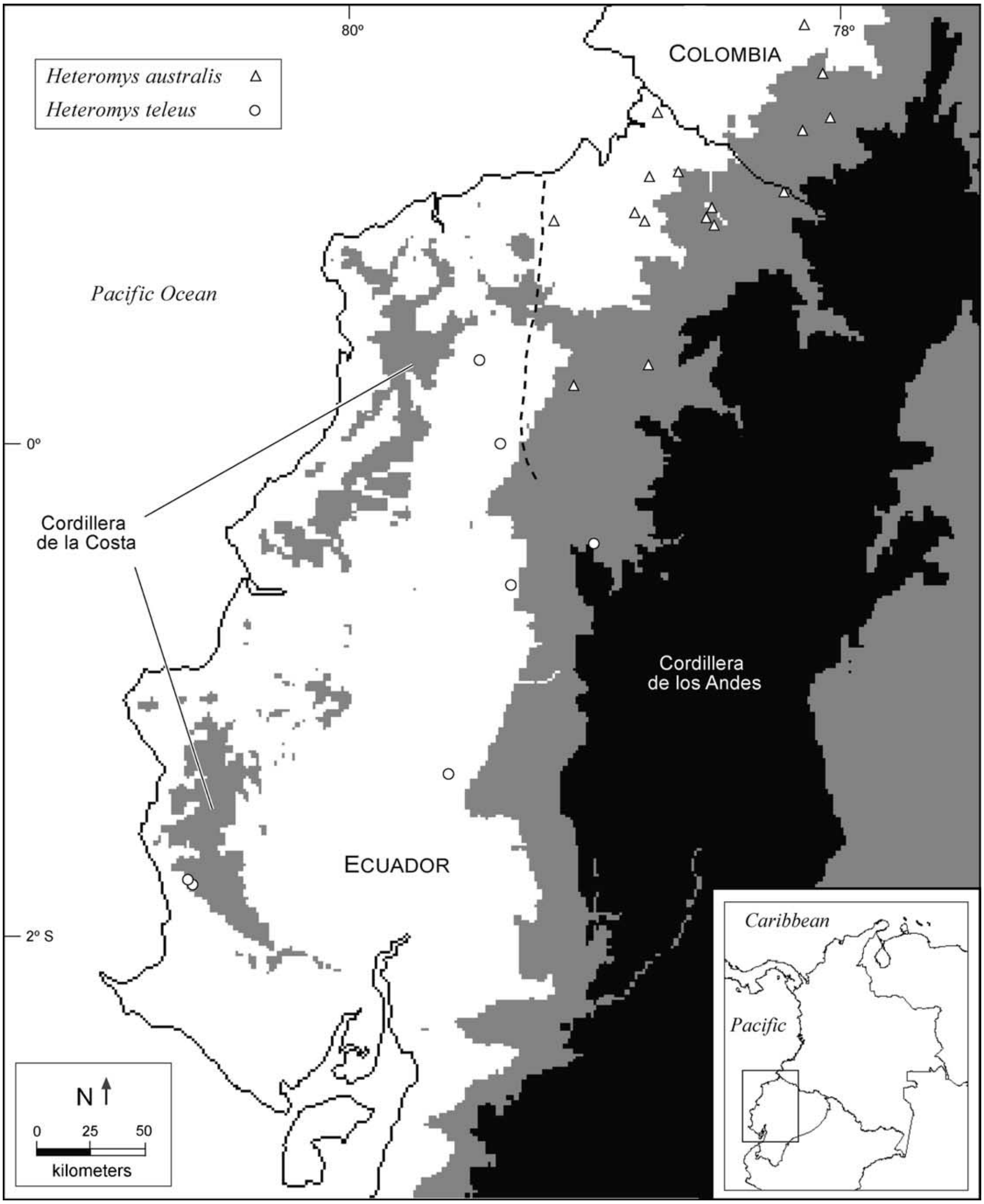

Fig. 1. Map showing collection localities for *Heteromys australis* (triangles) and *H. teleus* (circles) in Ecuador and southwestern Colombia (models were made using only Ecuadorian localities; data from Anderson and Jarrín-V., 2002). Regions above 300 m are shown in gray, and areas above 2000 m appear in black. The dashed line in the northwestern part of Ecuador denotes the division between coastal regions with a dry season more than 5 months long (southwest of the line) and areas with a shorter dry season (northeast of the line), adapted from Sierra et al. (1999b).

(Anderson and Jarrín-V., 2002). These disturbed forests correspond to several forms of low-intensity human use. Some contain small cultivated plots and/or are occasionally entered by free-ranging livestock. In addition, wood and other products have been selectively extracted from many of them by local inhabitants. However, no Ecuadorian collection locality of either species derives from a truly secondary site (recovering from being clearcut recently), deciduous forest, or open, non-forested area. Although *H. anomalus* is known to tolerate low-intensity or "subsistence" agricultural areas (Anderson, 1999; Utrera et al., 2000), species of *Heteromys* characteristically inhabit closed-canopy forests (Sánchez-Cordero and Fleming, 1993). All data available for *H. australis* and *H. teleus* indicate that they are restricted to closed-canopy forests (Anderson and Jarrín-V., 2002).

These two species thus represent an ideal study system for the current approach using distributional modeling for preliminary conservation assessments (Chen and Peterson, 2000; Lizcano et al., 2002). Their examined distributions correspond to the southern end of the Chocó/Darién/Western Ecuador biodiversity hotspot, identified for its high species richness, endemism, and levels of habitat destruction (Myers et al., 2000). Within that region, deforestation has been most pervasive in western Ecuador, with estimates of up to 95% of the original forested areas there converted to agriculture (Albuja-V., 1999). Neither species is known from any governmentally protected area in the country. These factors led to concern for their long-term survival—particularly that of the recently described *Heteromys teleus*, which is endemic to a small region where deforestation is especially severe (Anderson and Jarrín-V., 2002).

Because so few locality records are available, some form of extrapolation is clearly necessary to estimate the species' distributions. Vegetation-surrogate methods (e.g., Scott et al., 1996; Lizcano et al., 2002) fail in this case, predicting virtually the same distribution for both species (Anderson and Jarrín-V., 2002). Thus, the addition of other variables, such as climatic data, is required to estimate their ranges. Digital maps of original vegetational zones, current landcover conditions, and protected areas in the country are available, making the project feasible (Sierra, 1999; Sierra et al., 1999a, b).

2.2. Model building and data sources

We employed the Genetic Algorithm for Rule-Set Prediction (GARP) to model the potential distributions of *Heteromys australis* and *H. teleus* in Ecuador. Chen and Peterson (2000), Peterson and Vieglais (2001), and Anderson et al. (2002a) provide general explanations of the GARP modeling process and interpretation of potential distributions; see Stockwell and Noble (1992) and Stockwell and Peters (1999) for technical details. GARP evaluates non-random associations between environmental characteristics of localities of known occurrence versus those of the overall study region to produce a heterogeneous rule-set characterizing the species' ecological requirements (Peterson et al., 1999). In some circumstances, the rule-set does not provide a presence/absence decision for the environmental combination present in a particular map pixel; such cells were considered as predicted absence (following Anderson et al., 2003). Owing to strong stochastic elements in the algorithm, no unique solution is produced. Hence, production of multiple models is necessary to account for variability among independent runs of model building (see below; Anderson et al., 2002a, 2003; Lim et al., 2002).

We used 13 geographic coverages for the base environmental data. Topographic data (elevation, slope, aspect, and topographic index) were derived from USGS (2001; http://edcdaac.usgs.gov/gtopo30/hydro/; original resolution 1 km on a side). Climatic data came from New et al. (1997; http://ipcc-ddc.cru.uea.ac.uk original resolution ca. 55 km on a side) and consist of annual values for: cloud cover, precipitation, solar radiation, vapor pressure, wet-day frequency, diurnal temperature range, and minimum, maximum, and mean temperature. We resampled all environmental coverages to a coincident grid of approximately 1×1 km.

Species' occurrence records in Ecuador came from Anderson and Jarrín-V. (2002; 12 unique latitude-longitude combinations for *Heteromys australis*; 7 for *H. teleus*). The quality of predictive models of species' distributions is commonly evaluated by dividing known localities randomly into two groups: a training data set used to create the models and a test data set used to evaluate them (Fielding and Bell, 1997; = split-sample approach of Guisan and Zimmermann, 2000). A one-tailed χ^2 statistic (or binomial probability, if sample sizes are small, as here) can then be employed to determine whether test points fall into regions of predicted presence more often than expected by chance, given the proportion of map pixels predicted present by the model (Anderson et al., 2002a). These test data sets thus provide extrinsic (independent) measures of model significance (better than random prediction). In addition to significance, good models also should show low extrinsic omission of localities in the test data set (Anderson et al., 2003; = "accuracy" of Anderson et al., 2002a).

Hence, to test our ability to predict the species' distributions, we produced preliminary models based on a subset of the localities. We first divided collection localities randomly into training and test data sets (50% each) for each species. With the respective training sets, we created 10 preliminary models. We eliminated any model showing intrinsic omission (omission of training localities), following Anderson et al. (2003). Because one locality of *Heteromys teleus* on the western slope of the Andes corresponds to environmental conditions quite different from those of all other known records of the species (Anderson and Jarrín-V., 2002; Fielding, 2002: 273), we made a second set of preliminary models for that species after stratifying the random sampling of training localities to include one locality from the Andes, one from the Cordillera de Chongón-Colonche, and two from the coastal plain. Since sample sizes were too small for χ^2 analyses, we calculated one-tailed exact binomial probabilities for the test data sets (Anderson et al., 2002a). Due to potential error in geographic coordinates, we also calculated binomial probabilities for the proportion of test localities falling within 5 km of areas of predicted presence (Anderson and Jarrín-V., 2002).

After demonstrating effective predictive ability in the preliminary models, we made 100 final models for each species using all available locality records. Once again, only models with zero intrinsic omission were considered further (see Anderson et al., 2003). We then summed 100 such models to create a composite prediction in which the value for each map pixel corresponded to the number of models predicting the species' presence in that cell. This composite model thus represents a surface indicating the suitability of various regions for the species, and we refer to it as the raw climatic model.

2.3. Model processing and interpretation

We cut each raw climatic model by the vegetation types in which the respective species has been found west of the Andes (*formaciones naturales* of Sierra et al., 1999a, b). This phytogeographic scheme differentiates between structurally similar vegetative formations that have different species compositions due to historical causes (e.g., lowland evergreen forest west and east of the Andes). Thus, it differs from a potential-vegetation classification and could not be included as an additional predictor variable in the GARP modeling process (e.g., as in Sánchez-Cordero and Martínez-Meyer, 2000; Anderson et al., 2002a; Feria-A. and Peterson, 2002; Lim et al., 2002). By so cutting the raw climatic models, we removed areas of deciduous forest and xeric non-forested areas from the predictions, leaving only various classes of evergreen forest. This was necessary because complex mosaics of deciduous and evergreen vegetation types are present in some regions suitable for the respective species based on overall climate (Best and Kessler, 1995). We did not include areas of potential presence falling into the corresponding vegetational categories east of the crest of the Andes; therefore, this step also removed areas of potential distribution there, where no *Heteromys* are known (probably due to historical restrictions; Anderson, 1999; Anderson et al., 2002a). We refer to these trimmed models as the species' potential distributions in western Ecuador and restrict our further analyses and discussion to that region.

Closely related, morphologically similar species commonly share ecological requirements that can prevent their coexistence (Gause, 1934; MacArthur, 1972). Thus, a species' geographic range may be restricted by related species (Miller, 1967; Koplin and Hoffmann, 1968; Brown, 1971). Throughout the subfamily Heteromyinae, congeneric species are seldom syntopic. Where their distributions come into contact, species generally segregate into distinct habitat types along narrow contact zones, indicating that in such situations their realized niches reflect a partitioning of habitable areas (Genoways, 1973; Rogers and Engstrom, 1992). In addition, ecogeographic patterns for *Heteromys australis* and *H. anomalus* strongly suggest that competitive interactions reduce species' potential distributions in this group (Anderson et al., 2002b).

Therefore, we overlaid the potential distributions for the two species, highlighting regions of potential sympatry where both were predicted present. To approximate reductions to their potential ranges due to the congener, we determined which species was predicted by a greater number of models in each map pixel. We then cut each species' potential distribution to include only those pixels where it was predicted with the same or greater frequency than the congener. This process yielded our estimates of the species' historical distributions in western Ecuador.

Then, we considered current and protected distributions for the species. To produce estimates of the species' current distributions, we cut the historical distributions by areas of remaining forest as of 1996 (Sierra, 1999). Finally, we cut the species' current distributions by the Ecuadorian governmental system of protected areas as of 1999 (Sierra, 1999; Sierra et al., 1999b), yielding approximations of their protected current distributions.

We provide a range of quantitative areal estimates for the species' potential, historical, current, and protected current distributions in western Ecuador. The lower (restrictive, conservative) estimates correspond to the pixels predicted by all 100 models, and the higher (permissive, liberal) ones to pixels predicted by any of them. Despite presentation to the nearest 100 km^2, the results must be interpreted as very general estimates due to the coarseness of some of the original environmental variables (the climatic ones). In addition, predictor variables were not available for small areas adjacent to the coast at Punta La Cabezona and Cabo San Lorenzo in Manabí and Guayas provinces, or for a region just inland from Cabo Pasado in Manabí. Given the modeling results for adjacent areas, we discuss the likely suitability of these regions for each species and consider such areas in the conservation assessments.

3. Results

3.1. Preliminary models

The preliminary models for *Heteromys australis* correctly predicted most sites in the test data set. Five of the six test localities lay in pixels predicted by at least one of the 10 models ($P = 0.0001$, one-tailed binomial). Furthermore, these sites all lay either in or within 1 km of pixels predicted by all models. The last test locality was not predicted by any model, but fell within 4 km of a pixel of predicted presence ($P < 0.0001$ for six out of six test sites) indicated by all 10 models.

The preliminary models for *Heteromys teleus* also correctly predicted most test sites. Two of the three test localities were predicted by at least one of the models ($P = 0.0994$) and also lay in or within 1 km of a pixel predicted by all 10 models. The last test locality (Bosque Integral Otonga; Jarrín-V., 2001) was not included by any model and fell 29 km from predicted areas. In the second set of test models for the species—with training localities stratified by each of the three environmental categories identified by Anderson and Jarrín-V. (2002)—two test sites (one from the Cordillera de Chongón-Colonche and one from the central coastal plain) were predicted by all 10 of the new preliminary models ($P = 0.1427$). The last locality lay within 5 km of a predicted pixel ($P = 0.0134$ for three of three test sites; Jauneche, the southernmost record on the coastal plain; see Albuja-V., 1992).

3.2. Final models

The climatic models trimmed by vegetation type represented the species' potential distributions in western Ecuador (Figs. 2A and 3A). The potential distributions of *Heteromys australis* and *H. teleus* overlapped broadly from the Colombian border to near the southern extent of continuous evergreen forest in the western part of the country. However, *H. teleus* was predicted farther south than *H. australis*, and only *H. teleus* showed potential distribution in the Cordillera de Chongón-Colonche. These differences derived from the underlying climatic models (not shown), not from slight discrepancies in the vegetation types that the species inhabit. For *Heteromys australis*, the area predicted by at least one model was much more extensive than that predicted by all 100 models (Table 1). The full potential distribution for *H. teleus* was slightly larger than that of *H. australis*, and a much larger proportion of it was indicated by all 100 models (Table 1).

Despite the large overlap in potential distributions, the species differed greatly in the *support* for their potential presence in various portions of those regions. The potential distribution for *Heteromys australis* was strongly supported in extreme northwestern Ecuador (primarily in Carchi, Esmeraldas, and Imbabura provinces), with most pixels there predicted by the vast majority of the 100 models (Fig. 2A). Support for the species' potential distribution was moderate (less than 50% of the models) in areas slightly west and south, and even weaker farther south (50% threshold not shown). Complementarily, the potential distribution for *H. teleus* was indicated most strongly in the Cordillera de Chongón-Colonche and along the central portion of the coastal plain (Fig. 3A; mostly in Guayas, Los Ríos, Manabí, and Pichincha provinces). The prediction for *H. teleus* also included small areas with moderate support in central-western Ecuador just north of Chone and Bahía de Caráquez, as well as at the very tail end of the Chocó (sensu Cracraft, 1985) east of Balao and Naranjal. Support for its prediction was weak in the lowlands of northwestern Ecuador (where support for *H. australis* was especially strong) and in most of the southern extent of its potential distribution (south of known records on the coastal plain).

After cutting each species' potential distribution by removing pixels more frequently predicted for the congener, the species' reconstructed historical distributions differed greatly. The distribution of *Heteromys australis* in the country was restricted to northwestern Ecuador and a few small areas on the central-western coast and along the piedmont of the Andes (Fig. 2B; Table 1). In contrast, the analyses indicated the historical distribution of *H. teleus* throughout most of the central-western coastal plain, as well as in the Cordillera de Chongón-Colonche and some areas along the western slopes of the Andes (Fig. 3B; Table 1).

Deforestation has led to much smaller current distributions for both species. The results indicated a current distribution for *Heteromys australis* in Ecuador almost entirely restricted to the extreme northwestern part of the country (Fig. 2C). This represents ca. 52–63% of its historical distribution there (Table 1; note that the species also occurs in Colombia, Panama, and Venezuela). Despite a more extensive historical distribution in Ecuador for *H. teleus*, removal of deforested areas yielded an estimated current distribution much smaller than that of *H. australis* (Fig. 3C; Table 1). Those areas correspond to ca. 13–19% of its historical distribution and are scattered throughout the original range.

Only small regions of the species' current distributions in Ecuador lay in governmentally protected areas. Estimates of the protected current distribution for *Heteromys australis* in Ecuador encompassed ca. 11–13% of its historical range in the country and ca. 18–25% of its current one there (Fig. 2D; Table 1). The vast majority fell in either the Reserva Ecológica Cotacachi-Cayapas or in the Reserva Ecológica Mache-Chindul, but tiny areas were also present in the Reserva Ecológica Cayapas-Mataje and Reserva Ecológica Los Ilinzas. The protected current distribution for *H. teleus* was even smaller, corresponding to ca. 2–3% of its historical range and ca. 16% of its current distribution (Fig. 3D; Table 1). These areas occured in five reserves: the Parque Nacional Machalilla, Reserva Ecológica Cotacachi-Cayapas, Reserva Ecológica Mache-Chindul, Reserva Geobotánica Pululahua, and Reserva Ecológica Los Ilinzas.

Few areas excluded from our modeling effort (because geographic data were not available) represent regions of likely presence for either species. Map pixels adjacent to the region lacking environmental data inland from

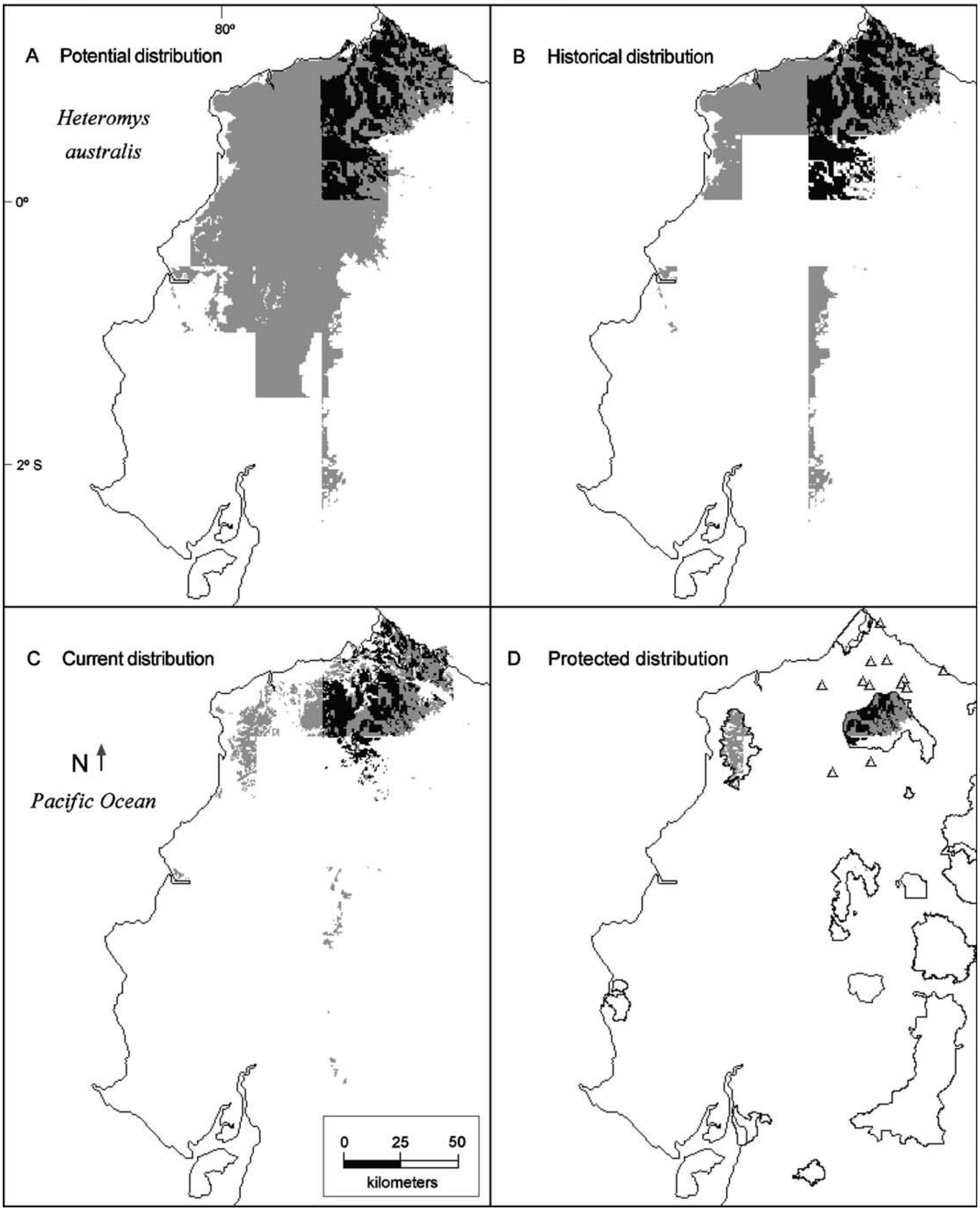

Fig. 2. Estimated geographic distributions for *Heteromys australis* in western Ecuador (all relevant areas occur in this region of central-western and northwestern Ecuador): (A) potential distribution, (B) historical distribution, (C) current distribution, and (D) protected distribution (with outlines of governmentally protected areas; triangles denote known locality records for the species in the country). Areas predicted by all 100 models appear in black and those indicated by 1–99 models in gray. The blocky nature of some environmental predictor variables (the climatic ones) is apparent here, especially in the 100-model threshold. A spectrum of gray portraying the full gradient from 1 to 100 (not shown) indicates a much more gradual transition between areas predicted with low vs. high support. See methods for details of model building and processing.

Cabo Pasado in Manabí province indicated potential presence for *Heteromys australis* with only low support (in the climatic prediction). The same pixels corresponded to potential presence for *H. teleus* with low-to-moderate support. In any case, most of the evergreen forests that once extended into this area have been removed (Sierra, 1999; Sierra et al., 1999b). In contrast, map pixels adjacent to Punta La Cabezona and Cabo San Lorenzo (also in Manabí) showed a well-supported climatic prediction for *H. teleus*. In this region, extremely small areas of evergreen forest are still present just north of the Río Ayampe directly east of Punta la Cabezona; in addition, a patch of evergreen forest is located east of Cabo San Lorenzo (Sierra, 1999).

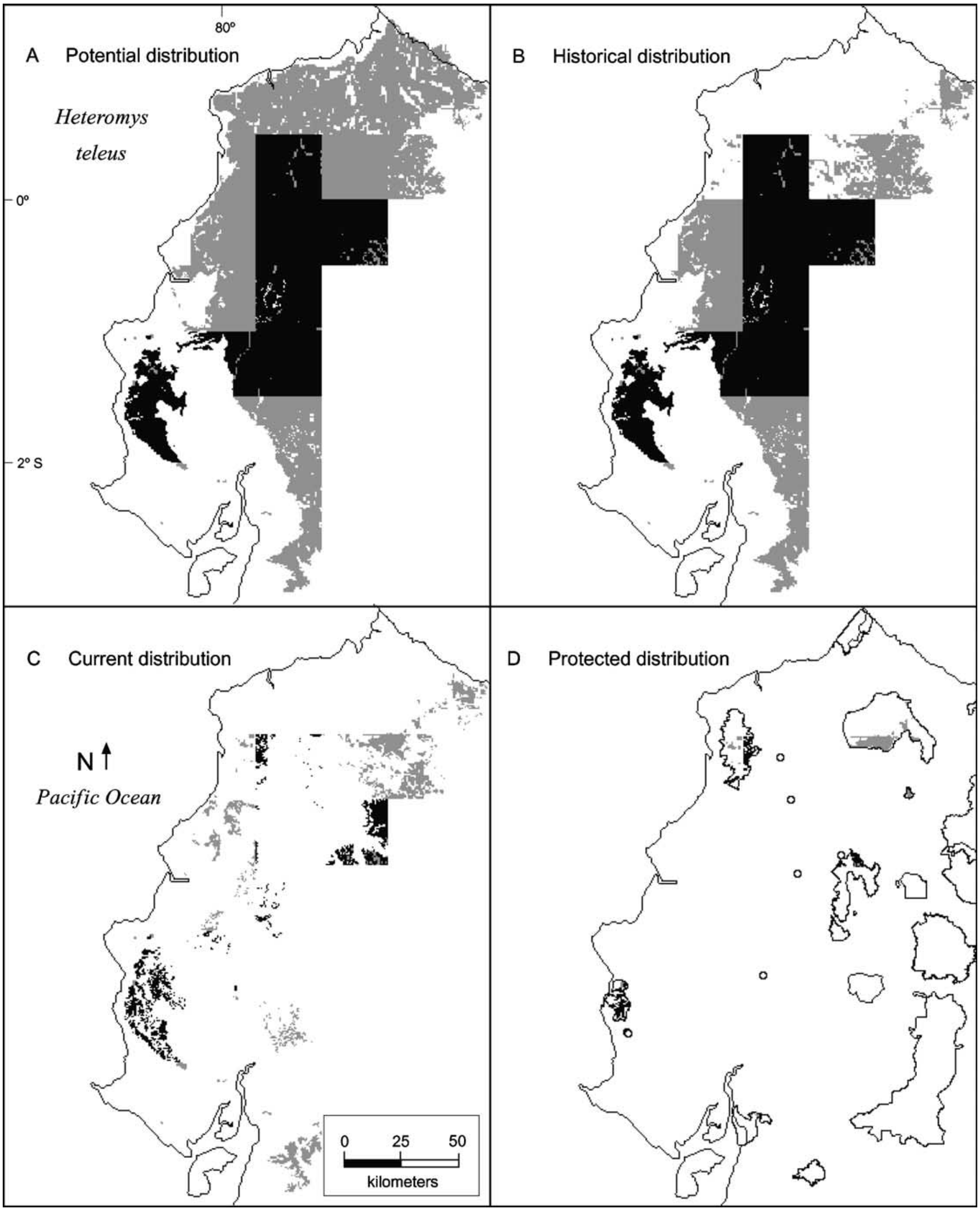

Fig. 3. Estimated geographic distributions for *Heteromys teleus* in western Ecuador (all relevant areas occur in this region of central-western and northwestern Ecuador): (A) potential distribution, (B) historical distribution, (C) current distribution, and (D) protected distribution (with outlines of governmentally protected areas; circles denote known locality records for the species). Areas predicted by all 100 models appear in black and those indicated by 1–99 models in gray. The blocky nature of some environmental predictor variables (the climatic ones) is apparent here, especially in the 100-model threshold. A spectrum of gray portraying the full gradient from 1 to 100 (not shown) indicates a much more gradual transition between areas predicted with low vs. high support. See methods for details of model building and processing.

Table 1
Ranges of estimates for the areal extent of modeled potential, historical, current, and protected distributions of *Heteromys australis* and *H. teleus* in western Ecuador

		Potential distribution (km^2)	Historical distribution (km^2)	Current distribution (km^2)	Protected distribution (km^2)
H. australis	(any)	37,100	17,600	9100	2300
	(all)	6300	6300	4000	700
H. teleus	(any)	47,200	33,400	6200	1000
	(all)	19,000	19,000	2500	400

Estimates (rounded to the nearest 100 km^2) are given for map pixels predicted by any of the models, as well as for those indicated by all 100 models.

4. Discussion

4.1. Models and distributions

Several factors require that these models be interpreted with caution. First of all, the original resolution of the climatic data is quite coarse. However, combining those data layers with much finer topographic variables and cutting by vegetational classes moderated somewhat the effect of the blocky climatic coverages. Secondly, only small numbers of localities are available for making the models (Guisan and Zimmermann, 2000; Stockwell and Peterson, 2002b). Despite these two potential sources of error in the predictions, preliminary models indicated satisfactory performance in predicting the test localities (better than random prediction and low extrinsic omission). Although geographic coordinates were assigned to localities carefully using a variety of sources, the low level of geographic detail provided by some collectors precluded exact location of all sites (Anderson and Jarrín-V., 2002). Furthermore, collecting typically occurs within a radius of walking distance around a field camp. Thus, accuracy of test points to within 5 km—much more precise than the original resolution of the coarsest predictor variables—is acceptable (see Anderson et al., 2002a) and indicates the ability of GARP to predict the species' macrodistributions using the present environmental data.

Thus, the final models made using all occurrence records provide objective *estimates* of the species' potential, historical, current, and protected distributions in western Ecuador (Figs. 2 and 3; Table 1). Overall, they agree with the general inferences made by Anderson and Jarrín-V. (2002) based on collection localities and climatic and vegetational patterns in the region. Furthermore, even given the coarse nature of the climatic data employed here (typical of that available for most tropical areas), the models provide finer-resolution hypotheses of areas meeting the species' requirements produced through an operational procedure (Figs. 2A and 3A). Also, they attach a degree of confidence to various regions of the predictions, based on the proportion of each species' models predicting potential presence in particular map pixels.

This information regarding support for the species' potential presence is especially useful given the parapatric distributions typical of congeneric species of spiny pocket mice (Genoways, 1973; Rogers and Engstrom, 1992; Anderson, 1999) and the likely role of competitive factors in limiting realized distributions in the genus (Anderson et al., 2002b). Even though the two species' potential distributions overlapped greatly, areas of high support for the respective predictions varied. Removal of areas more frequently predicted for the congener provided realistic predictions of their historical distributions (Figs. 2B and 3B; Table 1). Field work will be especially auspicious in these regions along the likely contact zones between the species where local factors may determine which species is present.

4.2. *Implications for conservation of* Heteromys australis *and* H. teleus

The distribution of *Heteromys australis* in Ecuador has been affected moderately by deforestation (Table 1). Fortunately, most of the map pixels that were consistently predicted by all models for this species still harbor forests (Fig. 2C). In general, deforestation is less pervasive in extreme northwestern Ecuador than in the rest of the coastal plain (Sierra, 1999). Because this region receives so much rainfall, it has not been developed for agriculture as much as the rest of the Pacific lowlands; however, logging for commercial extraction of timber and for plantations of oil palms is now proceeding rapidly (Parker and Carr, 1992; Best and Kessler, 1995; Anderson and Jarrín-V., 2002).

The results indicate that the largest areas of protected current distribution for *Heteromys australis* in Ecuador lie in the Reserva Ecológica Cotacachi-Cayapas and Reserva Ecológica Mache-Chindul, both of which should be surveyed to confirm the species' presence and assess the status of any extant populations there. Although *H. australis* has been captured in several disturbed or managed forests elsewhere (Anderson and Jarrín-V., 2002), monitoring is necessary to determine long-term population trends in such situations. Most of the species' distribution lies not in Ecuador, but rather to the north in Colombia, eastern Panama, and a small region of montane western Venezuela (Anderson, 1999; Anderson and Soriano, 1999). Although quantitative analyses have not yet been undertaken in Colombia, the species' distribution there has probably been substantially decreased in the Andes due to deforestation; its range in the Chocoan lowlands of Colombia appears much more intact, but few protected areas are present there (Garcés-Guerrero and De la Zerder-Lerner, 1994; IAvH and Etter-R., 1998; Anderson, 1999; Myers et al., 2000).

In contrast, the distribution of *Heteromys teleus* has been drastically reduced by deforestation (Table 1; Fig. 3C). Its historical range corresponds to a region with a long history of agriculture that now supports expansive plantations of bananas (Parker and Carr, 1992; Best and Kessler, 1995). Remaining evergreen forest patches in the species' range are small, reflecting a general and pervasive pattern of fragmentation. Furthermore, the protected current distribution of *H. teleus* represents a miniscule fraction of its original range (Fig. 3D).

Of the indicated protected areas, the presence of *Heteromy teleus* is most likely in areas predicted within the Parque Nacional Machalilla near the type locality in the Cordillera de Chongón-Colonche. However, that park has been heavily grazed by goats and cattle, impacting even those areas still harboring forests (L. Emmons, personal communication). The species has been captured recently under similar situations (Anderson and Jarrín-V., 2002), and further fieldwork is necessary to examine its susceptibility to various degrees of disturbance. Small areas are also predicted with moderate-to-high support in the Reserva Ecológica Cotacachi-Cayapas and Reserva Ecológica Mache-Chindul, but these reserves (especially the former) lie near known records of *H. australis*. Thus, it is especially important to undertake fieldwork there to determine if *H. teleus* truly inhabits them. Distributional areas for *H. teleus* in the Reserva Geobotánica Pululahua received only weak support in the predictions, and those in the Reserva Ecológica Los Ilinzas lie at high elevations at the edge of the species' tolerances (in a vegetation type from which only one specimen of the species is known). A few private reserves are known to hold populations of the species (Bosque Integral Otonga, Bosque Protector La Perla, Estación Biológica Pedro Franco Dávila, and Río Palenque Science Center), but three of those represent tiny, isolated forest patches lying within the ubiquitous coastal agricultural matrix (Anderson and Jarrín-V., 2002). Finally, like in many other tropical regions, protected areas in Ecuador face encroachment and various human uses, and the future of currently intact forests in them cannot be taken for granted (Anderson and Jarrín-V., 2002; see also Soulé, 1991; Sinclair et al., 1995).

The small, fragmented current distribution of *Heteromys teleus* bodes poorly for its long-term survival, especially considering current deforestation rates and limited overlap with the governmental system of protected areas (Harrison, 1991; Brooks et al., 2002). However, the current analyses present only an estimate of the most basic information regarding the species: its distribution. Due to the lack of other data regarding population sizes and long-term viability, this conservation assessment can only be considered preliminary. Fortunately, the species' predicted historical distribution includes a few small areas of naturally disjunct evergreen forest that still exist: isolated hills immediately west of Guayaquil (in the low Cordillera de Cerro Azul of Guayas province) and west of Portoviejo (in Manabí province). Fieldwork should target these sites, because discovery of relictual populations of *H. teleus* there would indicate an areal extent sufficient for population survival and signify considerable long-term resiliency to isolation. In some regions, the species has only been found in association with small streams within the evergreen forest (especially along stream banks; G.H.H. Tate field notes; see Anderson and Jarrín-V., 2002). Thus, fieldwork should include intensive sampling in mesic microhabitats within predicted areas. Whereas most of the distribution of *H. australis* lies elsewhere, *H. teleus* is endemic to Ecuador, making its conservation situation there perforce synonymous with its global status.

4.3. Applicability to other systems

The approach employed here provides quantitative, operational estimates of a species' geographic range for use in preliminary conservation assessments. It represents a tractable geographic option when more data-intensive analyses are clearly unfeasible and untimely (e.g., population viability analysis; Boyce, 1992; see also Pimm et al., 1988; Bibby, 1994). In addition, it indicates regions of likely presence for productive fieldwork. This process is of general applicability for obligate forest species when occurrence records and environmental data (that coincide temporally with the occurrence data) are available in digital format. In contrast to the present case, vegetational coverages are not always necessary for distributional modeling or model-processing (Peterson et al., 2001, 2002d). However, if used in model-building itself, they must correspond to potential vegetation (e.g., DCN, 1977; IGAC, 1962; although edaphic associations also need be taken into account) not phytogeographic classifications (e.g., Huber and Alarcón, 1988; IAvH and Etter-R., 1998). Furthermore, if land-use/land-cover maps are included, they should only be used in conjunction with species' occurrence records from a small temporal span that corresponds to the land-use information. Finally, whereas the current models assume stable climates, more realistic ones would combine the current habitat-modification paradigm with distributional models that include scenarios of global climatic change (Huntley et al., 1995; Peterson et al., 2001, 2002b; McLaughlin et al., 2002).

Clearly, objective modeling of a species' geographic range holds promise in conservation biology as an important improvement over subjective, broad-stroke shaded outline maps. Although fine-resolution base environmental data are always desirable, the development of modeling techniques that provide general distributional hypotheses using even the relatively coarse environmental data currently available for most tropical regions (as here) is important. Similarly, many species of conservation concern are known from only a few localities, as in the present case. However, the existence of a recent taxonomic revision providing confirmed, georeferenced occurrence records is rare, yet highly desirable. According to the needs of the particular application, various thresholds of numbers of models predicting presence can be set: from permissive (e.g., any model; liberal scenario) to strict (e.g., all models; conservative scenario; see discussion of the costs of overprediction vs. underprediction in Fielding, 2002: 275). In addition, a prediction could be made more or less permissive by buffering it outside or inside by an arbitrary linear radius (e.g., 5 or 10 km). Future research should continue to evaluate these approaches with a wide variety of species and taxonomic groups and examine the necessary data requirements for both occurrence records and environmental coverages (Peterson and Cohoon, 1999; Stockwell and Peterson, 2002b; Anderson et al., 2003).

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