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Choosing reserve sites probabilistically: A Colombian Amazon case study

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ABSTRACT

This study demonstrates a method for modelling species habitats and selecting reserves for their conservation. The method has a number of advantages: It makes use of well-known techniques, is straightforward to implement, does not require species absence data, produces georeferenced digital maps for visual analysis and geographical identification, and can be adapted to any scale of analysis or data resolution. Using existing presence data for the Colombian Amazon and standard linear optimization techniques, the study models landscape level probabilities of reptiles and amphibian habitats and then uses this probabilistic habitat data to prioritize reserves for their protection. The first stage of the study uses an ecological niche factor approach to produce a series of spatially explicit probabilistic habitat suitability maps. The second stage implements an objective function that chooses appropriate sites for protection according to the suitability of these modelled habitats to support focal reptiles and amphibians. On the assumption that more suitable habitats (expressed as a probability between 0 and 1) will contain more individual numbers of amphibians and reptiles than those that are unsuitable, any objective function used with this approach will implicitly choose sites that maximize the expected number of *individual* animals comprising a taxa. This is in contrast to many standard selection algorithms that focus directly on species occurrences, usually seeking to cover a representative taxa at least once somewhere on the landscape.

1. Introduction

Despite growing resource demands of their populations, many tropical developing countries are trying to protect biodiverse areas before they are lost forever. However, many of these areas often face intense development pressures, exacerbated by their chronic poverty and rising populations. Hence there is a need for governments to trade off the costs of conservation of these lands against alternative uses in as informed and cost-effective manner as possible. Increasingly, government planners are resorting to more systematic methods, such as selection algorithms that can incorporate any number of biodiversity goals (e.g. rarity). These have been used to find optimal solutions to the problem of reserve selection for a variety of species (e.g. Margules and Pressey, 2000; Cabeza and Moilanen, 2001; Williams, 1998).

Like all reserve selection methods in conservation planning, the information generated by these algorithms depends crucially on the quality of the species information that informs them. Unfortunately, information on species occurrence and habitat requirements is often non-existent or incomplete. Typically, only species presence not absence data are available. The restricted geographical coverage of much of this presence data also precludes landscape level analyses (Margules et al., 1998). However, without comprehensive information on species habitat and distribution, efforts

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to prioritize species representation will remain ineffective.

Conservation planners often get around the problem of missing data by using existing information on known species habitats to infer the locations of species elsewhere. Typically, locations which pass a threshold of suitability will be assigned a binary value: 1 if the habitat is suitable and 0 otherwise. Thus, every location will have the same likelihood of housing a focal species if it passes an arbitrary "presence" threshold (Polasky et al., 2000). In contrast, some studies have used probabilistic data, modelling species occurrences as a range of probabilities between 0 and 1 (e.g. Polasky et al., 2000; Cabeza et al., 2004; Sarkar et al., 2004; Araújo and Williams, 2000; Williams and Araújo, 2000). This approach has the advantage that planners can consider all sites on the landscape based on their degree of conservation suitability. However, as in the use of binary data, most probabilistic approaches to modelling species distribution require the use of both presence and absence data.

This study demonstrates a simple to use methodology for the derivation of species distribution when absence data are unavailable and conservation planners must determine which areas should be set aside as reserves. Specifically, the study implements an ecological niche factor analysis (ENFA) to model habitat suitability, and then shows how this information can be used to guide the selection of reserves in a way that explicitly incorporates spatial ecogeophysical characteristics of the landscape. ENFA models species habitat suitability based on a range of ecogeophysical data. It models landscape characteristics using existing information on species locations to derive information on habitat suitability elsewhere.

As part of this modelling process, the ENFA methodology used in this paper produces a series of probabilistic maps, where any pixel represents the suitability of a georeferened location on the landscape to house a species of interest, expressed as a probability between 0 and 1. The paper then demonstrates how planners can use this information to choose reserve sites based on any objective function that their conservation goals dictate. Although the methodology outlined requires spatially georeferenced information on ecogeophysical attributes of the landscape, such information (contained in national land use and land cover assessment, geological surveys, precipitation and climate monitoring data), is more likely to be available for developing countries than are species presence/absence data. The methodology set out is straightforward, easy to use, and produces high quality georeferenced raster maps that can greatly assist in the identification of suitable habitats and reserves. In a way that is made clear in the following sections, it also implicitly maximizes the expected number of individual animals comprising a focal taxa since its focus is on maximizing habitat suitabilities rather than on maximizing expected species representation. This study demonstrates the viability of this method using presence data for the Colombian Amazon.

One omission in the application of this methodology to the Colombian Amazon is the lack of suitable land price data for the region. For this reason, the paper chooses reserves under the assumption that the cost of setting aside each piece of land will be the same. This approach can be formulated as: How can the planner maximize the number of species subject to the constraint that the chosen reserve must be a specified size (e.g. 400 km²)? This is equivalent to the problem: How can the planner maximize the number of species subject to the constraint that each reserve be at least 1 km² (e.g. have a minimum threshold size for habitat viability) and together cannot exceed more than 400 km²? Ando et al. (1998) demonstrate that a budget constrained approach to reserve selection will choose areas more cost effectively than will an approach such as this one based on size. Similarly, Polasky et al. (2001) find that the percentage cost savings under the budget constrained approach are significantly larger than that predicted by Ando et al. (1998). In view of the importance of economic considerations in reserve selection, the study carries out a site selection exercise that indirectly considers legal economic activities in the region. In addition, the study compare sites to officially protected parks.

2. Study area

The Colombian Amazon is situated in Colombia, South America. It borders the countries of Peru, Venezuela and Ecuador, and comprises about 35% of the total area of the country. A largely uninhabited region, it is isolated from the rest of the country west of it by the formidable Andean cordillera. The region is dissected by many rivers, which together with their tributaries, form part of the larger Amazon river basin. The latter covers an area in excess of 6 million km², of which the Colombian Amazon comprises approximately 400,000 km² (González Posso, 2000; McClain, 1999). The fluvio-geomorphological and climatic variations of the region have given rise to and sustain a variety of ecoregional profiles. The region contains a diversity of habitats, from llanos (savanna grass) to rich galley and primary rain forests. Topographically, the landscape is predominately lowland river basin, but plains and plateaux, steep hills, mountains and valleys are also present. The structure and composition of vegetation reflects topography, proximity to rivers, and differences in soil nutrients and climatic variations. The climate of the region is tropical and humid, although dry periods occur in some upland areas.

Colombia is rightly considered to be one of only five megadiverse countries in the world (Mittermeier et al., 1997, 1998). Although it accounts for only 0.7% of the Earth's continental area, Colombia has a high degree of biodiversity. In terms of vertebrates, Colombia ranks third in the world, with 2890 species, 1721 of which are birds (20% of the world's total) and 358 are mammals (7% of the world's total). Of particular importance for this study, Colombia is also home to 6% of the world's reptile species and 10% of its amphibian species, although new species are continually being recorded. The Amazon region itself houses 37% of the country's 583 amphibians and reptile species (Mittermeier et al., 1997, 1998). The warm temperatures, high humidity and the Amazon basin's extensive interconnected system of rivers and streams provide an ideal habitat and breeding ground for amphibians and reptiles.

The cultivation of illicit crops (coca and marijuana) is a major agricultural activity of the Amazon region impacting heavily on its biodiversity. The boom in coca (*Erythroxylum coca*) production has accelerated with the growth in population. The environmental impacts of this illicit activity range from defor-

estation to the pollution of soils and waterways with highly toxic herbicides and fertilizers (Alvarez, 2002; González Posso, 2000). Due to the interdependent and coevolved mutualisms of the region's ecosystems, these chemicals have the potential to cause extensive disruption (Farley, 2000). Other threats to biodiversity include mining, cattle-ranching, road-building, oil and pipeline developments, settlements, hunting, and wildlife trafficking, particularly in birds, reptiles and ornamental fish species (UNEP, 2002). Human-induced fires are also a problem, particularly in logged or fragmented areas (Laurance, 1998; Schlaepfer and Gavin, 2001).

3. Materials and methods

3.1. Species distribution variables

Data on amphibian and reptile species are from Conservation International's Center for Applied Biodiversity Research. Data were compiled in conjunction with the Fundacion Puerto Rastrojo in Colombia (Conservation International Fundacion Puerto Rastrojo, 2001). Since many of the data set's individual species of amphibians and reptiles contain insufficient observations, the study models habitat suitability for species by amphibian and reptile families. Despite this approach, at least half of the amphibian and reptile families in the data set had to be omitted from the study due to insufficient observations. Nonetheless, the families modelled in this study represent a wide variety of the Amazon region's species of toads, frogs, snakes, turtles and crocodiles/alligators. Such variation is necessary for predictive modelling on a regional scale.

The scale of the study's resolution also provides sufficient enough landscape coverage of the area to ensure that the selection of reserves considers many human threats to the region (much of which remains untouched by human activities) and allows for the potential inclusion of fragmentation and metapopulation effects into planning initiatives once suitable reserves have been selected (Corsi et al., 1999). Due to space considerations, results for only 4 of the 12 modelled families are presented here. There is no one ecogeophysical rationale for choosing these 4 families out of the 12 families modelled in the study. Families for which results are presented were selected because they exemplify the range of animals, habitat characteristics, rarity status, and geophysical locations modelled in the study. Appendix A lists the names of all families omitted due to insufficient observations, and the names and number of species in each family of the 12 families modelled in the study. A full listing of species and family groups modelled in the study are not included due to space constraints but are available on request, as are all data and habitat suitability maps. Species data for each family were used to construct point vector maps in a GIS measuring the study's response variable: 1 if a species was present and 0 if not known. In order to avoid species maps giving higher weight to abundant species, each species map was then rasterized using a GIS option that allowed for the presence of 1 or more points to be recorded for each cell and then were added together to produce a single family distribution map. These maps were then used to prioritize reserve sites that maximize amphibian and reptile habitats for the Colombian Amazon. Note that the small number of families modelled relative to the large landscape area mean that complementarity and rarity criterion were not an issue as they are in other studies. However, if these are issues in a study, the objective function can be changed quite easily to accommodate them.

3.2. Ecogeophysical variables

Since animal distributions will differ according to ecogeophysical conditions, it is necessary to choose areas of the landscape that will likely represent the habitats of focal animals (and indirectly those belonging to unknown species). In this study, the environment of the Colombian Amazon is modelled using maps that reflect different ecogeophysical dimensions. Table B.1 provides a full listing of ecogeophysical predictor variables and their definitions. All variables are derived from the Conservation International-Rujado database. Ecogeophysical data are georeferenced digital maps produced from a wide range of government and scientific data sources. Several maps (e.g. soil and vegetation type) had to be converted from qualitative into continuous data by computing new surface maps from Boolean images that assigned to each cell a distance value to the closest qualitative category. In addition, two other boolean images were created, measuring human impacts (the study's disturbance variable) from the original data set. These maps represent areas where rates of deforestation ranges from low to moderate $\geq 1\% < 40\%$ and high ($\% \geq 40\%$). To minimize potential bias arising from the opportunistic observation of species, road networks and locations of airports were excluded from the analysis.

3.3. Habitat suitability modelling

Studies use a variety of approaches to predictive modelling of habitat distribution (see Guisan and Zimmerman (2000) for a review). However, for many species, these largely statistical approaches are not feasible due to a lack of absence data. This situation arises with most species data sets, especially those derived from museum collections. However, even when absence data are available, recorded absences may still be unreliable. Typically, absence data will reflect factors unrelated to species presence; for example, the reclusiveness of a species or degradation of its habitat. In these cases, predictive modelling may produce more reliable results if absence data are excluded from the analysis altogether (Hirzel et al., 2002).

Unlike regression approaches that model probabilities of species or family presences in a given location, the ENFA (ecological niche factor analysis) approach used in this study models habitat suitability. The study's family distribution maps indicate 1 km^2 information on the ecogeophysical characteristics of locations where animals have been observed. If another location also shares the same ecogeophysical characteristics as sites where these animals have been observed, then it is probable that they are present in this location as well. Beyond the obvious advantage that it does not require absence data, the ENFA method offers an ecologically intuitive approach to the measurement of habitat suitability.

Specifically, ENFA models habitat as a series of maps representing ecogeophysical variables that are required for the focal species' survival. This is the fundamental concept of the

ecological niche (Hirzel et al., 2002). More formally, ENFA models the niche as a continuous series of isometric cells. In this case a raster landscape of equal area 1 km^2 pixels, each one associated with a vector of ecogeophysical values (represented by all of the ecogeophysical maps) characterizing that area of the landscape. Pixels where the focal animals are recorded as present comprise a subset of the global distribution (i.e. the whole modelled landscape) of these ecogeophysical values. These distributions may differ with respect to their mean and their variances. ENFA measures both: (a) marginality, the departure of the mean for each of these subsets from the global mean for each family distribution map; (b) specialization, the ratio of the variance of each of these subsets to the variance of the global mean for each family distribution map (Hirzel et al., 2002). Like principal components analysis (PCA), ENFA works by transforming the original – in this case, ecogeographical variables – into new, uncorrelated axes. Unlike PCA analysis, which chooses axes so as to maximize the variance within the distribution (i.e. within the ecogeographical space), ENFA chooses axes so as to maximize family marginality (the first axis) and specialization (all remaining axes) (Hirzel et al., 2002, 2001).

The higher the absolute value of the coefficients of the marginality factor, the more the focal animal deviates from the mean habitat defined by that ecogeophysical variable for the entire study site (i.e. the global mean). A negative coefficient implies that the focal animal prefers lower values than the global mean for that variable. A positive coefficient implies a preference for higher than average global values of these variables (Hirzel et al., 2002). Likewise, the higher the absolute value of the specialization coefficient, the more restrictive the range of the focal family in respect to that variable. Note that the coefficient sign of the specialization factor has no meaning. More details on the statistical and ecological theory underlying ENFA can be found in (Hirzel et al., 2001, 2002; Hirzel and Arlettaz, 2003). ENFA is one of several methods in the literature for modelling habitat suitability when absence data are missing (e.g. Nix, 1986; Segurado and Araújo, 2004; Carpenter et al., 1993; Curnutt et al., 2000; Parra et al., 2004; Phillips et al., 2006). ENFA has a number of similarities with and advantages over existing presence data only techniques. For instance, it is computationally efficient, can accommodate a wide variety of environmental variables and their interactions, and produces easily interpreted probability distribution maps of habitat suitability.

All ENFA models of habitat suitability for the study's various families (12 in total) were run in BIOMAPPER (Ver 2.0, Hirzel et al., 2000), a freely available, integrated mapping and statistical software program. After extracting marginality and specialization factors, Biomapper uses the median algorithm to evaluate the suitability of each cell of the ecogeophysical maps to support each focal family. Biomapper then normalizes the resulting number for each cell by dividing twice its number by the total number of cells from each family distribution. From this information an overall suitability index for each cell is computed by adding each score count together on each factor. Habitat suitability for each cell for each family is expressed in terms of a "suitability index" ranging from 0 to 100, with 100 representing the optimal habitat (Hirzel et al., 2002). Before carrying out the ENFA analysis, Biomapper normal-

izes the ecogeophysical maps using a Box–Cox transformation.

3.4. Reserve selection analysis

Many possible objectives can be used to choose reserves. This section discusses a few such objectives. Map outputs of some of these modelled objective functions are presented in Section 4.2. The results of the previous section provided 12 probability location maps, one for each family. To recall, each cell represents a suitability index representing a number between 0 and 1, which is here treated as a probability. Thus, a site registering a probability of .60, for instance, would have a 60% chance of housing the family of interest.

Given the relatively small number of families represented (i.e. 12) in the study relative to the large area covered (502,643 km^2), objective functions that seek to preserve the maximum number of species from extinction are not relevant for this study's example. For example, we let the notation p_{ij} denote the probability that family type i (for $i = 1, \ldots, I$, in this study, $I = 12$) is present in cell j (where $j = 1, \ldots, J$). Also, each pixel (j) represents an areal unit on the ground, in this study 1 km^2 area. The following function can thus be written to express the problem of complementarity; that is, one that seeks to save as many species a possible, if only once on the landscape:

$$\max \sum_{i=1}^{I} P_i$$

where P_i is the probability species type i is present somewhere in the entire reserve network. With a small number of species or families, this objective function can be trivially pushed to its maximum value of $P_i = 1$ for $i = 1, \ldots, I$. In this study, if one site is simply chosen where each family has been observed this maximum value is obtained with at most 12 cells. Since the study is interested in larger reserves, this sort of objective function is not relevant. (Note that in all the reserve maps presented in Section 4.2, the study obtains $P_i = 1$ for all families but does not impose this as a constraint). However, it should be stressed that for other studies such an objective function may indeed be necessary. If so, habitat suitability maps can easily accommodate a change in objective function. Indeed, the planner can flexibly adjust the analysis to any objective function she wishes, depending on the objectives of the conservation planning exercise.

Let N_i (for $i = 1, \ldots, I$) be the number of cells containing amphibian or reptile family i and X_j define the reserve. That is, $X_j = 1$ if cell j is included in the reserve and $X_j = 0$ if it is not (for $j = 1, \ldots, J$). Then, using elementary rules of probability, the expected number of sites in the reserve containing amphibian or reptile family i is given by:

$$E(N_i) = \sum_{j=1}^{J} p_{ij} X_j \tag{1}$$

One sensible objective function is to simply add up this expected number of sites across all amphibian and reptile fam-

ilies as:

$$\max \sum_{i=1}^{I} E(N_i) \qquad (2)$$

Reserve prioritization problems also require the specification of a constraint. However, as noted, in many applications, data on land costs are unavailable so an alternative constraint can be placed on the number of cells set aside in the reserve:

$$\sum_{j=1}^{J} X_j \leq K \qquad (3)$$

where K is the number of cells allocated to the reserve.

From a technical viewpoint, the study's reserve prioritization problem comes down to choosing values for X_j (for $j = 1, \ldots, J$) that maximize the objective functions given in Eq. (2) subject to the constraint given in Eq. (3). The habitat suitability modelling exercise has provided values for p_{ij} and now values for K must be chosen. For the constraint represented in Eq. (3), the computational methods needed to find the optimal reserve proceed as follows: For each cell calculate $\sum_{i=1}^{I} p_{ij}$ for Eq. (2). Then select the K cells with the highest values for these as the reserve.

Eq. (2) treats all families as equivalent to one another. In practice, the researcher may have to consider the relative value of individual families or any other group. In addition, the researcher may have to simultaneously weight families or species by their scarcity level, charismatic status or some other criteria. For instance, some taxa may be rarer than others and thus, more "worthy" of protection, or some may have greater economic value (e.g. due to ecotourism). The above objective function can be extended to deal with such cases:

$$\max \sum_{i=1}^{I} w_i E(N_i) \qquad (4)$$

where w_i is the weight the researcher attaches to individual species, i. For each cell $\sum_{i=1}^{I} w_i p_{ij}$ can be calculated and then K cells selected with the highest values as the reserves to be set aside.

Likewise, a common constraint is to assume a fixed budget, B, for the purchase of land. If C_j is the cost of purchasing cell j, and it is included in the reserve network, the budget constraint becomes:

$$\sum_{j=1}^{J} C_j X_j \leq B \qquad (5)$$

This constraint is slightly more complicated than one that states that sites must be a certain size. Nonetheless, it too, can be handled using standard linear programming techniques. Note that, unlike the weights in (4), the land costs in (5) cannot be relative but must reflect the cost of purchasing land. For both objective functions (4) and (5), the first part of the study's methodology provides values for p_{ij} and the planner must now select values for C_j, w_i and B.

Moreover, the planner may wish to specify that reserves have a certain degree of compactness or shape. This is a more complicated exercise than the above in that this algorithm must treat the selection of each pixel square as dependent on

the value of adjacent squares. In the above each square was selected independently by the algorithm, with those having the highest habitat suitability value making up the resulting reserve. A constraint that requires reserves to have a certain shape is more difficult but can be allowed for in the study by extending the cost Eq. (5). That is, compactness can be interpreted in terms of costs; more specifically, the costs of "purchasing" an isolated piece of land can be considered higher than those involved in "purchasing" a piece of land that makes up part of a compact reserve. However, in this extended case of (5), the costs (C_j) are not simply selected by the planner but are included in the algorithm itself. In other words, if we assume that X_j^N in (5) can be interpreted to mean "squares that are the neighbours of square j", then (5) can be written to reflect compactness concerns:

$$\sum_{j=1}^{J} C_j(X_j^N) X_j \leq B \qquad (6)$$

where the term $C_j(X_j^N)$ is technical notation expressing the idea that "the costs of including square j depend on whether the neighbouring squares are in the reserve or not". This is a general constraint to ensure the selection of more compact reserves. To encourage compactness in the selection of reserves would require the objective function in (2) or (4) subject to the constraint (6), in addition to both a definition of neighbouring squares (e.g. a square which has a border or column touching square j is a neighbour such that every square (other than the ones on the borders) would have 8 neighbours)) and a definition of the cost function (e.g. using the preceding definition for a neighbour the algorithm could assign every square a value between 0 and 8 simply by counting the number of neighbours that are in the reserve). The cost could then be made to depend on these definitions (e.g. squares with 0 neighbours in the reserve receive a high cost, say 100, while squares with one neighbour in a reserve receive a lower cost, say 80, and so on, all the way down to a square that has all 8 neighbours in the reserve receiving a very low cost of inclusion, e.g. 1 or lower. Given that the cost algorithm must select pixel squares in view of the value of other neighbouring squares, the computational demands of such an exercise are far greater than for other constraints. However, it should be noted that reserves chosen for the families modelled in this study maximize suitable habitats around major riverways and smaller waterways. This is a reasonable finding, in view of the water requirements of amphibians and reptiles. These locations account for the elongated shape of many selected reserves described in Section 4.2.

4. Results

4.1. ENFA analysis of habitats

Statistical summaries of the ENFA analysis for the study's four example families are presented in Tables B.2–B.5. The first factor presented in the ENFA tables accounts for family marginality, and all remaining factors, family specialization. (Note that, while all the marginality component is measured in the first factor, it also accounts for some specialization.) Specialization factors are presented in decreasing level of importance (i.e.
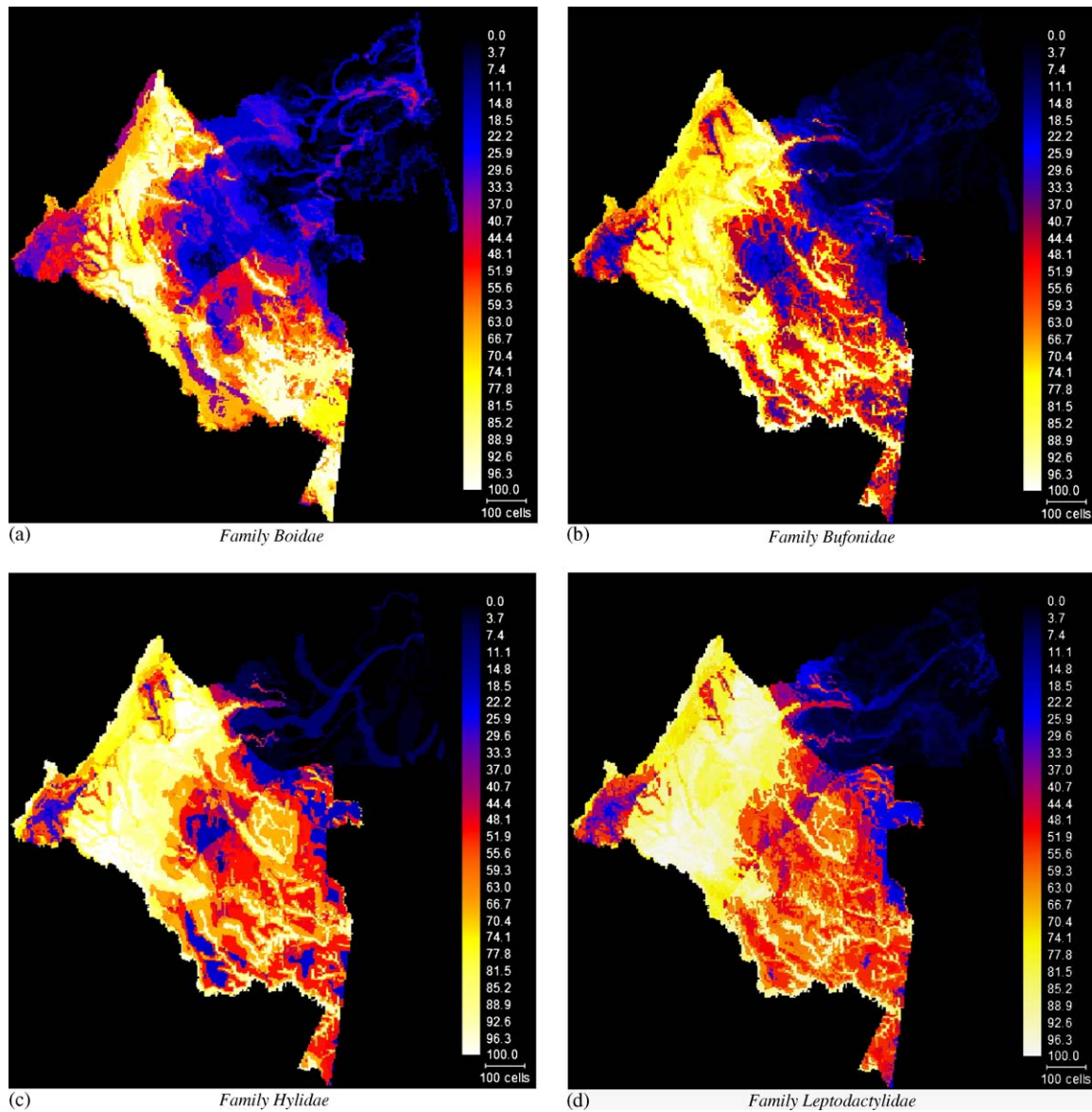
Fig. 1 – Habitat suitability maps: (a) family Boidae; (b) family Bufonidae; (c) family Hylidae; (d) family Leptodactylidae.

variance explained). Since the first five or fewer factors typically explain most of the variance in family habitat preference, the remaining factors can be excluded from the analysis without a significant loss of information. In this study, the number of factors for inclusion in the habitat suitability mapping was determined by the statistical significance of their respective scores. Only those scores whose distribution was larger than would have obtained by chance alone were included in the habitat suitability mapping exercise. The marginality factors for each family confirm what are well known habitat requirements for amphibians and reptiles. In particular, they indicate that all families prefer moist areas to dry and do not like to be far from rivers/streams. In addition, most represented families prefer low lying areas, and well-drained soils and dislike too much sun. Many prefer to live in or close to intact forests, with some tending to prefer open, mixed forests, herbaceous savannah and scrub vegetation.

For all representative families whose ENFA results are recorded in Tables B.2–B.5 that the first four to five factors account for 100% of the marginality and as much as 92 and 94% respectively of the specialization in the case of *Hylidae* and *Bufonidae*. For the *Hylidae* family, the marginality factor alone accounted for 61% of the total specialization. The marginality coefficients for members of this family and for *Leptodactylidae* suggest that they are especially "choosy" in respect to habitat requirements from which they differ from the global mean or background conditions observed in the Colombian Amazon. The other specialization factors suggest that like those of the *Leptodactylidae* family, members of the *Hylidae* family prefer the piedmont/Sierra de la Macarena region and do not like to be far from fast-flowing rivers. They are also sensitive to changes in the optimum in respect to cyperaceous savannah/scrub. Particularly in respect to members of the *Hylidae* family, who are also close to areas of high human
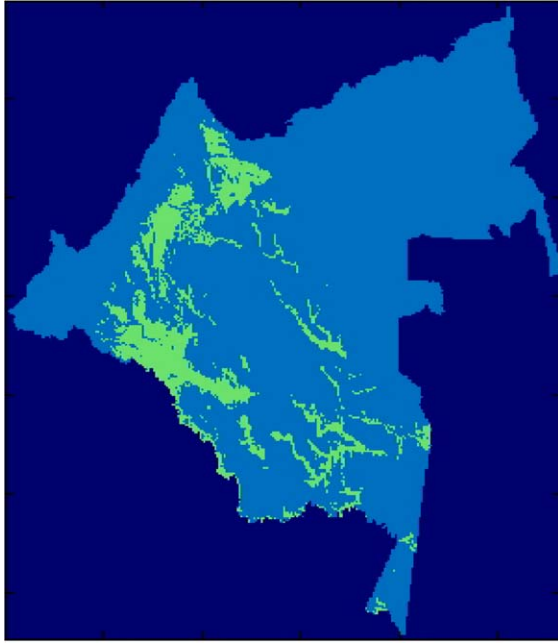
Fig. 2 – Reserves sites selected (11.43% of land area) (selected sites: light grey).
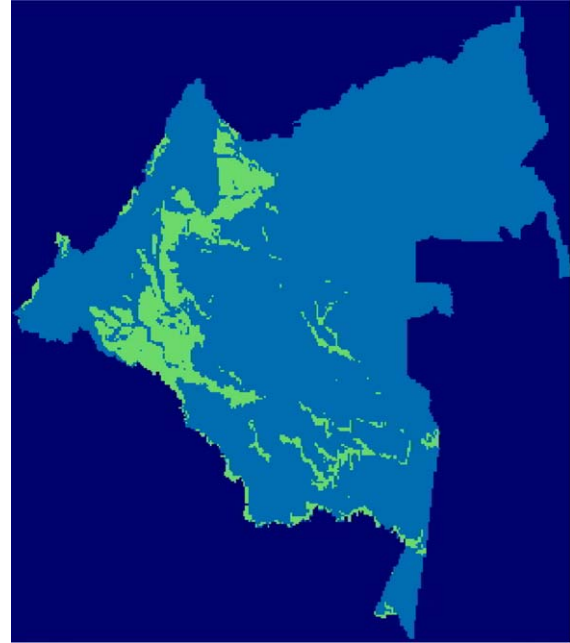
Fig. 4 – Reserves selected with species weightings (reserves selected: light grey).

impact, this finding suggests that their survivability would be adversely affected by impacts on their habitat arising from, say, the conversion of forest cover to scrub. In contrast, members of the *Bufonidae* and *Boidae* families do not share the same degree of restrictiveness of habitat. However, unlike *Hylidae* and *Leptodactylidae* members, they dislike to a greater
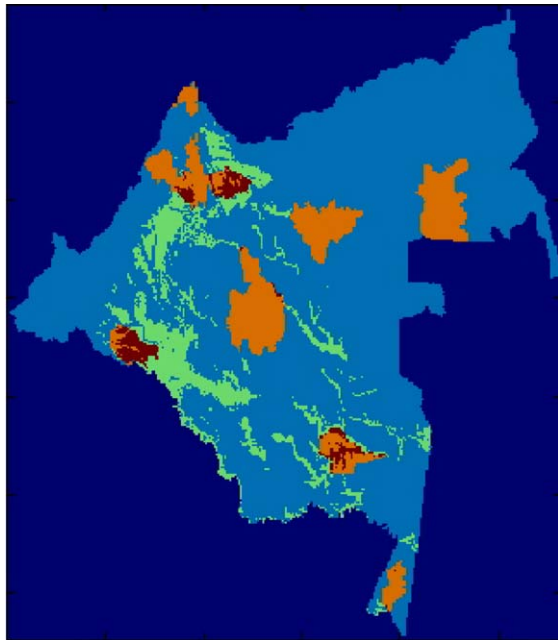

Fig. 3 – Comparism of reserve sites selected in Fig. 2 with officially protected areas (reserve sites selected: light grey; officially protected areas: medium grey; areas of overlap: black).

degree steep areas and areas of open, secondary growth and disturbed areas of vegetation, such as open broadleaved esclerofilo forest and shrub, herbaceaous savannah and ciperaceous/savannah shrub. All members demonstrate the fundamental need of reptiles and amphibians to be close to water and avoid dry areas. For example, *Leptodactylidae* (tropical frogs), exemplifies these habitat requirements well: precipitation = 0.23, evaporation = −0.27, days dry = −0.24, distance to water = −.017, distance to occasional fast-flowing rivers/subdentric/subparallel drainage = −0.22.

Computed habitat suitability maps using these factors for representative families are presented in Fig. 1. Suitable habitats range from 0 to 100; the higher the number the more suitable the habitat (and higher the probability that families will be found there). Each pixel expresses the expected probability that its corresponding $1\,km^2$ area on the ground is a suitable habitat for the focal family. Confidence intervals for each map were calculated using a Jack–Knife cross-validation procedure. This procedure computes a confidence interval for the predictive accuracy of each HS model, by partitioning the habitat suitability map into k random but mutually exclusive identically sized partitions. This process is repeated k times, each time leaving out a different partition. The k partitions are then used to compute a HS model and the left-out partitions used to validate the map. A good model fit is one where 80% or more of the cells have a value over 50. This 80% threshold was obtained for all maps, but most had an HS-value > .87. In addition, Jack–Knife results were robust to a wide number of partitions for all maps.

4.2. Reserve selection analysis

This section presents georeferenced maps of the reserve selection algorithms discussed in Section 3.4. Due to space con-
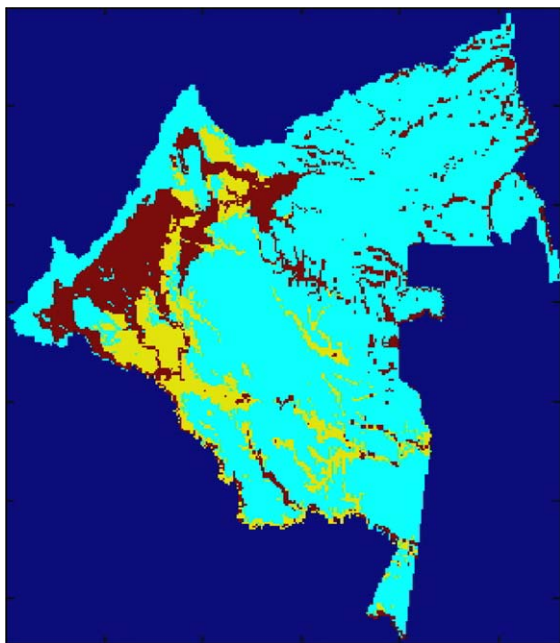
Fig. 5 – Reserves selected when areas of commercial legal activity are excluded (reserve sites selected: light grey; areas of commercial activity: black).

straints, not all examples of selected reserve maps for iterations of the objective functions discussed in Section 3.4 are presented here. However, these are available on request (as are all accompanying programs).

Fig. 2 depicts resulting reserve for the constraint represented in Eq. (3), which specifies reserves must be a specific size. In this case, they must not exceed 502,643 km^2, which is approximately equal to the current amount of officially protected land area (11.43%). Fig. 3 is an overlay comparing legally protected sites with those in Fig. 2. Protected areas are in medium grey, areas of overlap in black, and reserve selected areas in lighter grey. Note the strong disjunction between the two sets of reserve locations in Fig. 3. Few sites overlap. If the objective is to conserve as many individuals as possible by careful selection of sites having a high probability of housing focal families (subject to present levels of protected area status) then many official reserves appear to be poorly located or are too small). This finding accords with inadequacies in coverage of sites found in Rodrigues et al. (2004).

Fig. 4 depicts reserve sites selected according to a weighting system introduced in Eq. (4) that values snakes and frogs families (Viperidae, Boidae, Hylidae and Leptodactylidae) more than others in the sample. The resulting reserve prioritization maps is based on the following relative valuation: Hylidae (1000), Leptodactylidae (100), Viperidae (50), Boidae (25) and Colubridae (10).

Redefining the objective function slightly to reflect the loss of areas dedicated mostly to licit commercial activities (a proxy for the land price data constraint introduced in Eq. (5)), yields the site selection map, Fig. 5. In this figure black areas designate commercial activities and light grey areas, the selected reserves, many of which are close to sites of economic im-

portance. Note that in this example, almost all reserves are chosen as before, with the exception of commercial areas of activity. The objective function compensates for excluded areas by selecting additional land area around previously chosen sites. For example, chosen reserves in the south-western Amazon basin are slightly larger than in the unrestricted case.

5. Concluding remarks

This paper has demonstrated a methodology whereby conservation planners can use existing techniques and data sources to solve the problem of where to site protected reserves. Simple to implement and capable of exploiting fully the information in existing data sets, it is well-suited for reserve prioritization in countries where comprehensive data are lacking and resources for conservation planning are limited. The paper used species presence data to model family distribution, expressed as a series of "habitat suitability probabilities" that any given point on the landscape houses and sustains species of frogs, lizards, toads, crocodiles, alligators and snakes. Resulting maps indicate that many highly suitable locations were in or close to areas of human activity, especially the foothills region of the Sierra de la Macrena—a biodiversity hotspot arising from its unique position as a point of confluence between several ecosystems (llanos, Amazonian rainforest, Andean montane forest) (WWF, 2001). Although this finding may reflect habitat preference for the environmental impacts induced by these activities, quite a few families that had a high preference for these areas also preferred non-disturbed or closed forests. Hence it is likely that many of them suffer from the misfortune of being located in areas that are also under human threat.

Employing well known linear optimization techniques, the study used this probabilistic information to systematically choose reserves that maximize the number of expected amphibian and reptile habitats, subject to a constraint on reserve size. The reserve selection approach based on probabilistic rather than binary information has the advantage that it allows conservation planners to assess more accurately the potential opportunity costs of designating a site as a biological reserve. In this study, i represented a family, a group comprised of related species as opposed to one individual species. However, a planner could just as well substitute an individual species or even a higher classification for i. Since it models habitat suitability based on known habitat locations of taxa thought to live within them, this information, when combined with an objective function, allows for the maximization of as many suitable habitats as possible (and thereby the expected number of individual frog, toad, snake, etc. residing in them). Thus, the methodology explicitly selects against areas where habitat viability is low.

The approach is extremely flexible, and can be easily changed to suit any criterion weighting (including survival probabilities) or budget constraint. Unlike many existing approaches to reserve selection, the methodology does not require sophisticated programming skills or expensive software, a crucial feature for developing countries where technical expertise and tools are in short supply. It is also

flexible in that it can be accommodated to any landscape scale or data resolution, and can quite easily incorporate any degree of species information or objective function the researcher wishes to impose. Existing approaches to reserve selection either do not use probabilistic data or select reserves based on probabilistic occurrences derived largely using regression analyses of species presence/absence data (e.g. Cabeza et al., 2004). The latter data are often very limited in scope, particularly for the tropics. Indeed, comprehensive landscape data is a problem with logistic regression approaches due to the large number of observations to be modelled relative to species occurrence data (e.g. Araújo and Williams, 2000; Williams and Araújo, 2000). Moreover, many existing reserve selection approaches cannot so seamlessly incorporate such a diversity and range of spatial information on ecogeophysical attributes of the landscape since their starting-point is species occurrences rather than habitat. Neither can they produce such easily identifiable georeferenced outputs for visual display.

Finally, the methodology outlined here differs from existing reserve selection or "Noah's Ark" approaches that assume a species is "covered" if it is represented at least once somewhere on the landscape, whether this is based on a binary or probabilistic threshold measure (e.g. Araújo and Williams, 2000; Williams and Araújo, 2000). In contrast, the study's objective function aims to save the *greatest number* of frogs, toads, lizards, snakes, etc. as possible. It stresses the importance of habitats, and implicitly, the expected number of animals residing within them, according to the assumption that organisms of any given reptile or amphibian family can only maintain viable populations under a range of conditions and resource conditions. The more a location provides an optimal niche the greater the probability that it will house higher numbers of organisms than other locations.

Many species modelled in various family groups were recorded in difficult to access locations (e.g. deep within the Amazon basin). The possibility that the study's presence data may reflect human-species encounters more than species location is a potential problem with any study, not just this one. Given the size of the area under investigation it is not possible to thoroughly explore each sampling area. If information were known about the detectability of the study's species in various habitats, another route might be to use information to weight the presence points. For example, if it was three times more difficult to see an animal in a forest than in a meadow, then researchers could give a weight of three to every sightings of this species, say, located in a forest. Similarly, the ENFA modelling portion of the study revealed that several families were located close to areas subject to human settlements. The objective function could be easily changed to incorporate family survival characteristics in light of this finding. One approach would be to site reserves in a way that attaches greater weight to locations in and near areas of human activity. Such an approach may also implicitly incorporate the revenue benefits to be derived from ecotourism or other forms of wildlife based recreation. Alternatively, planners may decide that the economic value of some commercial activities may be so high as to preclude entirely the siting of reserves in these locations. In this case, the study's objective function could be easily modified to downweight such areas,

even going so far as to assign them a value of zero according to the reasoning that because species habitats will be irretrievably lost anyway money is better spent preserving them elsewhere.

The value assigned to a species or budget constraint will depend on the particular goals of the conservation plan and the economic and other resources allocated to it. More research on habitat requirements, population dynamics, and the economic trade-offs of reptile and amphibian protection vis-a-vis competing land uses is required before results can comprehensively inform conservation policy. Nonetheless, the approach outlined here can provide planners with important cues about habitat preferences and in light of this information, where to site reserves. It is a low cost and easy to implement approach that enables planners to overcome real world data limitations to create visual maps of probabilistic occurrences and systematically choose sites in a way that exploits to the fullest the information contained in the data. One way to supplement the species distribution data in this study would be to carry out ground surveys within selected areas indicated by the study's habitat suitability maps as having a high probability of housing focal taxa. This would be a way for planners to obtain more data on quantity and quality of habitats, and any other animal survivability characteristics. This refined data could then be incorporated into the initial objective function. Alternatively, the kind of maps produced in the analysis could be used to guide the field collection of absence data for use in statistical modelling of habitat suitability. However, a comprehensive ground-based approach will no doubt prove to be too costly for large areas and numbers of taxa. And if there is uncertainty about whether the absences recorded in these areas are in fact absences, the ENFA approach is a useful tool for obtaining probabilistic information using this refined data prior to the systematic selection of reserve sites.

Acknowledgements

Appendix A. Modelled and omitted species

Results for the majority of the families modelled in this study are not presented here but are available on request include: Crocodylidae–Aligatorindae (crocodiles/alligators, $n = 514$); Tropiduridae (tree runners and thorny tails, $n = 147$); Gekkonidae (gekos, $n = 127$); Testudinae (tortoises, $n = 100$); Colubridae (typical snakes, $n = 1,199$); Viperidae (pit vipers, $n = 168$); Chelidae (modern side-necked turtles, $n = 231$).

Modelled species whose results are presented in this study are: Hylidae ($n = 2779$); Leptodactylidae ($n = 2341$); Bufonidae ($n = 535$); Boidae ($n = 101$). Species comprising each family and their number are also available on request.

Omitted species are from the following families: Plethodontidae (lungless salamanders), Centrolenidae (glass frogs), Phyllomedusinae (leaf and monkey frogs), Microhylidae (narrow-mouth frogs), Ranidae (typical frogs), Pelomedusidae (primitive side-necked turtles), Kinosternidae (mud turtles), Amphisbaenidae (amphisbaenians or worm lizards), Gymnopthalmidae (ground lizards), Hoplocercidae (tree dragons), Polychrotidae (anoles & monkey lizards), Scincidae (skinks), Aniliidae (pipesnakes) and Elapidae (coral snakes). Three families – Dendrobatidae (poison & rocket frogs), Pelomedusidae (primitive side-necked turtles) and Caeciliidae (terrestrial caecilians) – had sufficient number of species observations to be included in the analysis. Resulting habitat maps for these families provided poor model fits and were therefore excluded from the analysis.

Appendix B

See Tables B.1–B.5.

Table B.1 – Ecogeophysical variables

Variable	Measure
Temperature	Average annual temperature (°C)
Solar radiation	Hours of solar brightness per year
Humidity	Average relative humidity (%)
Evapo-transpiration	Annual average evaporation (mm)
Days dry	Annual number of days with no rainfall
Precipitation	Annual average rainfall in mm
Steepness	Annual average percent slope (change in elevation/distance × 100)
Altitude	Average height above sea level (m)
Topography	Topographic contours (areas of average equal altitude (m above sea level))
Geomorphology 1	Distance to dissected sedimentary surfaces
	Distance to dissected peneplains/Guyana shield
	Distance to surface alluvial deposits
	Distance to mountains, heights/surface residuals
	Distance to piedmont
	Distance to piedmont/diluvial surfaces
	Distance to surface sedimentary structures
	Distance to piedmont/ Sierra de la Macarena
Geomorphology 2	Distance to alluvial fan of piedmont areas
	Distance to granite of Paraguaza
	Distance to exposed ignaceous rocks
	Distance to relict landforms
	Distance to alluvial plains
	Distance to denudational plains

Table B.1 – (Continued)

Variable	Measure
Drainage	Distance to Andean foothills
	Distance to plains associated with the Guyana Shield
	Distance to relict relief
	Distance to terraces
	Distance to terraces/alluvial plains
	Distance to dendritic drainage
	Distance to dendritic to subparallel drainage
	Distance to deep dendritic drainage; interfluvial channels
	Distance to parallel drainage
	Distance to parallel to subparallel drainage
	Distance to areas of subdentric drainage; diffuse drainage
	Distance to areas of subparallel to parallel drainage
	Distance to areas of superficial dendritic drainage
	Distance to areas of variable drainage along rivers
	Distance to areas of diffuse drainage
	Distance to slow-moving rivers and dendritic drainage
	Distance to occasional fast-flowing rivers; subdentritic/subparallel drainage
	Distance to fast-flowing rivers; subdendritic drainage
	Distance to fast-flowing rivers, wide valleys; shallow dendritic drainage
	Distance to fast-flowing rivers, narrow valleys, subdendritic drainage
Human disturbance	Distance to areas low to moderately deforested ($> 0\% \leq 40\%$ deforested)
	Distance to highly deforested areas (>40% deforested)
Distance to water	distance to rivers, tributaries and streams
Vegetation	Distance to dispersed casmofita vegetation
	Distance to herbaceous savannah of medium height
	Distance to ciperaceas open forest
	Distance to ciperaceas savannah/open forest
	Distance to ciperaceas savannah scrub
	Distance to esclerofilo thicket/casmofita vegetation
	Distance to broadleaf esclerofilo scrub
	Distance to esclerofilo scrub
	Distance to ombrophilous forest/escclerofilo scrub, thicket
	Distance to ombrophilous (small leaved) cloud forest
	Distance to ombrophilous montane forest
	Distance to ombrophilous alluvial riparian forest
	Distance to ombrophilous forest
	Distance to open broad-leaved esclerofilo forest

Table B.2 – ENFA analysis results (family Bufonidae (toads))						
Ecogeophysical variable	Marginality (65%)	Spec. 1 (16%)	Spec. 2 (5%)	Spec. 3 (3%)	Spec. 4 (3%)	Spec. 5 (2%)
Precipitation	0.28	0.07	0.00	−0.06	0.06	0.05
Evaporation	−0.28	0.02	−0.01	−0.02	0.04	0.04
Days dry	−0.27	0.11	0.01	−0.07	0.13	0.07
Distance to piedmont/Sierra de la Macarena	−0.25	0.02	0.01	0.05	0.00	−0.09
Distance to water	−0.21	0.00	0.00	0.00	0.00	0.00
Steepness	−0.20	0.00	0.00	0.00	0.00	0.01
Distance to ombrophilous alluvial riparian forest	−0.19	0.00	0.00	0.00	0.00	0.00
Distance to areas of variable drainage along rivers	−0.18	0.00	−0.01	0.01	0.03	0.01
Distance to terraces/alluvial plains	−0.18	0.00	−0.01	−0.01	−0.01	−0.01
Distance to areas of high human impact	−0.18	0.00	0.00	0.00	0.00	0.00
Distance to areas of moderate human impact	−0.18	0.00	0.00	0.00	0.00	0.00
Distance to surface alluvial deposits	−0.17	0.01	0.01	0.01	−0.01	−0.01
Distance to herbaceous savannah of medium height	0.15	0.54	0.38	−0.18	0.28	−0.50
Distance to piedmont/diluvial surfaces	−0.15	0.04	−0.01	0.10	−0.07	−0.17
Distance to open broadleaved esclerofilo forest	0.15	−0.09	−0.15	−0.12	0.08	−0.08

Variance explained by first six factors and coefficient values for most important 15 ecogeophysical variables.

Table B.3 – ENFA results (family Boidae (boas))					
Ecogeophysical variable	Marginality (25%)	Spec. 1 (32%)	Spec. 2 (18%)	Spec. 3 (8%)	Spec. 2 (5%)
Steepness	−0.27	0.00	0.00	−0.01	0.00
Distance to terraces/alluvial plains	−0.27	0.00	0.00	0.00	0.00
Days dry	−0.23	0.22	0.23	0.00	−0.03
Evaporation	−0.22	0.15	0.10	0.15	−0.01
Distance to alluvial surface deposits	−0.22	0.00	0.00	−0.01	0.00
Precipitation	0.22	0.19	0.07	0.09	−0.03
Distance to broadleaf esclerofilo scrub	0.20	−0.12	−0.41	0.00	0.07
Distance to water	−0.20	0.00	0.00	0.01	0.01
Distance to open broadleaved esclerofilo forest	0.19	0.50	0.14	−0.14	0.03
Distance to granite of Paraguaza	0.19	0.45	−0.70	−0.61	0.78
Distance to herbaceous savannah of medium height	0.19	−0.54	0.61	0.73	−0.41
Distance to areas of variable drainage along river	−0.18	0.00	0.00	0.00	0.00
Distance to ciperaceas savannah/open forest	0.18	0.02	0.09	0.07	−0.19
Distance to ciperaceas savannah/scrub	0.18	−0.16	0.10	0.08	−0.21
Distance to ombrophilous alluvial riparian forest	−0.17	0.60	0.00	0.00	0.00

Variance explained by first five factors and coefficient values for most important 15 ecogeophysical variables.

Table B.4 – ENFA results (family Leptodactylidae (tropical frogs))					
Ecogeophysical variable	Marginality (49%)	Spec. 1 (19%)	Spec. 2 (8%)	Spec. 3 (4%)	Spec. 4 (4%)
Distance to piedmont/Sierra de la Macarena	−0.31	0.00	0.02	−0.06	−0.03
Evaporation	−0.27	−0.03	−0.01	0.05	0.04
Days dry	−0.24	−0.05	−0.06	0.05	0.00
Precipitation	0.23	−0.03	−0.04	0.05	0.00
Distance to occasional fast-flowing rivers; subdentric/subparallel drainage	−0.22	0.01	−0.07	0.13	0.21
Distance to piedmont/diluvial surfaces	−0.21	0.03	−0.04	−0.07	0.12
Distance to alluvial fan of piedmont	−0.20	−0.01	0.03	0.00	−0.01
Distance to parallel drainage	−0.19	−0.01	0.02	0.04	−0.07
Distance to Andean foothills	−0.18	0.01	0.01	−0.05	−0.02
Distance to parallel to subparallel drainage	−0.18	−0.03	0.08	0.09	−0.18
Solar radiation	−0.17	0.03	0.04	−0.09	−0.00
Distance to piedmont	−0.17	0.02	−0.02	0.03	0.01
Steepness	−0.17	0.00	0.00	0.00	0.00
Distance to water	−0.17	0.00	0.00	0.00	−0.01
Distance to ciperaceas savannah/open forest	0.17	0.67	−0.34	−0.18	−0.27

Variance explained by five first factors and coefficient values for most important 15 ecogeophysical variables.

Table B.5 – ENFA results (family Hylidae (tree frogs))				
Ecogeophysical variable	Marginality (61%)	Spec. 1 (17%)	Spec. 2 (11%)	Spec. 3 (3%)
Distance to piedmont/Sierra de la Macarena	−0.32	0.00	−0.02	0.00
Evaporation	−0.29	0.01	−0.02	0.02
Days dry	−0.27	0.05	−0.06	−0.01
Precipitation	0.25	0.02	−0.04	−0.01
Distance to high human impact	−0.23	0.00	−0.01	0.00
Distance to ombrophilous montane forest	−0.20	0.02	0.05	−0.02
Distance to piedmont and diluvial surfaces	−0.20	0.01	−0.03	−0.04
Steepness	−0.19	0.00	0.00	0.00
Distance to ombrophilous alluvial riparian forest	−0.19	0.00	0.00	0.00
Distance to terraces/alluvial plains	−0.19	0.00	0.00	0.00
Distance to parallel drainage	−0.18	−0.01	0.00	0.01
Distance to alluvial surface deposits	−0.17	0.00	0.00	0.00
Distance to slow-moving rivers and dendritic drainage	0.17	0.00	−0.01	0.00
Distance to ciperaceas savannah/open forest	0.16	−0.81	0.06	−0.56
Distance to parallel to subparallel drainage	−0.16	−0.02	0.02	0.08

Variance explained by first four factors and coefficient values for most important 15 ecogeophysical variables.

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