Ecological Applications, 5(1), 1995, pp. 215–231

IDENTIFYING CONSERVATION PRIORITIES IN MEXICO THROUGH GEOGRAPHIC INFORMATION SYSTEMS AND MODELING[1]

Luis A. Bojórquez-Tapia, Iván Azuara, and Exequiel Ezcurra
Centro de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70-275, México, D.F., 04510

Oscar Flores-Villela
Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México, Apartado Postal 70-399 México, D.F., 04510

Abstract. Environmental assessments of regional development projects have been used in Mexico to determine where conflicts between conservation of biodiversity and resource extraction are likely to occur. Species-rich areas have been acknowledged as a priority for conservation. However, biological information is incomplete and biased toward accessible sites, so species-rich areas cannot be depicted directly from current biological knowledge.

An alternative approach to predicting species-rich areas is presented in this article. It is based on the gap analysis technique and involves the use of ordination analysis and generalized linear models integrated with a geographic information system. This approach was used for locating species-rich areas in the Mexican states of Guerrero and Oaxaca, where a regional forestry development project was proposed. Baseline information consisted of geo-referenced collection sites of terrestrial vertebrates. Thirty-two species assemblages were identified by the ordination analysis, as well as by 25 generalized linear models. Validation of six of these models showed no significant differences between observed and predicted species frequencies.

Results demonstrated that species-rich areas could be depicted even under the constraints of environmental assessment in Mexico. A large number of species could be used in this analysis due to the minimal information required for each species record. This predictive approach optimized available biological information for the integration of conservation into regional development planning.

Key words: biodiversity; conservation priorities; environmental assessments; gap analysis; GIS; GLIM; gradient analysis; identifying species-rich areas; Mexico; modeling; species-distribution maps; terrestrial vertebrate community.

Introduction

Concern over global change and widespread loss of biological diversity has resulted in laws and policies in favor of environmentally sound development and biodiversity conservation (UNEP 1992). Governments all over the world and multinational development banks are implementing environmental assessments (EA) as environmentally sound procedures aimed at development planning (Goodland 1988, Davis 1989). In Mexico, EAs are prerequisites for the approval of development projects (Bojórquez-Tapia 1989).

Consequently, EAs must provide elements for integration of natural resources management and conservation endeavors into regional development projects. Such integration implies that areas with the greatest potential for conflict between conservation and resource extraction have to be located and protected (Blockstein 1990, Davis et al. 1990).

Conflicts between conservation and resource extraction are prone to occur on species-rich areas, which are critical for biodiversity protection. Species-rich areas are critical because they tend to support more uncommon species (Patterson 1987, Wright and Reeves 1992) and their protection optimizes resources for conservation (Rapoport et al. 1986, Scott et al. 1987, 1988, 1993). Gap analysis is an approach used for identification of such areas. The technique consists of geographic information system (GIS) overlays of biological distribution data on a map of existing nature reserves, so results depict which species-rich areas are or are not protected (Scott et al. 1987, 1988). Alternatively, if the relationships between species richness and ecological factors are known, modeling through gap analysis can predict where species richness is likely to be the greatest (Davis et al. 1990). This approach has been recommended to locate possible nature reserves when biological inventories are incomplete (Austin et al. 1984, Margules and Stein 1989, Nicholls 1989).

This article presents the results of modeling through gap analysis to identify priority areas for conservation in the Mexican states of Guerrero and Oaxaca. The study is timely because, despite the biological importance of these states, a forestry development project is

[1] Manuscript received 27 May 1993; revised 20 January 1994; accepted 21 January 1994.

being planned without proper regard to conservation (Bojórquez-Tapia and Ongay-Delhumeau 1992). We also describe how a map of species-rich areas can be obtained with a minimum of information from biological inventories. The approach yields results useful for identification of critical areas for conservation, under the typical conditions of EAs and biological data constraints in Mexico (Bojórquez-Tapia 1989, Bojórquez-Tapia et al. 1994).

Study Area

The Mexican states of Guerrero and Oaxaca comprise ≈160 230 km², along the southwestern Pacific coast of Mexico (see Fig. 9). The region is characterized by a complex mosaic of vegetation types and ecological conditions (Flores-Villela and Gerez 1988), produced by its location along the biogeographic transition zone between neotropical and boreal biota (Rzedowski 1991), with rough topography, and variable climate (García and Falcón 1980). Mean annual temperature ranges between 8° and 30°C, and mean annual precipitation ranges between 500 and 4000 mm (INEGI 1982*a*).

Guerrero and Oaxaca are, respectively, the fourth and the first states in number of terrestrial vertebrate species in Mexico (Flores-Villela and Gerez 1988). Vascular plant diversity is equally high: estimations of the total number of species for the two states range from ≈8000 (Lorence and García Mendoza 1989), to 9000 species (Rzedowski 1991), and around 30% of the plant species probably are endemic to Mexico (Rzedowski 1991). The biological importance of the two states increases when one considers that Mexico is a "megadiversity" country because of its total number of species and high levels of endemism (McNeely et al. 1990).

Twenty vegetation types are found in Oaxaca, and thirteen in Guerrero. Coniferous forest, oak forest, tropical deciduous forest, and tropical evergreen forest are the main vegetation types in Oaxaca, while oak forest and tropical deciduous forest are the main vegetation types in Guerrero (Flores-Villela and Gerez 1988).

The two states contain extensive unmanaged forest. It is estimated that commercial forests in the two states cover 4.2×10^6 ha (32% of Mexico's total) and contain 24% of the nation's total timber volume (SARH 1980). A development project has been proposed to capitalize on those forest resources, but without proper consideration of biodiversity conservation (Bojórquez-Tapia and Ongay-Delhumeau 1992).

Despite their biological importance, <2% of the total area of the two states is under some form of protection (Flores-Villela and Gerez 1988).

Methods

Typical environmental assessments in Mexico are short-duration studies, performed with limited funds and baseline information (Bojórquez-Tapia 1989). Given these constraints, readily available biological data on endemic terrestrial vertebrates for the region were compiled from collections in Mexico and from the literature. A thorough description of the data is reported elsewhere (Bojórquez-Tapia et al. 1994).

Endemic species were used because of the following reasons: (1) It would be impossible to handle the total number of species of the region under the time restrictions of an EA; (2) endemics have been considered extinction-prone (Terborgh 1974, Terborgh and Winter 1983, Diamond 1986); and (3) endemics were assumed to be suitable indicators of species-rich areas, since it has been observed that species distributions exhibit nonrandom patterns (Patterson 1987, Patterson and Brown 1991). The criteria used for endemism were that species had to be endemic to Mexico and distributed in Guerrero and Oaxaca.

Data on endemic species were compiled from the literature and from biological collections. Literature data sources included: for amphibians and reptiles, Flores-Villela (1993); for birds, Friedman et al. (1957) and Flores-Villela and Gerez (1988); and, for mammals, Ramírez-Pulido et al. (1982). The consulted collections were the Instituto de Biología (IBUNAM) and the Museo de Zoología Alfonso L. Herrera de la Facultad de Ciencias (MZFC), both at the National Autonomous University of Mexico (UNAM) in Mexico City.

The data consisted of species names and collection sites. Each collection site was georeferenced mainly on a 1:250 000 topographic map (INEGI 1982*b*) and, if necessary, on 1:600 000 or 1:800 000 highway maps (SCT 1987*a, b*). Geographic coordinates of collection sites were also obtained from Binford (1989), Godwin (1969), and Office of Geography (1956). Repeated collection sites for a single species were not compiled into the data base.

The following 1:1 000 000 maps of the region were digitized by means of the geographic information system (GIS): soil types, soil phases, mean annual precipitation, mean annual temperature, vegetation, topography, and physiography (INEGI 1982*a*). The GIS consisted of three programs: AU2 (ICFA 1987), Roots (Corson-Rikert 1990), and CI/SIG (Conservation International 1992). The maximum resolution of our raster system (1-km² cell size) was used to minimize the "ladder effect" of digitized maps at the category boundaries of the environmental variables.

The geographic coordinates of all collection sites were transferred to the GIS. The digitized maps were then overlaid on the map of collection sites to characterize these sites environmentally. Results from the overlays were transferred to matrices of species and environmental variables. From these matrices, the corresponding contingency tables were prepared for the subsequent ordinations. The contingency tables consisted of the number of observations by species and by variable state or category (for example, number of observations of a species within the 8–10°C category).

Modeling was carried out by means of ordinations, through correspondence analysis of species and environmental variables (CASEV; Montaña and Greigh-Smith 1990), and generalized linear models (GLIM; Nicholls 1989, Atkin et al. 1990). We used both ORDEN version 1.4, by E. Ezcurra (unpublished program), and GLIM version 3.77 (Royal Statistical Society 1985) for all the statistical analyses.

CASEV was used to detect the relations between ecological factors and species distributions. The relationships between ordination axes and environmental variables were evaluated by visual examination. Thus, it was possible to: (1) select the environmental variables that better explained distribution patterns, and (2) identify groups of assemblages of species with similar ecological requirements. For each of these groups, a frequency matrix was prepared, using the environmental variables. To avoid altering the total deviance, nonexistent combinations of values between the environmental variables were eliminated from the analysis.

Log-linear models were fitted to the frequency matrix of each species assemblage (Atkin et al. 1990). The models were evaluated by coefficients of determination (r^2) and significance ($P < 0.001$) for the linear terms, and by significance ($P < 0.05$) for the quadratic terms. Coefficients of determination were estimated by:

$$r^2 = \frac{(\text{total deviance} - \text{residual deviance})}{\text{total deviance}},$$

where the "deviance", or measure of goodness of fit of the model to the data, was the chi-square function:

$$\Sigma\ \{(\text{observed})[\ln(\text{observed}/\text{expected})]\}.$$

The selected models were then used to predict the frequency of species for each species assemblage. The input values for the models were obtained from the species and environmental variables matrices (nonexistent combinations of values were omitted). Results were plotted as a function of the two main variables to obtain a response surface for each species assemblage (Ezcurra et al. 1987).

Some models were validated using available information that was not included in our data base. By means of a chi-square test, predicted and observed frequencies were compared for one species assemblage of reptiles, two species assemblages of birds, and three species assemblages of mammals. Observed frequencies were obtained from the following data sources: Morales-Pérez and Navarro-Sigüenza (1991), Flores-Villela and Muñoz-Alonso (1993), Jiménez-Alvarez et al. (1993), Navarro and Escalante-Pliego (1993), L. A. Peña-Hurtado (*unpublished manuscript*).

The GIS was employed to identify where species-rich areas were likely to occur. The combinations of variables that predicted the highest frequencies of species were mapped. This was in fact a map of predicted distribution of species assemblages. However, if a model could not be fitted to a species assemblage, the observed variable combinations with the highest frequencies were mapped. The final map was drawn by means of overlaying all the predicted distributions together and, to increase the accuracy of the predictions, the vegetation-type map. Predicted species-rich areas were ranked according to the number of species assemblages that coincide in the same zone; thus, category 1 corresponded to one species assemblage, category 2 corresponded to two species assemblages, and category 3 corresponded to three or more species assemblages.

Results

The following matrices (species × environmental variables) resulted from the overlays: amphibians (376 × 7), reptiles (1166 × 7), birds (388 × 7), and mammals (530 × 7). From these matrices the following contingency tables (species × categories of environmental variables) were obtained: amphibians (62 × 55), reptiles (159 × 62), birds (50 × 61), and mammals (55 × 64).

Thirty-two groups of species with similar ecological requirements (7 assemblages for amphibians, 10 for reptiles, 8 for birds, and 7 for mammals) were obtained from correspondence analysis of species and environmental variables (CASEV; Montaña and Greigh-Smith 1990) (Table 1, Figs. 1–4, Appendix). The variables that explained the highest variance differed between classes of terrestrial vertebrates but, in general, they were mean annual temperature, mean annual precipitation, elevation, and vegetation type (Table 2). However, other variables contributed greatly to the variance: landform, soil phase, and soil unit for mammals, and soil unit for amphibians, birds, and reptiles (Table 2). Nevertheless, elevation and mean annual temperature were highly correlated ($r^2 = -0.8$), so elevation was discarded from further analyses. Likewise, vegetation type was an ordinal variable, so we decided not to include it in GLIM (generalized linear models; Nicholls 1989, Atkin et al. 1990), but rather to use it as an additional overlay to increase mapping accuracy.

Frequency matrices were built from mean annual temperature (12 categories) and from mean annual temperature and mean annual precipitation (15 categories). Since nonexistent combinations of values between these orthogonal environmental variables were eliminated, the frequency matrices contained a total of 106 cells.

Significant fits of GLIM were possible for 25 assemblages (Table 3, Figs. 5–7) of the original 32 groups of species (Table 1). The general model consisted of five terms:

$$y = e^{(a+bt+cp+dt^2+fp^2+gpt)},$$

where y is the predicted frequency of number of species, t is mean annual temperature, and p is mean annual precipitation. The importance of each term (indicated by the coefficients b–g) varied between models (Table 3). Validation of the models through the chi-square test

TABLE 1. Environmental characterization of assemblages of endemic terrestrial vertebrate species in Guerrero and Oaxaca, Mexico.

Assemblage	Mean annual temperature (°C)	Mean annual precipatation (10^2 mm)	Vegetation type*	Elevation (10^2 m)
		Amphibians		
1	12–20	10–40	PO	20–36
2	12–26	8–40	PO, TD	10–20
3	12–26	5–8	TS	10–20
4	24–30	5–8	OF, MTE	10–16
5	24–30	8–40	TD, TS	10–16
6	24–30	8–40	TD	2–10
7	12–14	6–7	NA	30–36
		Reptiles		
1	26–30	4–7	M, TS	0–6
2	26–30	4–7	TD, TS	2–6
3	24–30	4–10	TD, G	6–10
4	22–24	6–20	OF	10–12
5	18–24	6–20	OF, CH	16–20
6	20–22	20–25	OF, PO	20–26
7	18–20	20–25	PO, CF	20–26
8	10–18	20–25	CF, MCF	26–36
9	NA†	25–35	TE	NA†
10	18–22	20–30	MC	20–36
		Birds		
1	10–16	20–45	CF, MC	26–36
2	16–20	8–35	PO, OF	16–28
3	20–24	8–35	OF	16–26
4	20–22	4–8	OF, CH	16–26
5	22–26	4–8	OF, CH, G, DV	10–16
6	22–26	8–45	TE, DV	10–16
7	26–28	8–35	TD, TS	8–16
8	28–30	8–35	TS, M	0–10
		Mammals		
1	26–30	10–35	CF, M	0–10
2	22–26	7–35	TD, TS, OF, G	2–16
3	22–26	4–5	DS, TD	6–20
4	18–24	7–12	DS, OF	16–20
5	18–22	8–40	CF, PO, MC, TE	20–25
6	18–22	30–40	CF, PO, MC	26–36
7	12–18	10–40	CF, PO, MC	26–36

* CF = Coniferous forest; CH = Chaparral; DS = Desert scrub; DV = Disturbed vegetation; G = Grassland; M = Mangrove; MC = Montane cloud forest; OF = Oak forest; PF = Palm forest; PO = Pine–oak forest; TD = Tropical deciduous forest; TE = Tropical evergreen forest; TS = Tropical semideciduous forest.
† NA = data not available.

demonstrated that the differences between predicted and observed frequencies of species were not significant (Table 4).

The response surfaces depicted the distribution gradients for 23 species assemblages (Figs. 5–7). Within the plotted range, some predicted frequencies for species assemblages responded to low mean annual temperature and low mean annual precipitation (mammals 1, 2, and 3; reptiles 2, 3, and 4; amphibians 6; and birds 7 and 8), some responded to moderate mean annual temperature and low mean annual precipitation (reptiles 6 and 7), some reacted to low mean annual temperature and from low to high mean annual precipitation (mammals 6 and 7; reptiles 6 and 7; amphibians 1; and birds 1 and 2), and others reacted to rather extensive gradients (birds 3, 5, and 6; mammals 4 and 5; and amphibians 2 and 5).

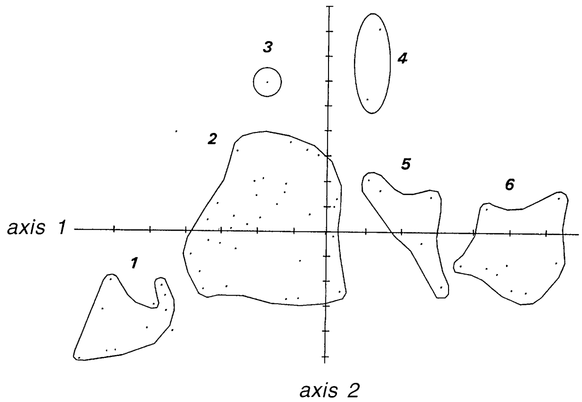


FIG. 1. Ordination analysis for 62 endemic species of amphibians of Guerrero and Oaxaca, Mexico. The numbers indicate groups or species assemblages distributed along similar environmental gradients. Axis 1 combines gradients of elevation, mean annual temperature, and vegetation type; axis 2 includes a mean annual precipitaton gradient. Non-grouped points belong to the 7th assemblage, on axis 3 (perpendicular to both of the axes shown).

Predicted distributions of species assemblages covered a large proportion of the study region (Fig. 8). However, when the areas were ranked with respect to the number of taxonomic classes contained, the predicted species-rich areas could be easily detected (Fig. 9). These areas are located along the Sierra Madre del Sur and Sierra de Juárez (Fig. 9). Given a 1-km² cell size, category 3 covered 1526 km², category 2 extended over 7788 km², and category 3 occupied 24 735 km².

DISCUSSION

Environmental policies in most countries demand comprehensive land-use planning aimed at long-term

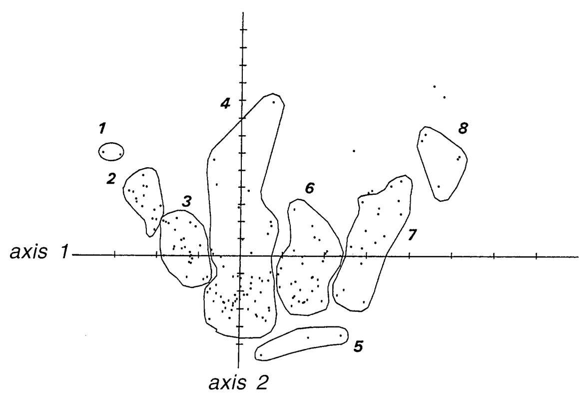


FIG. 2. Ordination analysis for 159 endemic species of reptiles of Guerrero and Oaxaca, Mexico. The numbers and axes are as in Fig. 1. Non-grouped points belong to assemblages 9 and 10 on axis 3.

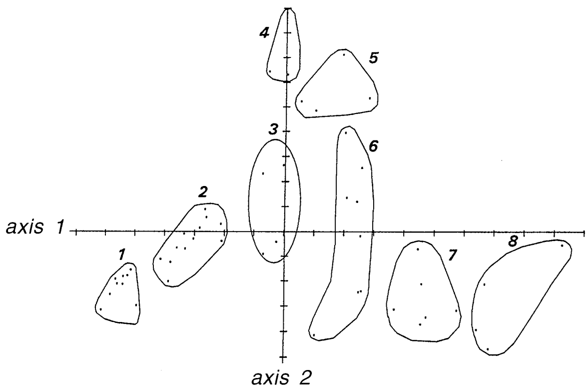


FIG. 3. Ordination analysis for 50 species of birds of Guerrero and Oaxaca, Mexico. The numbers and axes are as in Fig. 1.

conservation of biological diversity (UNEP 1992). As part of these policies, environmental assessments (EAs) are required for regional development projects. EAs are procedures aimed at environmentally sound development planning. Likewise, EAs are expected to use biological inventories as baseline information to achieve two important objectives: (1) to evaluate if a project conflicts with biodiversity protection, and (2) to set the basis for a regional conservation strategy (Goodland 1988). The two objectives require pinpointing areas with the greatest potential for conflict between conservation and resource extraction (Blockstein 1990). Such conflicts are likely to occur in species-rich areas, since they are critical for biodiversity protection (Rapoport et al. 1986, Scott et al. 1987, 1988).

Gap analysis is a technique designed to identify priority areas for conservation by comparing the location of existing nature preserves with the location of species-rich areas (Scott et al. 1987, 1988). To locate species-rich areas, this approach utilizes GIS (geographic information system) maps of species distributions, which are generated from four sets of information: (1) a digitized map of vegetation types; (2) a digitized map of geographic entities; (3) a data base that assigns the presence or absence of a species to the geographic units; and (4) a data base that associates each wildlife species with a set of preferred vegetation cover types (Scott et al. 1993).

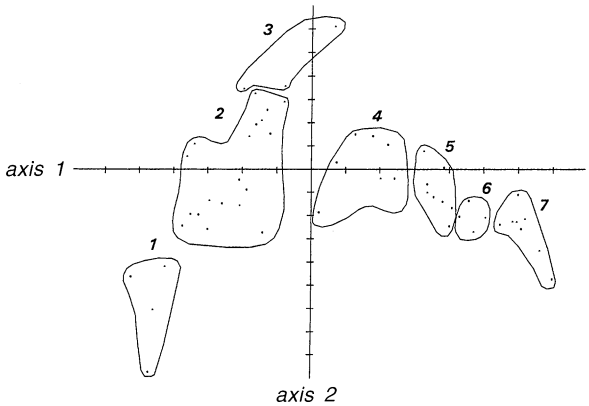


FIG. 4. Ordination analysis of 55 species of mammals of Guerrero and Oaxaca, Mexico. The numbers and axes are as in Fig. 1.

TABLE 2. Contribution (%) of the environmental variables to the first five ordination axes of endemic terrestrial vertebrates from Guerrero and Oaxaca, Mexico.

Variable	Amphibians	Reptiles	Birds	Mammals
Mean annual precipitation	22	37	15	16
Mean annual temperature	20	8	13	19
Elevation	21	10	20	11
Vegetation	14	19	36	12
Soil phase	3	7	4	18
Soil unit	15	17	10	11
Landform	5	2	3	13
Total	100	100	100	100

TABLE 3. Generalized linear models of the distribution of endemic terrestrial vertebrates from Guerrero and Oaxaca, Mexico.

Assemblage	Model terms*	df	r^2 †
	Amphibians		
1	$a + b$	3	0.74
2	$a + b + c$	5	0.51
5	$b + c + a$	5	0.43
6	$a + b + c$	5	0.62
	Reptiles		
2	$a + b$	4	0.69
3	$b + a$	4	0.77
4	$b + a$	4	0.73
6	$b + a$	4	0.63
7	$a + b$	4	0.55
8	a	2	0.34
10	b	2	0.34
	Mammals		
1	$a + c + b$	5	0.67
2	$a + b + c$	5	0.27
3	$a + b$	4	0.26
5	$a + b$	2	0.37
6	$b + a$	4	0.32
7	$a + b + c$	5	0.62
8	$a + b$	4	0.66
	Mammals		
1	$a + b + c$	5	0.90
2	$a + b$	4	0.62
3	$a + b$	4	0.61
4	$a + b$	4	0.48
5	$a + b$	4	0.43
6	$a + b + c$	4	0.49
7	$a + c + b$	5	0.72

* a = mean annual temperature; b = mean annual precipitation; c = interaction between mean annual temperature and mean annual precipitation. The order of the terms signifies their order of importance for fitting the model.

† r^2 = (total deviance − residual deviance)/(total deviance); $P < 0.001$ for all assemblages.

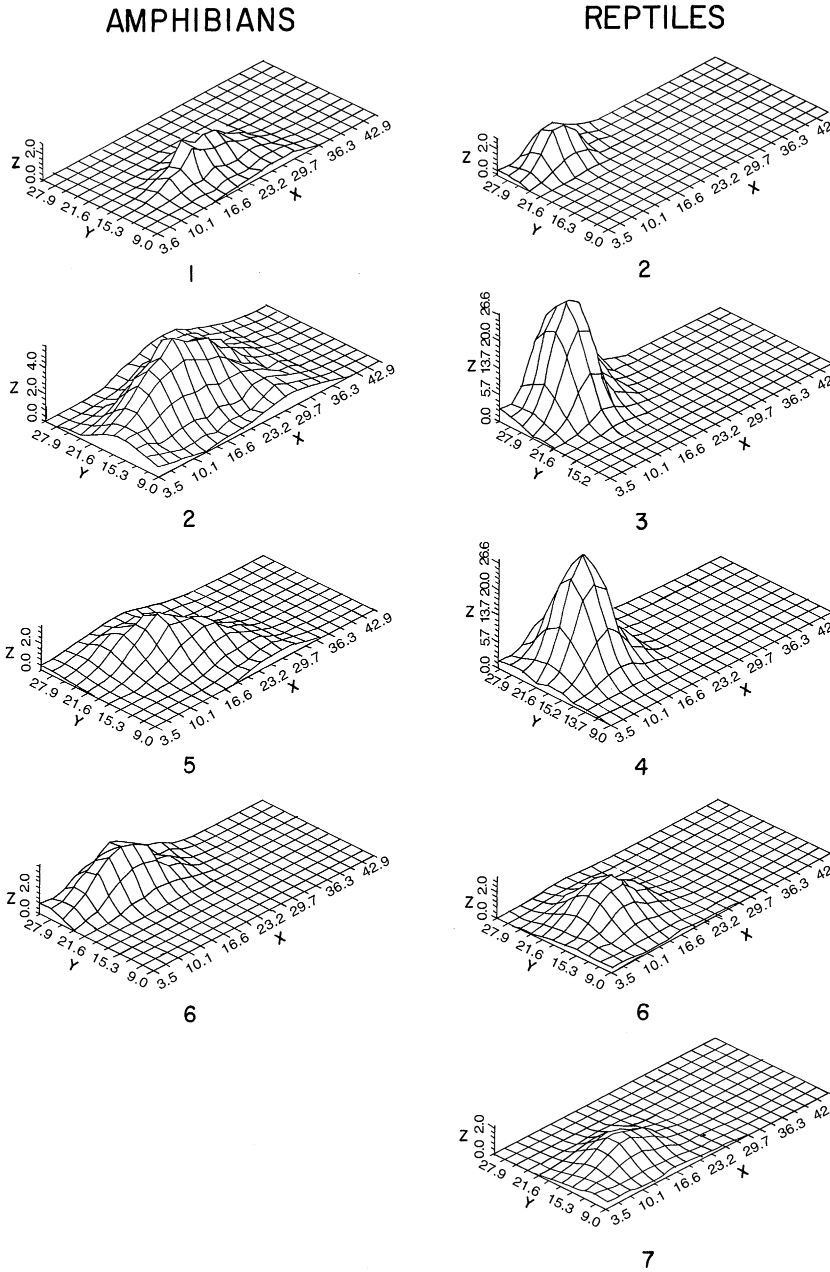


FIG. 5. Response surfaces for endemic amphibians and reptiles of Guerrero and Oaxaca, Mexico. X = mean annual temperature; Y = mean annual precipitation; Z = frequency.

However, incomplete biological data and lack of up-to-date cartography hamper comprehensive assessments of biodiversity through the original gap-analysis approach. In most parts of the world, current biological data is limited by sampling artifacts, such as biases towards field stations or accessible sites (Nelson et al. 1990, Pearson and Cassola 1992). In the case of Guerrero and Oaxaca, biological data are concentrated along major highways and accessible sites (Bojórquez-Tapia et al. 1994), and vegetation type maps are based on 15-yr-old baseline information (INEGI 1982*a*).

An alternative approach is essential, since it is unrealistic to postpone a development project until complete information is available. Consequently, a predictive approach is needed to assess species distribution patterns and to identify species-rich areas. Such an approach must yield a sound assessment in a short time and with limited baseline information. Multivariate models have been used to predict species distribution patterns with limited biological data (Austin et al. 1984, Miller 1986, Ezcurra et al. 1987, White and Miller 1988, Margules and Stein 1989, Nicholls 1989, Mon-

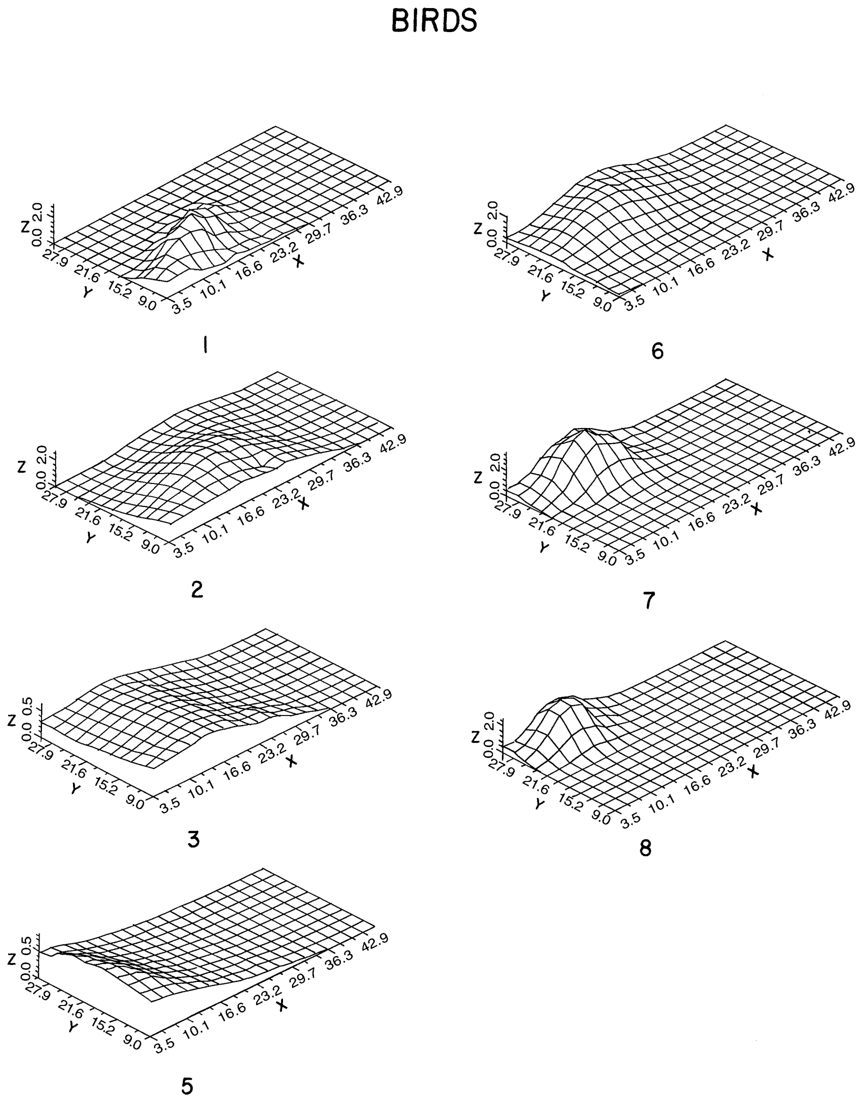


FIG. 6. Response surfaces for endemic birds of Guerrero and Oaxaca, Mexico. X = mean annual temperature; Y = mean annual precipitation; Z = frequency.

taña and Greigh-Smith 1990, Kramen 1992). Likewise, GISs have been utilized to map the species distribution patterns predicted from the multivariate models (Miller et al. 1989, Davis et al. 1990, Walker 1990).

Thus, a feasible procedure is to generate a map of predicted species-rich areas that can be overlaid on maps of projected land use. The end product would be a map that shows conflicting areas that should be protected and surveyed in more detail. Furthermore, specific biodiversity protection guidelines can be prescribed for those areas to withhold development until field validations take place (for example, restrictions on forestry operations).

Our study demonstrates that a map of predicted species-rich areas can be generated under conditions of EAs in Mexico. To overcome the limitations imposed by baseline data and regional scale, the approach consists of: (1) the use of a data base of collection sites, (2) relating that data base to a set of environmental variables through a GIS, (3) using ordination techniques (CASEV; Montaña and Greigh-Smith 1990) to depict the relations between richness and environmental variables, (4) using the main variables to formulate the generalized linear models that predict the greatest likelihood of finding a species-rich area, and (5) mapping the predictions of the model by means of a GIS.

This statistical procedure utilizes almost all the available information on endemic species (see Bojórquez el al. 1994), takes into account the data constraints, and produces areas with precise boundaries at an adequate scale for an EA. In contrast, global (Vane-Wright et al. 1991, Pearson and Cassola 1992) or regional (Fa 1989) biogeographic analyses are inappropriate for an EA because they do not identify specific areas, since maps

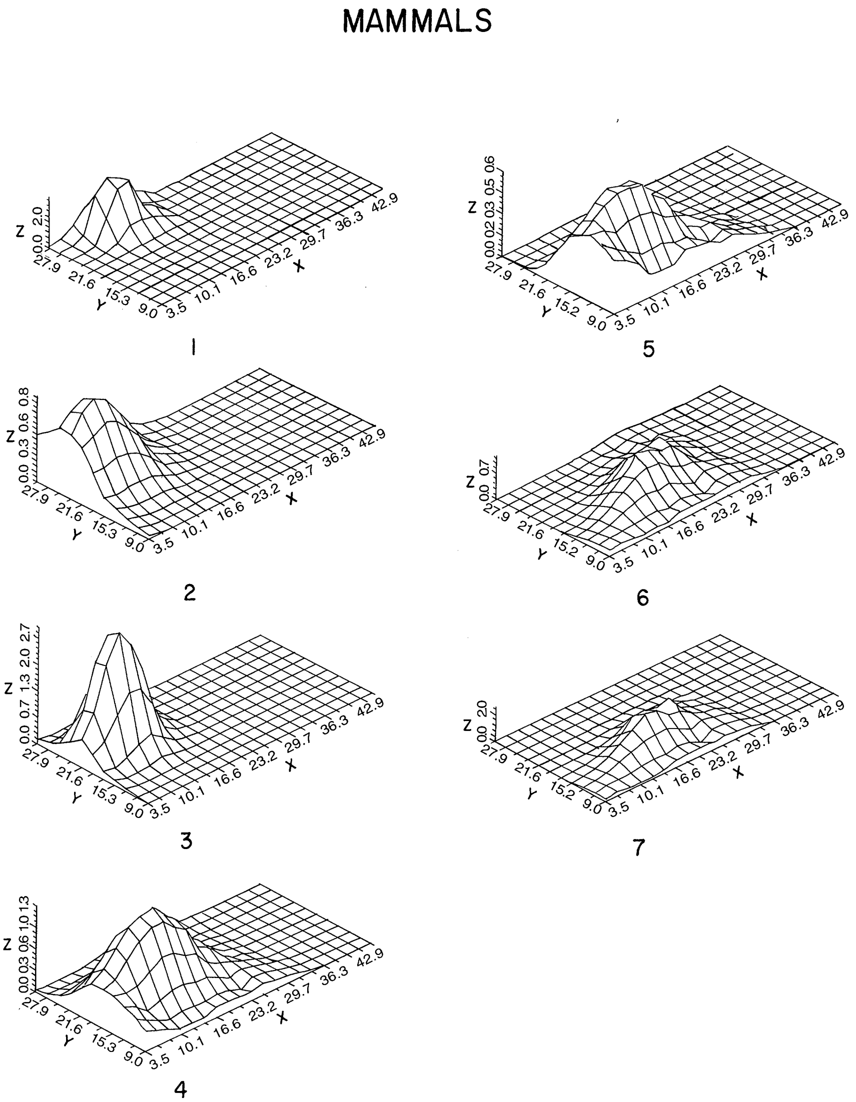


FIG. 7. Response surfaces for endemic mammals of Guerrero and Oaxaca, Mexico. X = mean annual temperature; Y = mean annual precipitation; Z = frequency).

at rather small scales are not useful for identifying specific areas.

Although the validation of some of the linear models makes us think that the analysis is robust (Table 3), it has to be noted that the results depend on the accuracy of small-scale maps, and the number and composition of species assemblages derived by ordinations. Therefore the models are vulnerable to error propagation, and the results may vary depending on the spatial resolution and the criteria used in the ordinations for obtaining species assemblages.

The results (Table 2) show that mean annual precipitation, mean annual temperature, elevation, and vegetation are, in general, good predictors of species richness, while the other variables are good predictors for distinct groups: soil unit for amphibians, birds, and reptiles, and landform, soil phase, and soil unit for mammals. Similar patterns have been found by other authors. For example, Miller et al. (1989) report that soil and vegetation are good predictors of rare bird distribution in Tanzania; Rabinovich and Rapoport (1975) correlate passerine bird species richness to temperature, precipitation, topography, and vegetation; and Fa (1989) and Robertson (1975) associate mammal species richness and abundance with elevation and vegetation.

In general, patterns of species richness have been related to environmental productivity (Abramsky and Rosenzweig 1984, Owen 1990), while endemism in Guerrero and Oaxaca has been correlated with elevation (Peterson et al. 1993). Therefore, our results can be partly explained by the relationship of the environmental variables to productivity at the scale of our study. Habitat productivity is correlated with climatic

TABLE 4. Validation of six generalized linear models of distribution of endemic terrestrial vertebrates from Guerrero and Oaxaca, Mexico.

	Assemblage		Observed frequency, f	Predicted frequency, f_1	
Locality*	No. (Table 1)	No. of species			$(f - f_1)^2/f_1$
		Reptiles			
1	7	18	5	5	0.00
		Birds			
2	1	9	2	7	3.57
1	2	12	2	3	0.33
		Mammals			
1	5	8	3	1	4.00
3	6	5	1	1	0.00
3	7	8	4	3	0.33
Totals		60	20	17	8.23†

* 1 = Omiltemi, Guerrero; 2 = Sierra Norte de Guerrero; 3 = Sierra de Juárez, Oaxaca.
† χ^2, $P = 0.14$.

variables, such as precipitation and temperature, and to landform and soils. Climatic variables explain variation at small scales; at medium scales, the broad climatic patterns are modified by landform because landforms control the intensities of key factors important to vegetation productivity and soil development; and at microscales, the broad patterns are controlled by edaphic factors (Bailey 1985, 1987). Considering that most endemic species are small, a case can be made that the high contribution of soil phase to the variance for mammals and of soil unit for the other three classes is related to distinct habitat requirements controlled by edaphic factors.

Our approach permits the use of a large number of species in the analysis because a minimum of data is necessary: geographical coordinates of collection sites and maps of environmental variables. These kinds of data are readily available in herbaria, museums, literature (Bojórquez-Tapia et al. 1994), and official cartography (INEGI 1982*a*). Consequently, both data on species habitat preferences and a digitized map of geographic entities are unnecessary. This is crucial for cases analogous to our study because habitat preferences are unknown for most species and geographic entities maps are yet to be produced in most parts of the world.

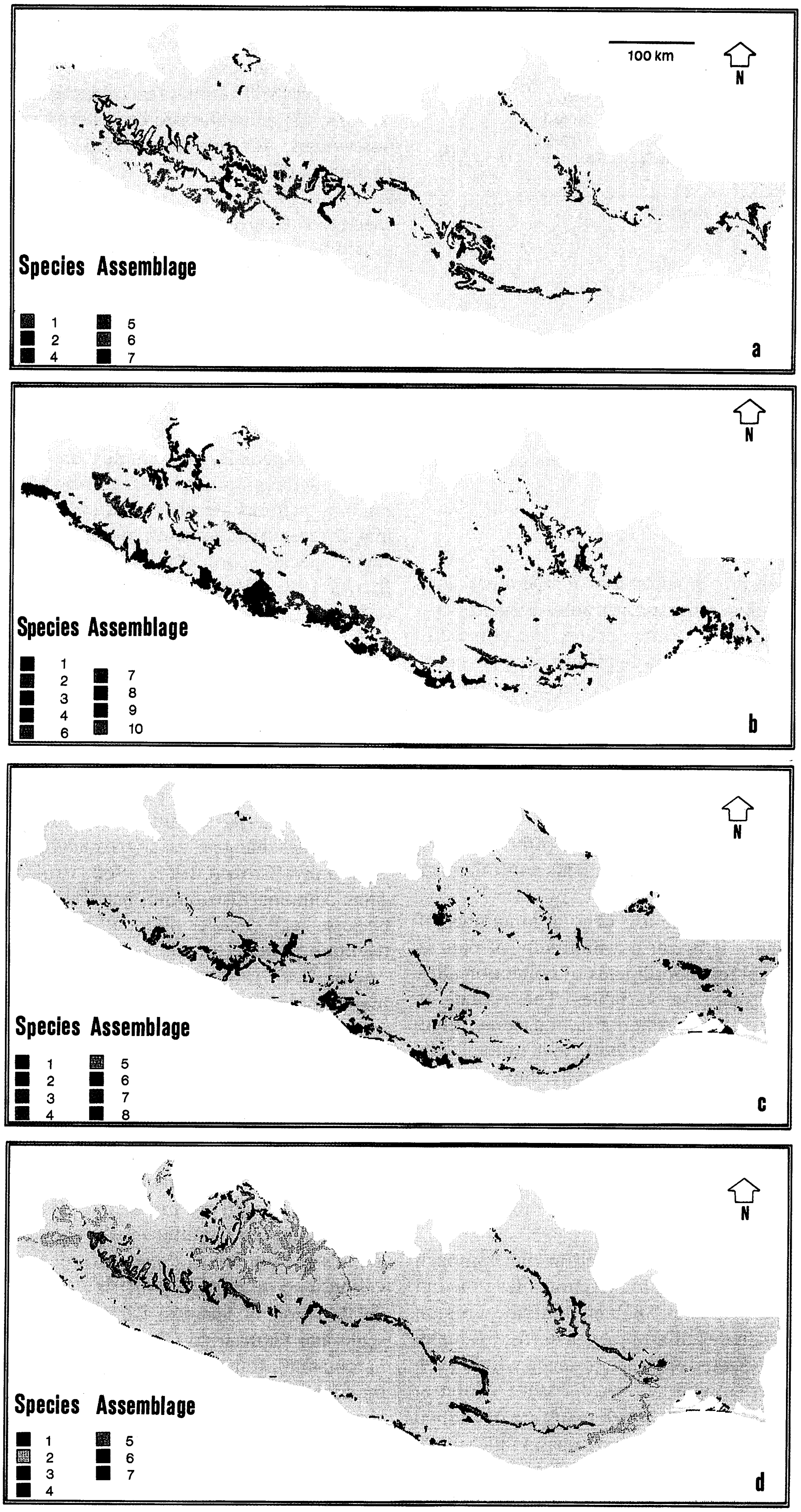
Species distributions are predicted in our approach from georeferenced records of collection sites to avoid the use of a coarse grid map. Such maps divide a region into rather large squares of arbitrary size (for example, 10 × 10 km) and species presence/absence within each square of the grid is recorded (see Fa 1989, Miller et al. 1989, Davis et al. 1991). These maps are of limited application for our case because of the complexity of the region, biases of biological data (Bojórquez-Tapia et al. 1994) and the lack of a habitat-range map with precise boundaries to minimize overestimation of the distributions (Davis et al. 1991).

An important aspect of our study is the use of endemic terrestrial vertebrates. Endemics are used for two reasons: (1) endemics are considered extinction-prone but suitable for protection with relatively small investments (Terborgh 1974, Terborgh and Winter 1983, Diamond 1986), and (2) data on the total number of species of Guerrero and Oaxaca would be impossible to handle under the time restrictions of an EA (Bojórquez-Tapia et al. 1994). Endemic species have been used to identify priority areas for conservation elsewhere (Terborgh and Winter 1983, Diamond 1986).

Therefore, the detected species-rich areas in our study correspond to centers of endemism. Though this might be regarded as a bias towards endemics, species distributions have been observed to follow nonrandom patterns, especially in complex and environmentally fragmented regions such as Guerrero and Oaxaca. Nonrandom patterns of species distributions presuppose that different species assemblages are samples from the same species pool (Patterson 1987, Patterson and Brown 1991, Wright and Reeves 1992); hence, sites occupied by assemblages of narrowly distributed species must correspond with sites occupied by more widely distributed species. Since richer sites support a greater number of uncommon species (Wright and Reeves 1992), endemic distribution patterns should reflect specific conditions that are related to local species richness.

The use of endemics also assumes that current biodiversity patterns should result from ecological and geographic changes, as suggested by vicariance biogeography (Croizat 1958, 1962, Croizat et al. 1974). Thus common distribution patterns of biota may exist because such changes affect all biota. Evidence of distribution patterns of biota has been detected: (1) the "generalized tracks" (similar distribution patterns) of highly mobile groups, such as butterflies and birds, and sedentary groups, such as apterous insects (Croizat 1958, Nelson 1973, Croizat et al. 1974); (2) the relationship between distribution patterns and centers of endemism; and (3) the relation between speciation of birds and centers of endemism (Cracraft 1982).

Consequently, at least in principle, species-rich areas can be located by means of identifying centers of endemism. Through the protection of species-rich areas, it is possible to simultaneously preserve both the endemics (which are the ones in urgent need of preservation) and more widely distributed species. However, the location of species-rich areas depends upon the scale and taxon used (Davis et al. 1991). If the scale is too small, transition zones may not be detected, and the location of the species-rich areas of one taxonomic class may be separated from other classes' positions. In our study, the detection of species assemblages through ordination allows us to determine species-rich areas independently from the taxa. Therefore, richness


100 km
N
Species Assemblage
1
2
4
5
6
7
a
N
Species Assemblage
1
2
3
4
6
7
8
9
10
b
N
Species Assemblage
1
2
3
4
5
6
7
8
c
N
Species Assemblage
1
2
3
4
5
6
7
d

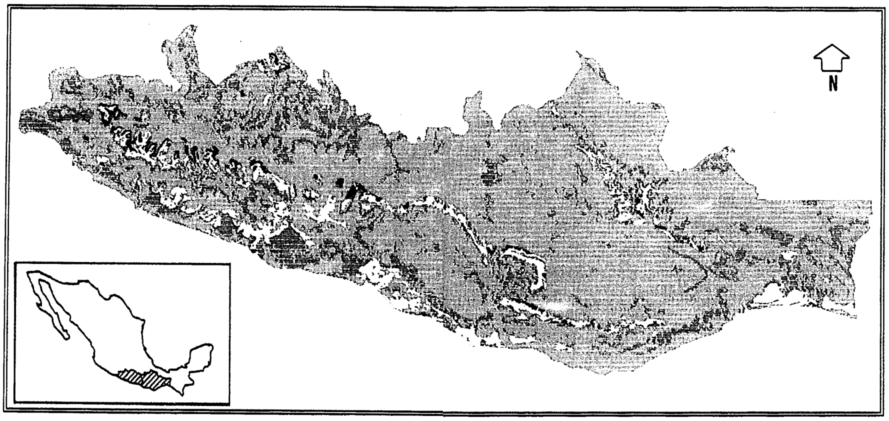


FIG. 9. Location of study area and predicted species-rich areas ranked by the number of classes of terrestrial vertebrates included within the area. Red = rank 3 (three or more species assemblages); yellow = rank 2 (two species assemblages); and green = rank 1 (one species assemblage).

is depicted by analyzing the distribution patterns of species assemblages (we ranked the species-rich areas as the ones that contained species assemblages of 1, 2 or 3 taxonomic classes; Figs. 8 and 9).

With respect to transition zones, these can be examined by means of the response surfaces (Figs. 5–7). As an aftermath of the ordination analysis, predicted highest frequencies for species assemblages within a class are obtained from different combinations of values of the main variables. Since the highest predicted frequencies never coincide, transition zones can be depicted by examining the response surfaces of two or more species assemblages and pinpointing where the lower frequencies cross. If necessary, the values of the variables can be read directly from the corresponding charts and then mapped through the GIS.

Examination of response surfaces serves to determine which additional species assemblages are contained by a predicted species-rich area, regardless of its rank. Response surfaces can also be classified according to a threshold value relative to the maximum predicted frequencies; in this way, overlapping of species distributions can be increased since wider variable value combinations are involved. For example, consider the maximum frequencies and a category-2 species-rich area, namely, the one that is composed of species assemblages 6 for amphibians and 7 for birds (Fig. 9); this should also contain species assemblages of birds 5, 6, 7, and 8, amphibians 5, reptiles 2, 3, and 4, and mammals 1, 2, and 3 (Figs. 5–7).

Priority consideration for establishing new nature preserves should be given to ranks 3 and 2 (Fig. 9), so these areas should be surveyed in detail. For areas of rank 1, the legally required environmental impact assessments for the forestry operations should give special attention to the protection of important habitats for the particular species assemblages.

A more accurate priority ordering can be obtained by overlaying the species-rich areas map on both a map of proposed forestry operations and a vulnerability map. Consequently, detailed surveys should include, on the one hand, (1) a biological inventory, (2) a field-verified vegetation map, (3) an appraisal of minimum areas needed for biodiversity protection, and (4) location of landscape corridors connecting areas of high species richness, and, on the other hand, (5) an appraisal of development pressure, including such factors as population, road density, land ownership, and land management. Thus, our species-rich area map can be viewed as a first step in a multistage sampling system (see Myers and Shelton 1980) that provides preliminary information about where detailed conservation surveys should be conducted.

CONCLUSIONS

Biased and limited biological data on species distributions are a major obstacle for identifying priority areas for conservation. Hence, a predictive approach is needed to supply timely information for EAs of regional development projects. Multivariate models and GIS can be used to identify species-rich areas and centers of endemism on which to base conservation decisions.

The approach presented in this article optimizes the use of current biological information for environmental planning. By ranking the predicted species-rich areas, appropriate surveys and mitigation measures can be

←

FIG. 8. Predicted distribution areas for species assemblages of endemic amphibians (a), reptiles (b), birds (c), and mammals (d) of Guerrero and Oaxaca, Mexico (see Appendix for species lists).

planned to mitigate conflicts between conservation and resource extraction.

ACKNOWLEDGMENTS

This research was supported by the Centro de Ecología, UNAM, the Consejo Nacional de Ciencia y Tecnología, and the Conservation International Foundation. This article was a contribution from the second author's dissertation, presented at the Facultad de Ciencias, UNAM. The valuable commentaries of the two anonymous reviewers improved this article. We also acknowledge the highly efficient and indispensable technical assistance of M. Alquicira, C. Alvárez, B. Estrada, L. Peña, and A. Ramírez.

LITERATURE CITED

Abramsky, Z., and M. L. Rosenzweig. 1984. Tilman's predicted productivity–diversity relationships shown by desert rodents. Nature **309**:150–151.

Atkin, M., D. Anderson, B. Francis, and J. Hinde. 1990. Statistical modeling in GLIM. Clarendon, Oxford, England.

Austin, M. P., R. B. Cunningham, and P. M. Flemming. 1984. New approaches to direct gradient analysis using environmental scalars and statistical curve-fitting procedures. Vegetatio **55**:11–27.

Bailey, R. G. 1985. The factor of scale in ecosystem mapping. Environmental Management **9**:271–276.

———. 1987. Suggested hierarchy of criteria for multisclae ecosystem mapping. Landscape and Urban Planning **14**: 313–319.

Binford, L. C. 1989. A distributional survey of the birds of the Mexican state of Oaxaca. Ornithological Monographs **43**.

Blockstein, D. E. 1990. Toward a federal plan for biological diversity. Journal of Forestry **88**:15–19.

Bojórquez-Tapia, L. A. 1989. Methodology for prediction of ecological impacts under real conditions in Mexico. Environmental Management **13**:545–551.

Bojórquez-Tapia, L. A., P. Balvanera, and A. D. Cuaron. 1994. Biological inventories and computer databases: their role in environmental assessments. Environmental Management **18**:775–785.

Bojórquez-Tapia, L. A., and E. Ongay-Delhumeau. 1992. International lending and resource development in Mexico: can environmental quality be assured? Ecological Economics **5**:197–211.

Conservation International. 1992. CI/SIG, Sistema de información geográfica, 2.0: manual del usuario. Conservation International, Washington, D.C., USA.

Corson-Rikert, J. 1990. Roots user's manual. Harvard University Graduate School of Design, Laboratory for Computer Graphics and Spatial Analysis, Cambridge, Massachusetts, USA.

Cracraft, J. 1982. Geographic differentiation, cladistics, and vicariance biogeography: reconstructing the tempo and mode of evolution. American Zoology **22**:411–424.

Croizat, L. 1958. Panbiogeography. Published by the author. Caracas, Venezuela.

———. 1962. Space, time, form: the biological synthesis. Published by the author. Caracas, Venezuela.

Croizat, L., G. Nelson, and D. E. Rosen. 1974. Centers of origin and related concepts. Systematic Zoology **23**:265–287.

Davis, F. W., J. E. Estes, B. C. Csutti, and J. M. Scott. 1991. Geographic information system analysis of biodiversity in California. Final Report. Department of Geography, University of California, Santa Barbara, California, USA.

Davis, F. W., D. M. Stoms, J. E. Estes, J. Scepan, and J. M. Scott. 1990. An information system approach to the preservation of biological diversity. International Journal of Geographical Information Systems **4**:79–86.

Davis, G. 1989. Environmental assessment: operational directive adopted by the bank. Environment Bulletin **1**:2.

Diamond, J. 1986. The design of a nature reserve system for Indonesian New Guinea. Pages 485–503 *in* M. E. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer, Sunderland, Massachusetts, USA.

Ezcurra, E., M. Equihua, and J. López-Portillo. 1987. The desert vegetation for el pinacate, Sonora, Mexico. Vegetatio **71**:49–60.

Fa, J. E. 1989. Conservation-motivated analysis of mammalian biogeography in the Trans-Mexican Neovolcanic Belt. National Geographic Research **5**:296–316.

Flores-Villela, O. 1993. Herpetofauna mexicana. Carnegie Museum of Natural History Special Publication **17**.

Flores-Villela, O., and P. Gerez. 1988. Conservación en México: síntesis sobre vertebrados terrestres, vegetación y uso del suelo. Instituto Nacional de Investigaciones sobre Recursos Bióticos-Conservation International, Xalapa, Mexico City, Mexico.

Flores-Villela, O., and A. Muñoz-Alonso. 1993. Anfibios y reptiles. Pages 411-442 *in* I. Luna and J. Llorente, editors. Historia natural del Parque Ecológico Estatal Omiltemi, Chilpancingo, Guerrero, México. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad/UNAM. Mexico City, Mexico.

Friedman, H. L., L. Griscom, and A. H. Miller. 1957. Distributional checklist of the birds of México. Part I. Pacific Coast avifauna. Number 29. Ornithological Club, Berkeley, California, USA.

García, E., and Z. Falcón. 1980. Nuevo atlas Porrúa de la República Mexicana. Editorial Porrúa, S.A., Mexico City, Mexico.

Godwin, G. G. 1969. Mammals from the state of Oaxaca, Mexico. Bulletin of the American Museum of Natural History **141**:256–265.

Goodland, R. 1988. A major new opportunity to finance the preservation of biodiversity. Pages 437–441 *in* O. E. Wilson, editor. Biodiversity. National Academy Press, Washington, D.C., USA.

ICFA [Ingenieron Civiles y Fotegrametristas Asociados]. 1987. AU2 Paquete general de cartografía: manual del usuario. Publicación 88-AU-2-01. ICFA, Mexico City, Mexico.

INEGI [Instituto Nacional de Estadística Geografía e Informática]. 1982*a*. Atlas nacional del medio físico. Secretaría de Programación y Presupuesto, Mexico City, Mexico.

———. 1982*b*. Carta topográfica 1:250,000. Secretaría de Programación y Presupuesto, Mexico City, Mexico.

Jiménez-Alvarez, T., J. Juárez-Gómez, and L. León-Paniagua. 1993. Mamíferos. Pages 503–549 *in* I. Luna and J. Llorente, editors. Historia natural del Parque Ecológico Estatal Omiltemi, Chilpancingo, Guerrero, México. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad/UNAM. Mexico City, Mexico.

Kramen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. Ecological Applications **2**:203–217.

Lorence, D. H., and A. García Mendoza. 1989. Oaxaca, Mexico. Pages 253–269 *in* D. G. Campbell and H. D. Hammond, editors. Floristic inventory of tropical countries: the status of plant systematics, collections, and vegetation, plus recommendations for the future. New York Botanical Garden, New York, New York, USA.

Margules, C. R., and J. L. Stein. 1989. Patterns in the distribution of species and the selection of nature reserves: an example from *Eucalyptus* forests in south-eastern New South Wales. Biological Conservation **50**:219–238.

McNeely, J. A., K. R. Miller, W. V. Reid, R. A. Mittermeier, and T. B. Werner. 1990. Conserving the world's biological diversity. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland; World Resources Institute, Conservation International, World Wildlife Fund–U.S., and The World Bank, Washington, D.C., USA.

Miller, R. I. 1986. Predicting rare plant distribution patterns in the Southern Appalachians of the south-eastern U.S.A. Journal of Biogeography **13**:293–311.

Miller, R. I., S. N. Stuart, and K. M. Howell. 1989. A methodology for analyzing rare species distribution patterns utilizing GIS technology: the rare birds of Tanzania. Landscape Ecology **2**:173–189.

Montaña, C., and P. Greigh-Smith. 1990. Correspondence analysis of species by environmental variable matrices. Journal of Vegetation Science **1**:453–460.

Morales-Pérez, J. E., and A. G. Navarro-Sigüenza. 1991. Análisis de distribución de las aves en la Sierra Norte del estado de Guerrero, México. Anales del Instituto de Biología UNAM. Serie Zoología **62**: 497–510.

Myers, W. L., and R. L. Shelton. 1980. Survey methods for ecosystem management. John Wiley & Sons, New York, New York, USA.

Navarro, A. G., and P. Escalante-Pliego. 1993. Aves Parque Estatal Omiltemi. Pages 443–501 *in* I. Luna and J. Llorente, editors. Historia natural del Parque Ecológico Estatal Omiltemi, Chilpancingo, Guerrero, México. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad/ UNAM. Mexico City, Mexico.

Nelson, B. W., C. A. C. Ferreira, M. F. da Silva, and M. L. Kawasaki. 1990. Endemism centres, refugia and botanical collection density in Brazilian Amazonia. Nature (London) **345**:714–716.

Nelson, G. 1973. Comments on Leon Croizat's biogeography. Systematic Zoology **22**:312–320.

Nicholls, A. O. 1989. How to make biological surveys go further with generalised linear models. Biological Conservation **50**:51–75.

Office of Geography. 1956. Mexico official standard names approved by the U.S. Board on Geographic Names. Department of the Interior, Washington, D.C., USA.

Owen, J. G. 1990. Patterns of mammalian species richness in relation to temperature, productivity, and variance in elevation. Journal of Mammalogy **71**:1–13.

Patterson, B. D. 1987. The principle of nested subsets and its implications for biological conservation. Conservation Biology **1**:323–354.

Patterson, B. D., and J. H. Brown. 1991. Regional nested patterns of species composition in granivorous rodent assemblages. Journal of Biogeography **18**:395–402.

Pearson, D. L., and F. Cassola. 1992. World-wide species richness patterns of tiger beetles (Coleoptera: Cicindelidae): indicator taxon for biodiversity and conservation studies. Conservation Biology **6**:376–391.

Peterson, A. T., O. A. Flores-Villela, L. S. León-Paniagua, J. E. Llorente-Bousquets, M. A. Luis-Martinez, A. G. Navarro-Sigüenza, M. G. Torres-Chávez, and I. Vargas-Fernández. 1993. Conservation priorities in Mexico: moving up in the world. Biodiversity Letters **1**:33–38.

Rabinovich, J. E., and E. H. Rapoport. 1975. Geographical variation of diversity in Argentine passerine birds. Journal of Biogeography **2**:141–157.

Ramírez-Pulido, J., R. López, C. Müdespacher, and I. Lira. 1982. Catálogo de los mamíferos de México. Editorial Trillas, Mexico City, Mexico.

Rapoport, E. H., G. Boroli, J. A. Monjeau, J. E. Puntieri, and R. D. Oviedo. 1986. The design of nature reserves; a simulation trial for assessing specific conservation value. Biological Conservation **37**:269–290.

Robertson, P. B. 1975. Reproduction and community structure of rodents over a transect in southern Mexico. Dissertation. University of Kansas, Lawrence, Kansas, USA.

Royal Statistical Society. 1985. GLIM 3.77. Royal Statistical Society, London, England.

Rzedowski, J. 1991. Diversidad y origenes de la flora fanerogámica de México. Acta Botánica Mexicana **15**:47–64.

SARH [Secretaría de Agricultura y Recuersos Hidráulicos]. 1980. Vademecum forestal mexicano. Dirección General de Información y Sistemas Forestales, Secretaría de Agricultura y Recuersos Hidráulicos, Mexico City, Mexico.

Scott, J. M., B. Csuti, J. D. Jacobi, and J. E. Estes. 1987. Species richness, a geographic approach to protecting future biological diversity. BioScience **37**:782–788.

Scott, J. M., B. Csuti, K. Smith, J. E. Estes, and S. Caicco. 1988. Beyond endangered species: an integrated conservation strategy for the preservation of biological diversity. Endangered Species Update **5**:43–48.

Scott, J. M., F. Davis, B. Csuti, R. Noos, B. Butterfield, C. Groves, H. Anderson, S. Caicco, F. D'Erchia, T. C. Edwards, J. Ulliman, and R. G. Wright. 1993. Gap analysis: a geographic approach to protection of biological diversity. Wildlife Monographs **123**.

SCT [Secretaría de Comunicaciones y Transportes]. 1987*a*. Mapa de carreteras del estado de Guerrero 1:600 000. Secretaría de Comunicaciones y Transportes, Mexico City, Mexico.

———. 1987*b*. Mapa de carreteras del estado de Oaxaca 1:800 000. Secretaría de Comunicaciones y Transportes, Mexico City, Mexico.

Terborgh, J. 1974. Preservation of natural diversity: the problem of 155 extinction-prone species. BioScience **24**:715–722.

Terborgh, J., and B. Winter. 1983. A method for siting parks and reserves with special reference to Colombia and Ecuador. Biological Conservation **27**:45–58.

UNEP [United Nations Environmental Program]. 1992. Draft convention on biological diversity. Conference for the adoption of the agreed text of the convention of biological diversity. UNEP/Bio.Div/Conf/L.2. United Nations Environmental Program, Nairobi, Kenya.

Vane-Wright, R. I., C. J. Humphries, and P. H. Williams. 1991. What to protect? Systematics and the agony of choice. Biological Conservation **55**:235–254.

Walker, P. A. 1990. Modelling wildlife distributions using a geographic information system: kangaroos in relation to climate. Journal of Biogeography **17**:279–289.

White, P. S., and R. I. Miller. 1988. Topographic models of vascular plants in the Southern Appalachian High Peaks. Journal of Ecology **76**:192–199.

Wright, D. H., and J. H. Reeves. 1992. On the meaning and measurement of nestedness of species assemblages. Oecologia **92**:416–428.

APPENDIX

Assemblages of endemic vertebrate species from Guerrero and Oaxaca, Mexico.

Order Family	Species
	AMPHIBIANS
	Assemblage 1
Anura	
Hylidae	*Hyla bogertae*
	H. echinata
	H. sabrina
	H. thorectes
	H. trux
	Ptychohyla ignicolor
Leptodactylidae	*Eleutherodactylus uno*
	E. syristes
	Assemblage 2
Anura	
Bufonidae	*Bufo occidentalis*
Hylidae	*Hyla altipotens*
	H. bistincta
	H. chaneque
	H. chryses
	H. erythromma
	H. hazelae
	H. juanitae
	H. melanomma melanomma
	H. mykter
	H. pellita
	H. pentheter
	H. pinorum
	Ptychohyla leonhardschultzei
Leptodactylidae	*Eleutherodactylus megalotympanum*
	E. mexicanus
	E. dilatus
	E. nitidus nitidus
Ranidae	*Rana omiltemana*
	R. sierramadrensi
	R. spectabilis
Caudata	
Ambystomatidae	*Rhyacosiredon rivularis*
Plethodontidae	*Bolitoglossa hermosa*
	B. macrinii
	B. riletti
	Thorius pulmonaris
	Pseudoeurycea anitae
	P. bellie belli
	P. mystax
	Thorius macdougalli
	T. minutissimus
	T. narisovalis
	Assemblage 3
Caudata	
Plethodontidae	*Pseudoeurycea conanti*
	Assemblage 4
Anura	
Hylidae	*Hyla crassa*
	H. miotympanum
Caudata	
Plethodontidae	*Pseudoeurycea cochranae*
	Assemblage 5
Anura	
Bufonidae	*Bufo marmoreus*
	B. preplexus
Hylidae	*Hyla smithii*
	H. sumichrasti
Ranidae	*Rana zweifeli*
	Assemblage 6
Anura	
Bufonidae	*Bufo gemmifer*
Hylidae	*Hyla sartori*
	Pachymedusa dacnicolor
	Triprion spatulatus reticulatus
Leptodactylidae	*Eleutherodactylus lineatus*
	E. silvicola
	E. spatulatus
Caudata	
Plethodontidae	*Bolitoglossa platydactyla*
Gymnophiona	
Caeciliaidae	*Dermophis oaxacae*
	Assemblage 7
Anura	
Hylidae	*Hyla cembra*
	H. siopela
Caudata	
Plethodontidae	*Nototriton adelos*
	REPTILES
	Assemblage 1
Squamata	
Polychridae	*Anolis taylori*
Colubridae	*Salvadora lemniscata*
	Assemblage 2
Squamata	
Anguidae	*Abronia bogerti*
Iguanidae	*Ctenosaura acanthura*
Phrynosomatidae	*Sceloporus edwardtaylori*
	S. macdougalli
Polychridae	*Anolis cuprinus*
	Ficimia ramirezi
	Thamnophils valida isabelleae
	Tantilla calamarina
	T. striata
	Tantillita brevissima
Elapidae	*Micrurus distans michoacanensis*
Viperidae	*Porthidium dunni*
Testudines	
Bataguridae	*Rhinoclemmys rubida perixantha*
	Assemblage 3
Squamata	
Gekkonidae	*Phyllodactylus lanei lanei*
	Phyllodactylus muralis
Iguanidae	*Cetnosaura pectinata*
	Enyaliosaurus clarki
Polychridae	*Anolis subocularis*
	A. isthmicus
Phrynosomatidae	*Sceloporus horridus oligoporus*
	S. pyrocephalus
	Urosaurus bicarinatus anonymorphus
	U. gadovi
Teiidae	*Cnemidophorus calidipes*
	C. communis communis
	C. guttatus immutabilis
	C. lineattissimus lividus
Colubridae	*Conophis vittatus vittatus*
	Leptodeira maculata
	Leptophis diplotropis diplotropis

APPENDIX. Continued.

Order / Family	Species
Colubridae	*Manolepis putnami*
	Pseudoleptodeira latifasciata
	Salvadora mexicana
	Sibon annulifera
	Symphimus leucostomus
	Toluca lineata
Elapidae	*Micrurus laticollaris laticollaris*
	M. ephippifer
Testudines	
Bataguridae	*Rhinoclemmys rubida rubida*
	Assemblage 4
Squamata	
Anguidae	*Mesaspis viridiflava*
	Celestus enneagrammus
Gekkonidae	*Phyllodactylus bordai*
	P. delcampoi
Phrynosomatidae	*Phrynosoma taurus*
	Sceloporus gadoviae
	S. horridus horridus
	S. internasalis
	S. ochoterenae
	S. utiformis
	S. salvini
	Urosaurus bicarinatus bicarinatus
Polychridae	*Anolis dunni*
	A. gadovi
	A. megapholidotus
	A. microlepidotus
	A. compressicaudus
	A. macrinii
	A. simmonsi
	A. nebulosus
Scincidae	*Eumeces ochoterenae*
	E. brevirostris
	Scincella gemmingeri
	S. silvicola
Teiidae	*Cnemidophorus costatus costatus*
	C. costatus zweifeli
	C. sacki gigas
	C. sacki sacki
	C. mexicanus
	C. parvisocius
Xantusiidae	*Lepidophyma radula*
Colubridae	*Conophis vittatus viduus*
	Ficimia ruspator
	F. variegata
	Geagras redimitus
	Leptodeira splendida bressoni
	Pseudoficimia frontalis
	Rhadinaea cuneata
	R. hesperia
	R. macdougalli
	R. omiltamana
	R. quinquelineata
	Salvadora bairdi
	S. intermedia
	Sibon zweifeli
	Sonora michoacanensis
	Tantilla bocourti bocourti
	T. coronadoi
	Trimorphodon tau latifascia
Leptotyphlopidae	*Leptotyphlops maximus*
Viperidae	*Crotalus basiliscus*
Testudines	
Kinosternidae	*Kinosternon integrum*
	K. oaxacae
	Assemblage 5
Squamata	
Phrynosomatidae	*Sceloporus jalapae*
Colubridae	*Geophis sieboldi*
	Rhadinaea taeniata aemula
	Tantalophis discolor
	Assemblage 6
Squamata	
Anguidae	*Abronia ornelasi*
	Barisia imbricata planifrons
	Mesaspis gadovii gadovii
Phrynosomatidae	*Sceloporus formosus scitulus*
	S. mucronatus omiltemanus
	S. spinosus
	S. stejnegeri
	S. formosus formosus
Polychridae	*Anolis liogaster*
	A. omiltemanus
	A. quercorum
Scincidae	*Eumeces brevirostris brevirostris*
	E. brevirostris indubitus
Xantusiidae	*Lepidophyma dontomasi*
	L. tuxtlae
Colubridae	*Geophis dubius*
	Pituophis deppei lineaticollis
	Rhadinaea fulvivittis
	Storeria storerioides
	Tantilla flavilineata
	Thamnophis chrysocephalus
	T. scalaris godmani
	Toluca conica
Viperidae	*Ophryacus undulatus*
	Sistrurus ravus exiguus
	Assemblage 7
Squamata	
Anguidae	*Abronia deppei*
	A. fuscolabialis
	A. mixteca
	A. oaxacae
	Mesaspis gadovi laevigata
Polychridae	*Anolis nebuloides*
	A. breedlovei
Phrynosomatidae	*Sceloporus cryptus*
	S. subpictus
Colubridae	*Geophis anocularis*
	G. dubius
	G. omiltemanus
	Tantilla oaxacae
	Toluca amphisticha
	T. megalodon
Viperidae	*Cerrophidion barbouri*
	Crotralus intermedius omiltemanus
	Sistrurus ravus brunneus
	Assemblage 8
Squamata	
Anguidae	*Abronia mitchelli*
Phrynosomatidae	*Sceloporus adleri*
Polychridae	*Anolis milleri*
Colubridae	*Rhadinaea bogertorum*
Tropidopheidae	*Exiliboa placata*
	Assemblage 9
Squamata	
Polychridae	*Anolis polyrhanchis*
Colubridae	*Geophis duellmani*
	G. sallaei
	Assemblage 10
Squamata	
Colubridae	*Cryophis hallbergi*
	Geophis russatus
	G. sallaei

APPENDIX. Continued.

Order Family	Species
BIRDS	
	Assemblage 1
Falliformes	
Phasianidae	*Dendrortyx macroura*
Passeriformes	
Tyrannidae	*Empidonax affinis*
Troglodytidae	*Campylorhynchus megalopterus*
Emberizidae	*Pipilo ocai*
	Atlapetes pileatus
Parulidae	*Geothlypis nelsoni*
	Ergaticus ruber
Corvidae	*Cyanolyca nana*
	C. mirabilis
	Assemblage 2
Caprimulgiformes	
Caprimulgidae	*Nyctiphrynus mcleodii*
Apodiformes	
Trochilidae	*Atthis heloisa*
Passeriformes	
Dendrocolaptidae	*Lepidocolaptes leucogaster*
Troglodytidae	*Thryothorus sinaloa*
Mimidae	*Melanotis caerulescens*
	Toxostoma ocellatum
Muscicapidae	*Ridgwayia pinicola*
	Catharus occidentalis
Emberizidae	*Oriturus superciliosus*
	Atlapetes albinucha
	Piranga erythrocephala
Vireonidae	*Vireo brevipennis*
	Assemblage 3
Passeriformes	
Troglodytidae	*Thryothorus felix*
Emberizidae	*Aimophila humeralis*
	Pipilo albicollis
	Melozone kieneri
	Assemblage 4
Piciformes	
Picidae	*Piculus auricularis*
Passeriformes	
Emberizidae	*Aimophila notosticta*
Vireonidae	*Vireo nelsoni*
	Assemblage 5
Apodiformes	
Trochilidae	*Calothorax pulcher*
Passeriformes	
Troglodytidae	*Campylorhynchus jocosus*
Emberizidae	*Aimophila mystacalis*
Vireonidae	*Vireo hypochryseus*
	Assemblage 6
Galliformes	
Cracidae	*Ortalis poliocephala*
Phasianidae	*Philortyx fasciatus*
Psittaciformes	
Psittacidae	*Amazona finschi*
Apodiformes	
Trochilidae	*Cynanthus sordidus*
Piciformes	
Picidae	*Melanerpes hypopolius*
Passeriformes	
Tyrannidae	*Tyrannus crassirostris*
Troglodytidae	*Hylorchilus sumichrasti*
Muscicapidae	*Turdus rufopalliatus*
	Assemblage 7
Trogoniformes	
Trogonidae	*Trogon citreolus*
Piciformes	
Picidae	*Melanerpes chrysogenys*
Passeriformes	
Emberizidae	*Passerina rositae*
	Granatelus venustus
	Cacicus melanicterus
Corvidae	*Cyanocorax sanblasianus*
	Assemblage 8
Strigiformes	
Strigidae	*Otus seductus*
Passeriformes	
Tyrannidae	*Deltarhynchus flammulatus*
Emberizidae	*Aimophila sumichrasti*
	Passerina lenclancherii
MAMMALS	
	Assemblage 1
Lagomorpha	
Leporidae	*Lepus flavigularis*
Rodentia	
Geomyidae	*Orthogeomys cuniculus*
Carnivora	
Mustelidae	*Spilogale pygmaea pygmaea*
	S. pygmaea australis
	S. pygmaea intermedia
	Assemblage 2
Marsupialia	
Didelphidae	*Marmosa canescens canescens*
	M. c. oaxacae
Insectivora	
Soricidae	*Notiosorex gigas*
Chiroptera	
Phyllostomidae	*Artibeus hirsutus*
	Choeronycteris harrisoni
Vespertilionidae	*Rhogeessa parvula*
	R. gracilis
	Myotis fortidens fortidens
Lagomorpha	
Leporidae	*Sylvilagus cunicularius pacificus*
Rodentia	
Sciuridae	*Spermophilus adocetus adocetus*
	S. annulatus annulatus
Heteromyidae	*Liomys pictus pictus*
Cricetidae	*Peromyscus banderanus banderanus*
	P. b. vicinior
	P. perfulvus perfulvus
	P. melanophrys melanophrys
	Sigmodon mascotensis
	Rheomys mexicanus
Dasyprotidae	*Dasyprocta mexicana*
	Assemblage 3
Chiroptera	
Vespertilionidae	*Rhogeessa alleni*
Rodentia	
Heteromyidae	*Liomys pictus plantinarensis*
	L. irroratus torridus

APPENDIX. Continued.

Order / Family	Species
	Assemblage 4
Lagomorpha	
Leporidae	*Sylvilagus cunicularius cunicularius*
	Lepus callotis callotis
Rodentia	
Heteromyidae	*Liomys pictus annectens*
	L. irroratus irroratus
Cricetidae	*Peromyscus thomasi thomasi*
	Sigmodon leucotis alticola
	S. alleni planifrons
	Assemblage 5
Insectivora	
Soricidae	*Cryptotis mexicana mexicana*
	C. goldmani goldmani
	C. mexicana peregrina
Rodentia	
Heteromyidae	*Liomys irroratus guerrerensis*
Cricetidae	*Peromyscus melanurus*
	P. megalops
	Sigmodon alleni vulcani
	Microtus fulviventer

Order / Family	Species
	Assemblage 6
Insectivora	
Soricidae	*Sorex ventralis*
Lagomorpha	
Leporidae	*Sylvilagus insonus*
Rodentia	
Cricetidae	*Peromyscus lepturus lepturus*
	P. melanocarpus
	Microtus umbrosus
	Assemblage 7
Insectivora	
Soricidae	*Cryptotis magna*
Rodentia	
Cricetidae	*Oryzomys caudatus*
	Peromyscus chinanteco
	P. lepturus ixtlani
	P. furvus
	P. thomasi cryophilus
	Microtus quasiater
	M. oaxacensis