

Determinants of diversity in a naturally fragmented landscape: humid montane forest avifaunas of Mesoamerica

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We used a published data set summarizing avifaunas of 31 montane patches of humid forest in Mesoamerica to analyze avian distributions with respect to site characteristics. This forest type was originally widespread in the lowlands, and became restricted to mountains during Pleistocene climatic changes. Hierarchical partitioning, a recently developed regression procedure, was used to examine independent factor effects. Total species richness, richness of Mesoamerican endemic species, richness of narrowly endemic species, and richness of habitat specialists were considered separately, each analyzed at three spatial scales. For total richness and Mesoamerican endemics, regional-level variables, notably latitude, were most influential. Narrow endemics exhibited more complex patterns, driven by foci both in western Mexico and in Costa Rica and western Panama. Historical factors are suggested to have contributed to this latitudinal pattern, such that the isthmuses of Tehuantepec and Panama acted as barriers to range expansion and peninsular effects catalyzed speciation, elevating numbers of endemic species. In contrast to many anthropogenic fragmentation studies, area and other local-scale patch attributes had little influence on avifaunas. This discrepancy may be related to fundamental differences in spatial and temporal scaling, with patterns uncovered herein more indicative of long-term community processes.

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Exploring the distribution of diversity is a central goal of ecology, serving as the basis for many questions regarding structure and function of communities. The relative importance of historic factors, species' autecology, species interactions, and abiotic factors has been examined in numerous ecosystems using diverse approaches (Culver 1969, Brown 1971, Johnson 1977, Lomolino 1984, Douglas and Lake 1994, Yu 1994). These studies typically examined diversity in single areas, and generally were restricted to single spatial scales. Increasingly-used landscape-level analyses (e.g., Bauer 1989, Oehler and Litvaitis 1996, Riitters et al. 1997) reveal patterns that vary widely across regions, such that patterns observed at one site may have little or no bearing on those in nearby areas. With differ-

ences in habitat quality and patch area, concomitant changes in the distribution of diversity might be expected, especially for endemic and restricted forms. Questions can then be formulated regarding the distribution of diversity across a landscape. What processes affect patterns of species richness? Do the same processes affect habitat specialists and endemic forms similarly? Do these processes operate differently at different spatial scales, or can large-scale effects be extrapolated from local dynamics? To answer these and other questions, detailed distributional data from multiple sites within a region are required.

For this study, data on the distribution of birds in montane patches of humid forest in Mesoamerica were used. Humid montane forest was defined as middle-

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Table 1. Summary of dependent and independent variables used in the analysis. Tot = total species richness, Res = richness of species restricted to humid montane forest, End = richness of species endemic to Mesoamerica, and Nar = richness of narrowly endemic species (known from ten sites or fewer). Independent variables are arranged from regional to local, where Lat = rank order of latitude, Elev = mean elevation, Dist = distance to nearest coastline, Cld = presence of cloud forest, Shp = shape index described in text, Area = patch area, and Num = number of distinct stands within patch.

Name	Tot	Res	End	Nar	Lat	Elev	Dist	Cld	Shp	Area	Num
TAMPS	103	14	8	0	31	2166	86	1	1341	25	1
HIDAL	136	27	15	1	29	708	15	1	3185	151	7
CVERA	175	41	23	2	27	3617	36	1	3230	163	4
TUXTL	104	24	14	2	22	1320	5	1	845	1	2
CUATR	172	10	5	0	14	2483	36	0	647	15	1
JUARE	154	38	22	1	20	2583	62	1	1843	362	1
FELIP	104	17	9	1	18	2817	71	0	870	37	1
ZEMPO	154	36	20	1	16	2250	61	1	1065	125	1
SCRIS	165	51	36	1	17	1650	50	1	1108	200	1
MONTE	166	51	36	1	12	1662	71	1	1230	75	1
SINDU	95	10	4	1	30	1817	27	0	2419	301	8
NAYJA	122	17	9	1	28	2666	20	0	3370	800	14
MICHO	113	14	8	0	23	1523	12	0	1625	350	2
GUERR	133	27	15	2	19	2510	14	1	1585	250	2
YUCUN	103	16	6	2	15	2217	28	0	1465	300	2
MIAHU	124	24	12	2	13	2700	10	0	1288	112	1
SOCON	155	56	37	2	10	1973	7	1	1708	87	1
TACAN	156	57	38	2	8	2424	25	1	798	89	1
TANCI	93	11	5	0	25	2952	69	1	777	16	1
TEMAS	91	11	6	0	26	3000	90	0	857	113	1
TAXCO	80	7	4	0	21	1613	72	0	1893	38	4
MALIN	74	7	3	0	24	2373	80	0	599	17	1
GUAPA	178	58	38	3	7	2809	21	1	2022	19	6
GUACU	183	59	39	2	11	2432	56	1	1353	58	1
GUAMI	181	58	38	1	9	2149	28	1	1625	125	1
HONDU	183	62	39	2	6	1891	23	1	678	1300	1
CRGUA	145	58	28	18	5	1442	10	1	871	350	1
CRTIL	170	79	40	28	4	1356	9	1	687	300	1
CRcen	195	97	54	41	3	2694	19	1	907	275	1
CRTAL	195	99	56	43	2	2921	12	1	852	250	1
WPANA	200	150	72	45	1	2045	9	1	1853	201	1

independent of area; Area, the area of the patch in square kilometers; and Num, the number of discernible fragments that constitute the patch.

We distinguished whether a patch was pure humid pine-oak forest or if there was associated cloud forest. These two habitats grade into one another in Mexico, typically along altitudinal gradients (Rzedowski 1986), and while the faunas of these two habitats are similar (Navarro 1992), they contain complementary species in some cases (Skutch 1967). Shp was calculated as $2A/ RP$, where A is the area of the patch, P is the perimeter, and R the radius of the circle with an area of A. Dist was used, not as a measure of isolation, but as an indirect measure of vegetation, because proximity to the coastline is often associated with relatively high humidities, and hence more mesic forests (Rzedowski 1986). Similarly, Lat and Elev were used as indirect measures of local climate, while Cld provided a more direct biological measure of local climatic conditions. Num was included to assess whether diversities were depressed owing to fragmentation, when "patches" were actually "archipelagoes" (after Burkey 1995).

The patches were arranged into three groups to examine the importance of spatial scaling. Regional-

scale analyses (Mesoamerica) were carried out using all sites. Because distinct floras and faunas are associated with different slopes, we examined separately the 19 sites located on the Atlantic slope. Furthermore, because the Isthmus of Tehuantepec corresponds to northern or southern range limits for many species, we examined separately the 13 sites south of the Isthmus (Central America).

The 31 patches extended from Sinaloa and Tamaulipas in northern Mexico south to western Panama, and varied in mean elevation from 708 m to > 3600 m (Table 1). Patch area ranged from < 1 to almost 1300 km², with a mean of 690 km². Distance to nearest coastline varied from 1 to 90 km, with a mean of 33 km. While several sites north of the Isthmus of Tehuantepec did not have associated stands of true cloud forest, all Central American sites did; therefore this variable was only useful at the regional scale.

A total of 335 species of birds was included in the database, based on Hernández-Baños et al. (1995). Waterbirds, migrants, vagrants, winter residents, and aerial foragers (e.g., swifts, swallows) were excluded, such that the data set contained only species dependent on humid montane forest as primary habitat. The data

represent a historical collection, with many records > 100 yr old, and hence likely summarize avifaunas prior to recent extensive anthropogenic perturbation. We used only actual occurrence records, excluding the “probable occurrences” of Hernández-Baños et al. (1995).

In addition to species richness for each site (i.e., all 335 species), three subsets were analyzed (Table 1): species ecologically restricted to humid montane forests (147 species), species endemic (sensu Peterson and Watson, in press) to Mesoamerica (101 species), and narrowly endemic (known from 10 patches or fewer) species (78 species) (Hernández-Baños et al. 1995). Separate analyses were conducted for each subset, regressing each against the seven independent variables. Loehle (1987) advocated the testing of many hypotheses concurrently, thereby minimizing effects of subjectivity on outcomes or interpretation of results.

Multiple regression techniques (typically stepwise algorithms) are usually employed to elucidate patterns of dependence and infer causality (Freemark and Merriam 1986, Blake and Karr 1987, but see Loman and von Shantz 1991, Knick and Rotenberry 1995 for robust alternatives). Several difficulties, however, are associated with using these methods with community-level data (Neter et al. 1985, Ludwig and Reynolds 1988, Chatterjee and Price 1991), and because ecological data rarely fulfill the assumptions their utility has been questioned (James and McCulloch 1990, Philippi 1993, Mac Nally 1996). Our aim in this study was to unravel interrelationships between independent variables, so we used hierarchical partitioning.

This statistical approach generates a more detailed and reliable basis for inferring causality in multivariate data sets (Chevan and Sutherland 1991, Christensen 1992, Mac Nally 1996). The aim of hierarchical partitioning is not identification of a single optimal submodel, nor does it generate a predictive equation. Rather, all possible regression submodels are calculated and arranged hierarchically to identify variables with high independent correlations with the dependent variable. In some situations, statistically significant independent effects can be suppressed by antagonistic joint effects. This technique is designed for such scenarios, converting antagonistic effects into negative joint contributions, effectively unmasking the independent contributions, which can be larger than the univariate squared partial correlation (Chevan and Sutherland 1991). Thus, for this class of investigation, hierarchical partitioning is superior to other multiple regression techniques, because it is a superset of other approaches.

Hierarchical partitions were run using programs written and generously provided by A. Chevan. All

graphs presented summarize hierarchical partitions, with variance explained equivalent to R^2 values. Although there currently is no way to assign statistical significance to the independent contributions of each explanatory variable (Mac Nally 1996), “significance” was regarded as the level corresponding to normal univariate levels; a 5% α level using a stepwise regression model (Anon. 1985). Significance values thus changed at different spatial scales as a function of diminishing sample size.

Results

Latitude was the single most important descriptor across all spatial scales and species groups examined (Fig. 2), although it had less influence on richness of narrow endemics (Fig. 2j, k). For total species richness, at all spatial scales, latitude was the most important factor (Fig. 2a–c). At the regional level (Fig. 2a), presence of cloud forest also was associated with increased total richness. This shift was driven both by high species richness in southern cloud forests, and by the relatively simple communities of humid pine-oak habitats in Mexico (Hernández-Baños et al. 1995). Once these high elevation, low diversity sites were removed, distance to coast became a significant descriptor for remaining (Central American) sites (Fig. 2c). All factors affecting species richness (latitude, distance to coast, presence of cloud forest) were regional-scale variables.

Richness of endemic species was related primarily to latitude and, at the regional scale, to the presence of true cloud forest (Fig. 2g–i). Narrow endemics showed no latitudinal pattern across the entire region (Fig. 2j) or for Atlantic slope sites (Fig. 2k), with higher numbers in southern Mexico and southern Costa Rica/western Panama. Variance explained by latitude tripled once sites north of the Isthmus of Tehuantepec were removed (Fig. 2l), owing to the clear concentration of narrow endemics in Costa Rica and Panama.

Species ecologically restricted to humid montane forests displayed a strong relation to latitude at the Mesoamerican scale (Fig. 2d). This effect resulted primarily from the paucity of habitat specialists in northern Mexico (Hernández-Baños et al. 1995). This relationship broke down at the Atlantic slope scale (Fig. 2e) as elevation became more important. Focusing on Central America (Fig. 2f), latitude and patch shape explained significant amounts of variance in richness of restricted species: more contiguous patches with simple edges contained more habitat specialists. This analysis was the only instance in which local-scale effects were found to influence avifaunal composition.

Discussion

Latitudinal gradients

The most important variable for all spatial scales and species groups was latitude. Latitudinal effects have been observed in diverse taxonomic groups in many geographic scenarios (Pianka 1966, Huston 1979, McCoy and Connor 1980, Stevens 1989, Kaufman 1995, Rosenzweig and Sandlin 1997). As many authors have noted, however, this effect is likely not due to latitude per se, but rather to more proximate factors that covary with latitude and affect the fauna and flora directly (e.g., variance in diel temperature, evapotranspiration rate, precipitation).

What is especially striking in our analyses is that, for the most part, latitude was the only important descriptor. If, indeed, local climatic factors related to latitude were the driving force behind the observed gradients, one would expect elevation and distance to coastline to mediate this pattern. In twelve separate analyses, distance to coastline and elevation were found statistically significant in only one case each, suggesting that local climatic factors were not the primary cause for the latitudinal gradient in Mesoamerican bird diversity. Regional climatic variation is consistent with the latitudinal gradient, but it doesn't explain the elevated diversities in southern Mexico.

A more parsimonious explanation is related to historic factors. The highland fauna of Mesoamerica is

constrained to the south by the Isthmus of Panama, and several workers have suggested that this lowland area may have acted as a bottleneck to dispersal, leading to a piling up of species on either side (Martin and Harrell 1959, Skutch 1967, Juvik and Scatena 1995). Rather than species "piling up," it is perhaps more realistic to imagine populations relatively isolated at the extreme of a species' range, with isolation provided by the peninsular situation potentially leading to differentiation and ultimately, speciation. Janzen (1967) demonstrated that, given the lower variation in diel and seasonal temperatures in the tropics, temperature gradients associated with topographic disjunctions functioned as highly effective barriers to dispersal (see also Huey 1978). Increased diversity would thus be expected to result primarily from concentrations of endemic and narrowly endemic species. Elevation or distance to coastline would not be expected to affect this pattern, and a similar gradient would be expected in southern Mexico on either side of the narrow, lowland Isthmus of Tehuantepec.

These expectations are validated in the distribution of high elevation birds in Mesoamerica. The distribution of narrow endemics fulfills the expectations, with one major center of diversification in Costa Rica and western Panama, and another centered on the Isthmus of Tehuantepec. Indeed, only when sites north of the Isthmus of Tehuantepec were removed did latitude become statistically significant for richness of narrow

Fig. 2. Summary of the results of 12 separate hierarchical partitions, showing the importance of seven independent variables in explaining variance in four dependent variables at three spatial scales. Black bars correspond to independent effects, and white bars to joint effects. Statistically significant independent effects are denoted by an asterisk. Vertical axes correspond to explained variance, equivalent to R^2 values. Independent variables are arranged from regional to local, where Lat = rank order of latitude, Elev = mean elevation, Dist = distance to nearest coastline, Cld = presence of cloud forest, Shp = shape index described in text, Area = patch area, and Num = number of distinct stands within patch.

endemics. At a finer scale, diversity of narrow endemics was high on both sides of the Isthmus of Tehuantepec in southwestern Mexico and Chiapas (Hernández-Baños et al. 1995, Peterson et al. 1998), with lower diversities further east and west. The pattern is also borne out in the region surrounding the Panamanian Isthmus, with elevated diversities of highland birds both east and west of the Isthmus of Panama, and lower diversities in northern South America (Renjifo et al. 1997).

This complex distribution of diversity has been found in other taxonomic groups in Mesoamerica. Duellman (1966) studied humid montane herpetofaunas, and noted higher diversities in mountains either side of the Isthmus of Tehuantepec, due largely to endemic hylid frogs. Simpson (1964) presented data that further substantiates the pattern (although he didn't discuss it), with the two centers of species richness of North American mammals closely associated with the Isthmuses of Tehuantepec and Panama. Wilson (1974) re-analyzed Simpson's (1964) data at a finer scale, and found foci of mammal species richness both east and west of the Isthmus of Tehuantepec. Elevated richnesses on either side of the Isthmus are also evident in butterfly faunas, with most of the richness due to endemic and narrow endemic species (Llorente-Bousquets and Escalante-Pliego 1992).

Incorporating previous data with our findings further validates the idea that diversity patterns in Mesoamerica do not result solely from climatological conditions and their indirect effects, but are sculpted in part by historical factors and their effects on speciation. Rather than a mechanistic explanation for latitudinal effects, this hypothesis explains deviations from the comparatively smooth gradients observed in other regions. This hypothesis could be readily tested using other taxonomic groups, with the prediction being that diversities of highland taxa would have foci centered on either side of the two isthmuses, with narrow endemics accounting for this increased diversity.

Diversity patterns and spatial scale

All but two of the relationships detected in this study involved regional-scale variables unrelated to characteristics of the patch itself. Deemphasizing patch-level factors provides an interesting counterpoint to studies of anthropogenically fragmented landscapes. Most of those investigations focus at smaller spatial scales, e.g., bird assemblages in habitat fragments within an agricultural matrix (Saunders et al. 1991). In many such studies, patch area is consistently found to be important, whereas this variable had no observed effect in the present study. One explanation is that this discrepancy results from fundamental differences in

spatial scaling of the studies: the smallest patch in our investigation corresponds to the largest in many fragmentation studies. Area and similar patch-level effects may be influential for smaller patches, but not once they exceed a particular size threshold. Given the typical size of anthropogenic fragments, theoretical investigations may be required to test this idea.

Alternatively, the differences may be related to the temporal scale of fragmentation. This ecosystem was fragmented over thousands of years rather than decades, and thus may be affected by processes that are not observable in the short-term (Holt 1993). Patch-scale characteristics such as area and isolation may be critical in determining local diversities in the short term, but over longer time periods may be superseded by other factors, such as disturbance regime and geographic context. To investigate this contrast more fully, more studies in naturally fragmented habitats are needed, especially at local/landscape scales.

The only group for which local effects were found to be important was the ecologically restricted species. These species are found only in humid montane forests, and therefore are presumably more sensitive to subtle changes in the habitat quality and quantity. If this effect is indeed true of this group of birds, it suggests that they would be ideal candidates for focused study for conservation-based applications.

Neotropical montane forests generally constitute important foci of endemism in birds and other groups (Wake 1987, Wege and Long 1995, Stotz et al. 1996, Renjifo et al. 1997). This evolutionary richness, coupled with the remote and inaccessible nature of many of these areas, suggests that the full diversity of these forests is yet to be discovered and fully appreciated. Indeed, even in relatively well-studied vertebrate groups such as birds and mammals, new species and even genera continue to be discovered in Neotropical montane forests (e.g., O'Neill and Graves 1977, Robbins et al. 1994, Albuja and Patterson 1996, Stiles 1996). Being altitudinally restricted, these forests naturally are limited in their extent, and may not have the resilience of many lowland habitats. They are therefore, extremely vulnerable, and represent some of the most endangered ecosystems in the region (Collar et al. 1992, Stotz et al. 1996, Renjifo et al. 1997).

Existing inventories, while valuable for regional scale analyses such as those presented herein, are frequently inadequate for more specific inquiries. The analyses conducted here are concerned primarily with comparing relative richnesses, but for investigations requiring absolute measures of known reliability, current data are insufficient, particular for small mammals and bats (Timm, pers. comm.). Additional fieldwork is required, both to revisit known localities to update historic inventories, and to add new localities.

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