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Biological Conservation 111 (2003) 283–303

BIOLOGICAL
CONSERVATION

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Long-term consequences of habitat fragmentation—highland birds in Oaxaca, Mexico

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Received 10 April 2002; received in revised form 20 August 2002; accepted 25 August 2002

Abstract

Studies of habitat fragmentation have been restricted primarily to anthropogenically-altered habitats, with most research conducted 60–90 years post-fragmentation. It is unclear whether patterns in older systems concur with results from these dynamic landscapes, and hence the long-term viability of populations inhabiting habitat fragments remains largely unexplored. I focused on resident birds in fragments of humid pine-oak forest in Oaxaca, southern Mexico, isolated over 5000 years ago by climate-change. Seventeen fragments, ranging from 2 ha to over 150,000 ha were sampled in 1997 and 1998 yielding 141 species, of which 60 residents were used for analysis. Avian assemblages exhibited a highly nested structure and, with several notable exceptions, assemblages of birds in low-richness fragments were predictable subsets of those in more diverse fragments. Patch-scale factors—area, shape, elevation, habitat diversity and fractal dimension of edge—all exerted strong univariate influence on avian richness but were so closely inter-related that none had a significant independent effect. Thus, larger fragments were more complex in shape, included higher peaks, supported more diverse forests, and contained higher diversities of resident species. In contrast, the landscape-scale index used—distance from nearest large fragment (>50,000 ha)—had little effect on richness. This was reinforced by species-level analyses—one species was significantly influenced by isolation, compared with 31 species that displayed significant minimum-area distributions, restricted to patches larger than a particular threshold value. In terms of autecology, vagility, relative abundance and elevational breadth were closely related to distribution—those species with greater mobility, higher abundances and broader elevational tolerances were consistently more widespread. I suggest that more abundant species were less prone to extinction initially, more vagile species were better dispersers and species with broader elevational tolerances more likely to be successful colonists. As with previous research from older landscapes, patch-scale factors were consistently found to be influential, with high quality fragments supporting diverse communities regardless of landscape context. This suggests that the influence of landscape-scale factors noted in younger, anthropogenically fragmented systems may be transitory, overwhelmed by patch-scale factors with time. Which patch attributes are most influential could not be resolved, however, indicating that even thousands of years after fragmentation, they affect diversity patterns in concert. Rather than differentiating effects of area from habitat heterogeneity and other patch-level factors, I advocate resource-based approaches to understand and manage diversity in habitat fragments.

Keywords: Neotropical; Habitat diversity; Patchy environment; Temporal scale; Montane

1. Introduction

Distribution patterns of organisms inhabiting habitat fragments have been the focus of considerable scientific attention, resulting in an extensive literature on the biological consequences of fragmentation. Most studies have been conducted in anthropogenically-altered landscapes less than 100 years after fragmentation (Watson, 2002a), and a detailed understanding of the short-term responses of communities to fragmentation is emerging. Hierarchical patterns are commonly exhibited, with patch area, habitat diversity and degree of isolation typically identified as key determinants of richness (Saunders et al., 1991; Renjifo, 1999; Graham and Blake, 2001; Lee et al., 2002; Tscharntke et al., 2002). This progress notwithstanding, there have been few studies of landscapes fragmented by natural processes thousands of years ago, and the long-term effects of fragmentation are relatively unknown (McGarigal and Cushman, 2002). It is unclear whether patterns in older systems concur with those of recently modified habitats, and hence the future viability of populations inhabiting anthropogenic fragments remains largely unknown.

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PII: S0006-3207(02)00271-9

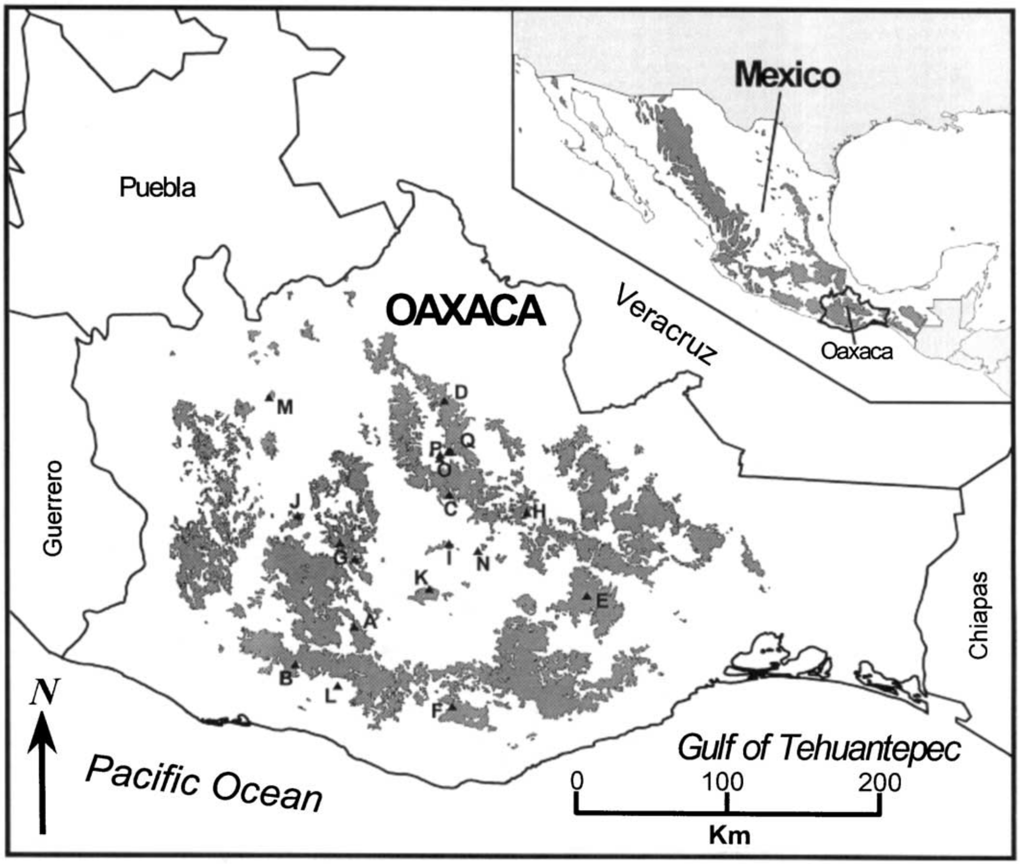

Fig. 1. Map of the study area, showing the distribution of montane humid forest including both humid pine-oak forest and cloud forest (the two habitats cannot be distinguished at this scale). Inset shows regional extent of habitat along both coastal ranges and the trans-volcanic belt in Mexico. Fragments are labeled in descending order of area, where A = Sierra de Yucuñacua (159,246 ha), B = Sierra de Miahuatlán-west (141,752 ha), C = Cerro San Felipe (120,189 ha), D = Sierra de Juárez (72,737 ha), E = Cerro Piedra Larga (68,932 ha), F = Sierra de Miahuatlán-east (31,582 ha), G = Sierra de Cuatro Venados (30,122 ha), H = Sierra de los Mixes (northern section; 11,334 ha), I = Cerro Labrador (9,131 ha), J = Cerro Peras (3,552 ha), K = Piedra del Sol (1,013 ha), L = Piedra de Leon (252 ha), M = Asunción Nochixtlan (91 ha), N = Santiago Matatlán (74 ha), O = Ixtlán (60 ha), P = El Punto (6 ha), Q = San Pablo Guelatao (2 ha). Names correspond to the names of the mountain ranges, peaks, or for the latter five fragments, nearest towns.

One class of naturally-fragmented landscapes includes altitudinally-restricted patches of habitat previously widespread in the Caenozoic and early Pleistocene, fragmented by climatic change in the mid-late Pleistocene (Simpson, 1974; Haper et al., 1978; Riebesell, 1982; Hadley, 1987). Most research conducted in these systems treated these relictual patches as ‘‘sky islands’’ and examined patterns of species distribution relative to ‘‘island’’ attributes (e.g. Brown, 1971; Johnson, 1975; see Watson, 2002a for full discussion). Indeed, most ecological studies in these landscapes were conducted more than 20 years ago and since that time, many new techniques have been developed and applied to geographical ecology. The burgeoning disciplines of geographic information systems, remote-sensing, and landscape ecology are matched with new methods for measuring physical and vegetative attributes of landscapes, and robust regression-based techniques to analyze these data. My aim in this investigation is to apply some of these tools to a naturally fragmented landscape to explore the detailed responses of faunal assemblages to habitat fragmentation over the long term.

The humid montane forests of Mesoamerica represent a naturally fragmented landscape, being widespread throughout lowland areas during the mid–late Pleistocene (Martin and Harrell, 1959). In a regional-scale study of montane forest avifaunas of Mesoamerica (Watson and Peterson, 1999), latitude and other regional-scale variables were found to exert the greatest influence on the distribution of avian diversity, supplanting patch-scale attributes such as area and isolation. The smallest fragment in this earlier study was approximately 1 km^2, and we suggested that while area had little explanatory power at the regional scale, area and other patch-scale effects may become important for smaller fragments.

In this study, I extend analysis of Mesoamerican forest avifaunas to local and landscape scales and explore relationships between fragment attributes and species richness. I assess whether there is a direct effect of area per se, or solely indirect influences via habitat heterogeneity or other patch-scale attributes. I also examine levels of nestedness and evaluate patterns of selective extinction and possible secondary recolonization. In addition to these patch-scale analyses, I adopt a species-level approach, exploring determinants of distribution in terms of autecological attributes of species: vagility, habitat preference and the three main macroecological variables (abundance, range size and body mass; Brown, 1995). A novel analytical method was devised to evaluate the importance of patch area and isolation in sculpting the distribution of resident bird species, allowing the relative importance of patch- and landscape-scale factors to be evaluated and critical thresholds to be estimated. I compare results of this study with general findings from anthropogenically-fragmented systems, commenting on the ecological and applied consequences of fundamental differences in temporal scaling. I detail the biogeographic and systematic issues affecting montane birds and highland biota in the region, and the implications for their conservation and management. Finally, I suggest that findings from naturally fragmented landscapes may provide valuable insight into the future viability of recently fragmented habitats, improving our ability to understand and preserve these systems.

2. Study area

This study was conducted in fragments of humid pine-oak forest in the state of Oaxaca, southern Mexico (Fig. 1). This habitat ranges from the highlands of northern Mexico south along the mountainous spine of Mesoamerica to Nicaragua, grading into oak-dominated cloud forests that extend to South America (Miranda and Sharp, 1950). Humid pine-oak forests are dominated by *Pinus*, *Quercus*, *Liquidambar*, *Alnus,* and other genera of Nearctic affinities (Leopold, 1950; Rzedowski, 1986). This habitat is typically associated with areas of medium to high rainfall (600–1200 mm annually) and cool-temperate climates (10–20 °C), and can withstand severe frosts (Gómez-Pompa, 1973; Toledo, 1982).

Table 1
Classification system used to characterize the diversity of vegetation in humid pine-oak forest fragments, after Johnson (1975)[a]

Class	Vegetation type
Primary habitats	Pure stands of pine Stands of pine saplings Pure stands of mature oak Pure thickets of young oak Fir (*Abies* sp.) forest Stands of alder (*Alnus* sp.)
Associated habitats	Bunch grasslands Moist riparian gulleys Lauraceous canopy trees
Understorey	Madroño (*Arbutus* sp.) Thick shrub layer Grassy ground cover Bracken (*Pteridium* sp.) Tree ferns (*Cyathea* sp.)
Micro-habitats	Mistletoe (Loranthaceae) Rocky outcrops Epiphytes

[a] Each of these habitat features was scored as absent (0), present (1), or abundant (2) for every fragment, and added to yield a composite measure of vegetation diversity.

Palynological data and analyses of pack rat (*Neotoma* spp.) middens reveal that humid pine-oak forests were more widespread historically in North America (Martin, 1963; Toledo, 1982). Archaeological studies of human settlement in the Oaxaca Valley have included detailed analysis of fossil pollen samples and microfossils (Schoenwetter and Smith, 1986), permitting a relatively complete reconstruction of the region's vegetational history. From the mid-Cenozoic until 15,000 years ago, the valley was dominated by humid pine-oak forest. In the following hypsithermal period (commencing 9000–7000 years ago), regional climates became consistently warmer and drier (Lorenzo, 1969; Ericson and Wollin, 1970) and this cool-temperate habitat migrated upslope, replaced in the intervening valleys by tropical evergreen forest and thorn-scrub (Smith, 1978; Schoenwetter and Smith, 1986; discussed in more detail in Watson, 1999a). Evidence from responses of coniferous forest to recent climatic fluctuations (Bergeron et al., 1997; Allen and Breshears, 1998) suggests this response may have been quite rapid, in contrast to gradual shifts typically associated with climate-change (e.g. McDonald and Brown, 1992). This process resulted in two large remnants of humid pine-oak forest associated with the mountain ranges forming the northern and southern boundaries of the Oaxaca Valley. Between 7000 and 5000 years ago, humid pine-oak forest was completely restricted to mountainous areas (Smith, 1978), and its distribution has remained essentially unchanged (Fig. 1).

Today, humid pine-oak forests occur primarily in the two mountain ranges of southern Mexico: the Sierra Madre Oriental and the Sierra Madre del Sur, with smaller patches associated with intervening highlands. The elevational extent of this habitat varies with rainfall and slope, typically descending to lower elevations on the coastal sides of mountain ranges (1000 m, occasionally lower) and grading into dry pine-oak forest at 1500–2000 m on interior slopes (Binford, 1989). While there has been additional habitat loss from anthropogenic activities, most of this is small scale harvesting which has been occurring for at least 9000 years (Flannery, 1986). Large-scale commercial logging is uncommon given the inaccessible location of most forests, restricted largely to subsistence collecting of firewood by local communities (personal observation).

3. Methods

Sampling was carried out in most accessible mountain ranges: the Sierra de Yucuñacua, Sierra de Cuatro Venados and the Sierra de Miahuatlán comprising the southern range, and the Sierra de Juárez, Cerro San Felipe, and the Sierra de los Mixes (Zempoaltepec) comprising the northern range. In addition, three isolated massifs in the Oaxaca Valley were sampled: Cerro Labrador, Piedra del Sol, and Cerro Piedra Larga (the latter by A.T. Peterson and others in 1995), constituting the first biological surveys for these areas. Finally, several small fragments were sampled, both between the two ranges in the valley interior and in outlying areas beyond the main mountain ranges (Fig. 1).

3.1. Fragment attributes

Pine-oak forests are variable, and within-patch habitat heterogeneity often exceeded between-patch differences. Quantitative approaches traditionally used to categorize vegetation in fragmentation studies (e.g. Watson et al., 2000) were therefore inappropriate, since any samples would be unrepresentative of the entire patch. To assess habitat heterogeneity at the fragment scale, I adopted a qualitative measure of habitat diversity (after Johnson, 1975). Seventeen micro-habitats and habitat features were identified with reference to appropriate sources (Leopold, 1950; Miranda and Sharp, 1950; Gómez-Pompa, 1973; Rzedowski, 1986), and scored as either absent (0), present (1), or well represented (2) in each fragment (Table 1). These scores were compiled for each fragment to produce an index of vegetation diversity (*Veg*), with a maximum possible value of 34.

Fragment boundaries were identified using a high resolution vector map produced by the Comisión Nacional para el Estudio y la Concervacion de la Biodiversidad (Anonymous, 1998), based on Landsat Thematic Mapper data collected in 1993 and geo-referenced localities of known vegetation type. The following metrics were then measured using ArcView, version 3.1: fragment area (*Area*), to the nearest hectare; maximum elevation (*Elevation*); and isolation (*Isolation*), measured in terms of distance in kilometers to the nearest large fragment (corresponding to the five fragments greater than 50,000 ha; after Lomolino et al., 1989; Lawlor, 1998). Two additional fragment attributes were computed using Fragstats version 2.0 (McGarigal and Marks, 1995) and a rasterized version of the map with a pixel dimension of 130m (smaller pixel sizes were not tractable given the areal extent of the study area). Fragment shape (*Shape*) was calculated by dividing patch perimeter by the square root of patch area, adjusted using a square standard to remove area effects, and fractal dimension of the fragment edge (*Edge*) was double the logarithm of patch perimeter divided by the log of patch area, adjusted to correct for perimeter bias (McGarigal and Marks, 1995 and references cited therein). Values for all six independent variables are summarized in Table 2.

Table 2
Summary of variables used in analysis of avian richness in naturally fragmented forest patches in Oaxaca, Mexico, ranked by patch area[a]

Fragment	Area[b] (Ha)	Edge	Elev (m)	Isol[b]	Shape[b] (km)	Veg	Rich_FR	Rich_HS
A	159246	1.175	3050	0.21	6.397	19	47	19
B	141752	1.195	2550	0.21	7.842	10	48	22
C	120189	1.206	3230	0.50	8.591	22	51	27
D	72737	1.197	3250	0.50	7.438	18	53	26
E	68932	1.139	2520	9.05	4.104	17	38	17
F	31582	1.156	2450	2.04	4.608	17	56	28
G	30122	1.201	2600	1.97	7.086	27	54	25
H	11334	1.161	2400	1.63	4.465	18	36	18
I	9131	1.117	2650	28.91	2.759	15	24	17
J	3552	1.120	2960	14.63	2.901	14	27	14
K	1013	1.063	2040	3.27	1.782	8	15	3
L	252	1.030	2500	59.17	1.225	9	6	1
M	91	1.063	1220	4.33	1.680	6	1	0
N	74	1.043	2080	4.28	1.333	9	10	3
O	60	1.000	2100	14.15	1.000	8	2	0
P	6	1.038	2000	5.26	1.296	10	10	2
Q	2	1.000	1720	0.57	1.000	3	0	0

[a] Area = total area of the forest fragment to the nearest hectare, Edge = fractal dimension of fragment edge, Elev = Maximum elevation in fragment, Isol = linear distance from nearest mountain range, Shape = fragment shape (larger values for more complex shapes), Veg = index of vegetation diversity described in Table 1. Rich_FR is he richest of forest residents in each fragment, and Rich_HS the richness of habitat specialists restricted to humid pine–oak forests.

[b] Raw values given here were transformed (natural logarithm) prior to analysis.

3.2. Avian data

Sampling was carried out over 2 years during the peak breeding season for resident bird species; April–June 1997 and May–June 1998. Larger patches were sampled during both years and visitation order randomized prior to sampling. Censusing was carried out in pre-determined sampling intervals (pre-dawn until midday, midday until dusk) by walking throughout the forest, both on and off trails, being sure to take a different route each period. During each sampling period, all species seen or heard were noted. Vocalisations were recorded, both for immediate playback to confirm species identities, and for subsequent verification. A results-based stopping rule was used to judge when a site had been censused adequately (Peterson and Slade, 1998; Watson, 1999a), ensuring all fragments were sampled to the same degree of completeness. Sampling was terminated only after two consecutive sampling periods in which a total of zero or one new species was added, resulting in 9–11 sampling periods (i.e. approximately 5 days of continuous censusing) for each inventory in the larger patches, and 3–7 sampling periods for the smaller patches. While the data matrix was initially augmented with historic records from museum specimens and published records (see Watson, 1999a), this contributed fewer than 5% of the inventory records due to the paucity of detailed inventories from the highlands in this region (Binford, 1989). Full analyses run with both datasets yielded the same qualitative results, so all data and analyses presented here are derived solely from field inventories (see Watson, 1999a for historic records and additional analyses).

Because the primary focus of this study is on landscape and patch-level effects, I restricted inquiry to those species for which humid pine-oak forest is primary habitat year-round. Thus, prior to analysis, I removed all migrants, waterbirds, transients, and species for which humid pine-oak forest is not considered primary habitat (after Binford, 1989; in litt.). Accordingly, only those 60 species dependent on humid pine-oak forest as their primary habitat year-round were included in analyses ("forest residents"; Table 3). A subset of this group was classified as "habitat specialists"—those 30 species dependent on humid pine-oak forest throughout the year that do not range into adjacent dry habitats nor occur solely in associated cloud forests (after Binford, 1989; Navarro-Sigüenza, 1992; Table 3). In addition to tallying up richness for each fragment, distributional data were summarised for each of the 60 forest residents by summing the number of fragments in which the species was recorded, from a maximum of 17 (i.e. recorded in all fragments) to a minimum of 1 (recorded in a single forest patch). This index provides a useful range-based measure of rarity, corresponding closely with other measures used by ornithologists (summarised by Gaston, 1994).

3.3. Autecological indices

Vagility is difficult to measure empirically and has typically been restricted to single species studies (Pradel, 1996). Many of the species examined here are poorly known and in the absence of banding and dispersal studies, the best information available is expert opinion. Species were ranked independently on a five-point scale (Table 4) by three ornithologists with extensive field knowledge of these taxa (not including the author). Standardised means were calculated for each of the three rankings and an overall mean calculated for each species, standardised to allow reference to the descriptive five-point scale (Table 4).

Avian abundance has also proven difficult to quantify (Emlen, 1971; Verner, 1985; Pendleton, 1995), and while point counts are often used, they are confounded by differing detectabilities and many other factors (Schieck, 1997; Verner and Milne, 1990). Capture-recapture techniques can be useful, but have numerous shortcomings when applied to community-level estimates of abundance (Remsen and Good, 1996). Mapping individual territories is arguably the most accurate method (Dawson, 1981; Svensson, 1981; Muller, 1987; but see Best, 1975), but is time-intensive and useful only for birds singing on established territories—a subset of most forest avifaunas (Emlen, 1971). Frequency of occurrence (i.e. number of times a species is recorded within a given site) is known to be closely allied to relative abundance (after Dawson, 1981; Verner, 1985) but is less prone to many of these confounding factors and can be readily derived from inventory data. Using inventories from all fragments to calculate this index would compromise the independence between occurrence and patch occupancy (Wright, 1991), so only data from four large fragments were used (Sierra de Cuatro Venados, Cerro San Felipe, Sierra de Miahuatlán-east and Sierra de Miahuatlán-west; Fig. 1). For every species recorded in these fragments, the number of samples in which it was recorded was divided by the total number of sampling periods (nine, ten or eleven). These values were computed separately for the four fragments and all non-zero values averaged to generate an estimate of relative abundance, based on sites in which it had been recorded. Given that a single record during a 6-h sampling period qualified as a presence, this estimate generated a conservative estimate of relative abundance, emphasizing subtle differences between those species that were seldom encountered and present in low numbers (Verner, 1985).

Other indices were derived from published sources. Habitat breadth and elevational range were taken from Parker et al. (1996), reflecting species tolerances throughout their distributional range. Habitat breadth was calculated by summing the total number of habitats from which the species is known—habitats

Table 3
Summary data for 60 forest residents recorded in humid pine–oak forest fragments in Oaxaca, Mexico

Scientific name	Class	Patch	Vagility	Abund.	Hab	Elev	Range	Mass	Min area
Dendrortyx macroura	H, CF	8	1.7	0.37	2	19	4.6	350	3552
Columba fasciata	PO	8	4.4	0.67	3	27	81	315	NS
Hylocharis leucotis	PO	10	4.2	0.74	2	22	18.1	3.7	NS
Amazilia beryllina	PO	6	3.5	0.56	4	16	26.8	4.5	NS
Lampornis amethystinus	H, CF	9	2.9	0.55	2	21	11.2	6	NS
Lampornis clemenciae	H	7	3.5	0.61	2	19	12.1	6.2	11 334
Lamprolaima rhami	H, CF	5	2.4	0.11	2	20	6.5	9.2	ID
Eupherusa cyanophrys	CF	2	1.2	0.10	2	19	0.4	4.3	ID
Eugenes fulgens	H, CF	8	3.6	0.44	3	20	18.7	9.6	5259
Trogon mexicanus	PO	11	2.8	0.95	3	19	13.4	70	3552
Trogon elegans	PO	3	2.8	0.33	2	25	21.5	78	ID
Aulacorynchus prasinus	CF	7	3.1	0.35	2	30	12	180	30 122
Melanerpes formicivorus	PO	11	5.0	0.59	2.5	33	52.2	85	NS
Picoides villosus	PO	8	3.3	0.71	3	25	56	42	9131
Colaptes auratus	PO	9	3.8	0.86	4	35	39	122	9131
Lepidocolaptes leucogaster	PO	9	2.4	0.63	2	30.5	12.2	32	NS
Lepidocolaptes affinis	H, CF	9	2.8	0.80	3	19	35	35	3552
Pachyramphus major	CF	6	1.3	0.31	3.5	15	13.8	21	30 122
Mitrephanes phaeocercus	PO	9	3.8	0.76	2.5	30	45.2	8.5	3552
Contopus pertinax	PO	11	4.1	0.74	3	25	13	27	NS
Empidonax affinis	H	8	3.1	0.55	2	22	13.2	11.5	NS
Empidonax occidentalis	H	9	3.8	0.72	3	21.5	11.8	12.5	3552
Vireo plumbeus	PO	10	2.8	0.55	2	21	32	17	NS
Vireo huttoni	PO	11	2.4	0.95	3	25	35.7	13	3552
Vireolanius melitophrys	H	6	2.4	0.11	2	26.5	6.8	30	31 582
Cyanocitta stelleri	PO	12	3.3	0.95	2	27	47.3	90	NS
Poecile sclateri	H	4	2.8	0.39	2	24	15.9	9.9	ID
Troglodytes brunneicollis	H, CF	9	2.4	0.61	2	25	16.2	12	3552
Henicorhina leucophrys	H, CF	6	2.1	0.50	2	21	34	16	11 334
Myadestes occidentalis	PO	11	2.8	1.00	3	21.5	14.1	38	3552
Catharus aurantiirostris	H, CF	4	3.5	0.50	5	19	22	27	ID
Catharus occidentalis	H	8	2.4	0.84	2	22	13	30	NS
Catharus frantzii	H, CF	9	2.4	0.79	2	18.5	9	28	3552
Turdus infuscatus	H, CF	3	2.8	0.44	2	22	9.1	85	ID
Turdus migratorius	PO	9	3.5	0.95	3	28	34.2	72	3552
Ridgwayia pinicola	H	5	3.5	0.53	2	13.5	13	75	ID
Melanotis caerulescens	PO	12	3.1	0.84	3.5	32	13.1	82	3552
Ptilogonys cinereus	PO	12	5.0	0.84	2	21	12.7	37	6
Peucedramus taeniatus	PO	9	3.5	0.71	2	14	20.2	10.2	91
Parula superciliosa	PO	10	3.1	0.89	2	25	14.9	9	3552
Dendroica gracei	PO	5	2.6	0.40	2	22	12.9	8	ID
Geothlypis nelsoni	H	5	1.9	0.33	1.5	11	8.8	10	ID
Ergaticus ruber	PO	7	2.4	0.63	2	11	10.4	8.2	11 334
Myioboris miniatus	H, CF	9	2.4	0.97	3	19	22.6	9.5	3552
Basileuterus belli	H, CF	8	2.4	0.79	2	18	11.2	10.3	11 334
Chlorospingus ophthalmicus	H, CF	5	2.4	0.61	2	15	59	20	ID
Piranga flava	PO	11	2.4	0.50	6	24	53.3	40	5.3 km[a]
Piranga erythrocephala	H	5	2.4	0.40	2	17	11.8	18	ID
Euphonia elegantissima	H, CF	10	3.5	0.54	3	15	15	15	NS
Diglossa baritula	H, CF	6	2.6	0.59	3.5	18.5	8.5	9	30 122
Atlapetes pileatus	H	11	2.8	0.45	2	21	10.8	22	3552
Buarremon brunneinucha	H, CF	9	2.1	0.83	3	24	37.2	42	3552
Pipilo ocai	H	8	2.4	0.43	2	22.5	4.4	45	3552
Pipilo erythrophthalmus	PO	13	3.3	1.00	5	35	26.7	38	NS
Junco phaeonotus	PO	8	2.8	0.84	2	31	18.7	18	11 334
Pheucticus melanocephalus	PO	10	4.2	0.95	2	22	10.4	47	5259
Icterus graduacauda	H, CF	10	3.5	0.76	4	21	10	55	NS
Loxia curvirostra	H	4	5.0	0.11	2	33	18.1	41	ID
Carduelis notata	PO	6	4.0	0.34	4	22	15.2	10	NS
Coccothraustes abeilli	H, CF	5	1.9	0.20	2	23	12.4	48	ID

Class = habitat classification of each species (based on Binford, 1989), where PO = arid and humid pine-oak forest, H = humid pine-oak forest specialist and CF = cloud forest. Patch = number of patches in which species was recorded; Vagility = the index of vagility described in Table 4; Abund = estimate of relative abundance derived from frequencies of occurrence in the four largest patches; Hab = the number of habitat types frequented by the species (half values are for marginal habitats, from Parker et al., 1996); Elev = elevational range in 100 m (taken from Parker et al. 1996); Mass = body mass of species in grams (absolute value given here, ranked for analysis) and Range = latitudinal extent within which species are present year-round (in degrees); Min. area is provided for those species found to exhibit significant minimum-area distributions, and refers to the smallest patch in which a species occurred (in hectares). ID = insufficient data for analysis and NS = no significant relationship. [a] This is the only species exhibiting a significant maximum-isolation pattern, and was restricted to fragments less than 5.3 km from the nearest mountain range. Scientific names and order follows AOU (1998)

Table 4
Classification system used to rank forest residents according to vagility

Rank	Name	Description
1	Sedentary	Very limited movements—wholly restricted to single forest patch
2	Occasional	Limited movements, but may occasionally move across unsuitable habitat to adjacent montane forest patch
3	Intermediate	Large home ranges within forest patch, dispersing to nearby patches; also capable of longer-distance dispersal through unsuitable habitat
4	Mobile	Readily able to move large distances through unsuitable habitat
5	Nomadic	Nomadic or transient species that moves large distances routinely (e.g. tracking ephemeral food source)

considered typical were given a score of one, while marginal habitats were given a score of 0.5. Body masses of birds were extracted from published accounts (primarily Stiles and Skutch, 1989; Dunning, 1993; Curson et al., 1994) and specimen data (KU Natural History Museum). Actual values are provided (Table 3), but these data were ranked prior to analysis. Finally, distributional ranges of species were quantified by scoring the latitudinal extent within which the species are year-round residents (after Brown, 1995), using published accounts of species (Stiles and Skutch, 1989; Curson et al., 1994; Howell and Webb, 1995; Isler and Isler, 1999).

3.4. Statistical analyses

Distribution patterns of species inhabiting habitat fragments are often highly non-random—assemblages of species inhabiting low-diversity patches are frequently predictable subsets of high-diversity patches—generating a nested arrangement of species distributions. Nestedness was quantified using the ‘‘Nestedness Calculator’’ program developed by Patterson and Atmar (1986), comparing the data matrix to a perfectly nested arrangement with departures classed as ‘‘holes’’ (unexpected absences) or ‘‘outliers’’ (unexpected presences; after Cutler, 1991). Matrix ‘‘temperature’’ was calculated, with a maximally packed, perfectly nested matrix having a temperature of 1. Statistical significance was determined by comparing the matrix to 100 random arrangements of the data (Cutler, 1991) approximating a normal distribution, using a t-test to calculate the probability of the observed pattern being due to chance. Analyses were run for the complete data set of 60 forest residents and for the 30 habitat specialists. Given that humid pine-oak forests are known to have split first into two large patches (corresponding to the two dominant mountain ranges) prior to contracting to their present-day distribution (Smith, 1978; Schoenwetter and Smith, 1986), the matrix was subdivided into two geographic areas for separate analysis—northern mountain ranges and associated fragments, and southern ranges and fragments.

Best subsets regression was used to identify the optimal combination of independent variables to explain variation in species richness. The ‘‘best’’ model was selected with reference to maximum adjusted R^2 values and minimum value of s (an estimate of σ, the standard deviation about the regression surface; Garside, 1971). In addition, attention was given to the value of C_P, or Mallows’ statistic, values higher than the number of parameters in the model (in this case, 6) indicating a lack of fit of data to the model and decreased predictive power (Chatterjee and Price, 1991). I also used hierarchical partitioning to quantify the influence of each independent variable on the response term (Chevan and Sutherland, 1991; Mac Nally, 1996). All 64 (2^6) possible regression submodels were calculated using the program ALLREG, and then analyzed using HIERPART (programs supplied by A. Chevan), using univariate critical values to assess statistical significance (two-tailed).

To evaluate further the relative influence of area and isolation, individual species occurrences were depicted using area-isolation plots (after Lomolino, 1986; Lawlor, 1998). Previous workers have used this primarily as a graphical technique, but here I used a novel statistical method to test the probability of the observed pattern being due to chance. Values of area (in hectares) and isolation (kilometres from nearest mountain range) were used to arrange the 17 fragments in graphical space for each species. Plots were assigned to one of three possible classes (minimum area, maximum isolation, interaction; Fig. 2) and the number of occupied sites used to partition the graphical space into two sections by either a vertical (area), horizontal (isolation), or diagonal (interaction) line. Thus, if nine of the fragments were occupied and the arrangement approximated a minimum-area pattern, a vertical line was imposed on the plot grouping nine fragments on the left and the remaining eight on the right, without regard to whether particular sites were occupied or not. A two-by-two table was constructed with number of fragments left and

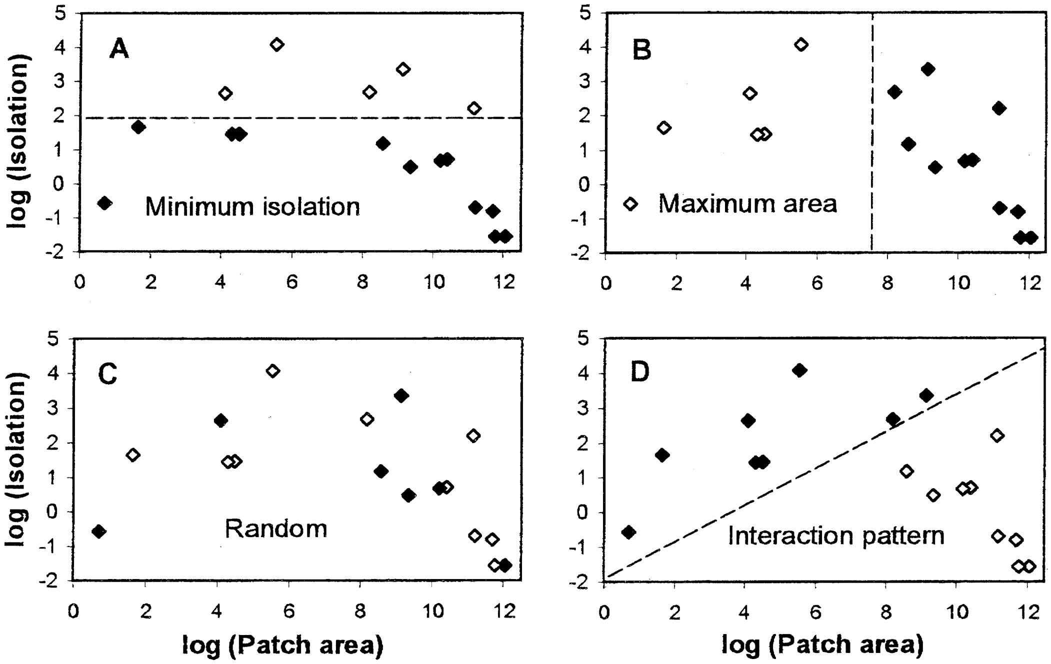

Fig. 2. Hypothetical distributions of species, arranged relative to fragment area and isolation (after Lomolino, 1986; Lawlor, 1998). Open diamonds are unoccupied fragments, while closed diamonds represent fragments in which the species occurs. (a) Maximum isolation pattern, in which species are dispersal limited, and recorded only in those fragments below a threshold-level of isolation. (b) Minimum area pattern, in which species are area-sensitive and inhabit only those fragments larger than a particular threshold. (c) Random pattern, in which the distribution of species is not affected by area or isolation. (d) Interaction pattern, in which isolated fragments are occupied when of sufficient size, and small fragments are occupied when close to larger patches.

right of the partition as columns, and number of fragments occupied and unoccupied as rows. A one-tailed Fisher's exact test was used to estimate the probability of obtaining the observed pattern by chance. Because the distribution of each species was simultaneously compared against three hypothetical distributions, the P value was multiplied by three. A final probability less than or equal to 0.05 was judged significant, which in this case ($n = 17$) corresponded to distributions with $\leqslant 1$ departure from the hypothetical pattern.

Prior to analysis, the distribution of the six ecological indices (vagility, relative abundance, habitat breadth, elevational range, mass and range-size) were checked for normality and transformed as required (natural logarithm transformation for vagility). Of all 15 pairwise correlations between independent variables, five were significant at the 0.01 level (Table 5). Given the confounding effects of multi-colinearity, multivariate methods were inappropriate and each variable was assessed for significance independently. Product–moment correlation co-efficients (Pearson) were calculated for pairwise comparisons and, given the number of comparisons and relatively high sample size (60), a significance level of 0.01 was used (one-tailed). Differences between habitat specialists and other forest residents were calculated using t-tests, with probabilities less than 0.01 judged significant (two tailed, not assuming equal variances).

4. Results

The 17 forest fragments sampled ranged in area from 2 ha to almost 160,000 ha for the Sierra de Yucuñacua, one of the largest remaining tracts of humid pine-oak forest. Maximum elevation within these patches ranged from 1220 m to 3230 m in Cerro San Felipe, with distance from the nearest mountain range varying from 200 m to 59 km. The vegetation index yielded values ranging from 3 to 27, with no patch containing all possible micro-habitats (Table 2). The shape index varied from 6.397 for the most complex patch, to 1.000 for the patch with the most simple edge, while fractal dimension of edge ranged from 1.175 to 1.000. Values of exactly one for these last two metrics indicate that the forest fragment was a perfect square, reflecting the lower bound in the resolution of the raster-based map (i.e. mapped fragments corresponded to a single pixel).

A total of 141 avian species was recorded from the 17 fragments, including many new and noteworthy records (Watson, 1999a, b). Several groups were especially well represented, with 11 species of diurnal raptor (Falconiformes), 12 species of hummingbird (Trochilidae), 12 species of tyrant flycatcher (Tyrannidae), 10 thrushes and allies (Turdidae), and 13 species of sparrow and allies (Emberizidae). For subsequent analyses and discussion, only those 60 forest residents listed in Table 3 were included (see Watson, 1999a for complete data).

Table 5
Comparisons of means and pairwise (Pearson) correlation analyses to evaluate the influence of autecology on distribution of highland birds in humid pine-oak forest fragments in Oaxaca, Mexico

Variable	Patch	Vagility[a]	Abundance	Habitat	Elevation	Range	Mass[b]
Mean±SD FR	8.9±2.7	3.2±0.9	0.7±0.2	2.8±1.0	24.4±6.1	25.9±18.2	51.0±64.3
Mean±SD HS	7.1±2.2*	2.7±0.7	0.5±0.2	2.4±0.8	20.4±4.1*	16.1±11.6	36.6±62.5
Vagility	0.36*						
Abundance	0.74*	0.33*					
Habitat	0.26	0.17	0.23				
Elevation	0.31*	0.36*	0.19	0.18			
Range	0.22	0.28	0.30	0.32*	0.31*		
Mass (Ranked)	0.20	0.16	0.14	0.14	0.42*	0.27	

* Significant at the 0.01 level (one-tailed for correlations, two-tailed not assuming equal variances for *t*-tests)

[a] Raw values of vagility given for means, log transformed values used to calculate correlations.

[b] Actual values of body mass given for means, ranks used to calculate correlations. FR refers to the 60 species of forest residents, HS to the 30 habitat specialists.

No species was recorded in all 17 patches—*Pipilo erythrophthalmus* was the most widespread species, recorded in 13 patches, followed by *Cyanocitta stelleri, Melanotis caerulescens* and *Ptilogonys cinereus* (all recorded in 12 patches; see Appendix for summary of records).

4.1. Nestedness

Fragments were ranked by species richness and the distribution of 60 forest residents was found to exhibit a highly nested pattern, with a matrix temperature of 16.44, [P (T $<$16.44)$<<$0.0001]. The 1020 cell matrix (17 fragments × 60 species) contained 182 departures from perfect nestedness—93 holes and 89 outliers—yielding a hole-rich overall matrix.

The matrix was divided into northern and southern sites for separate analysis. The nine northern fragments (comprising the Sierra de Juárez, Sierra de los Mixes-north, Cerro San Felipe, Piedra del Sol and associated smaller fragments) were ranked by species richness, and had a matrix temperature of 7.16, more than half the overall value (i.e. twice as nested). The remaining eight southern fragments (comprising the Sierra de Miahuatlán, Sierra de Yucuñacua, Sierra de Cuatro Venados, Cerro Piedra Larga, Cerro Labrador, and associated smaller fragments) were ranked by species richness, yielding a matrix temperature of 10.49, again considerably more nested than the overall matrix. Both analyses were highly significant when compared to null models [P (T $<$observed value) $<<$0.0001], and both were hole-rich. To assess whether the reduced temperature exhibited by the northern and southern fragments was an artifact of decreased matrix size, the overall matrix was split randomly 10 times into 20 groups of 8 and 9 fragments, yielding a mean temperature of 13.7.

Analysis of the 30 habitat specialists revealed a highly significant nested pattern with a temperature of 17.34 [P ($T$$<$17)$<<$0.0001]. The arrangement was similar to the overall data-set, with more holes (43) than outliers (39). Examined separately, northern fragments (temperature = 10.07) and southern fragments (temperature = 10.26), exhibited more nested arrangements than the overall matrix and both were hole-rich. Ten random splits of the data into 20 groups of nine and eight fragments yielded a mean temperature of 12.8.

4.2. Factors affecting species richness

Species richness of the 60 forest residents ranged from 56 in the Sierra de Miahuatlán-east to zero for one small fragment in northern Oaxaca (several species were recorded during inventories but none were recognized as forest residents; see Watson, 1999a for complete data). Richness of the 30 habitat specialists ranged from 28 in the Sierra de Miahuatlán-east to zero for three small northern fragments. Both richness measures were related separately to each fragment attribute to assess univariate influences. All independent variables except isolation had significant correlations with both measures of richness significant at the 0.01 level (R^2 $>$ 0.606, df = 15; Table 6). Richness of forest residents was significantly correlated with *Isolation* at the 0.05 level (R^2 $>$ 0.482, df = 15), while the only non-significant relationship was between richness of humid pine-oak specialists and *Isolation* (R^2 $<$0.482, df = 15). The independent variables displayed high degrees of inter-relatedness, with 12 of the 15 possible pairwise comparisons significant (Table 4), and ten highly significant (P $<$0.01). All five correlations which were not significant at the 0.01 level involved *Isolation*.

Best subsets regression was used to determine the optimal predictive model to explain variation in avian richness. For the 60 forest residents, the optimal model contained only a single variable, *Shape*. This model, while explaining marginally less variation in avian richness than the full model (R^2 = 0.925 compared with 0.942), had the highest adjusted R^2 (0.915) and the low-

Table 6
Univariate correlations (Spearman) used to infer determinants of avian richness in naturally fragmented humid pine-oak forests in Oaxaca, Mexico

	Area	Edge	Elev	Isol	Shape	Veg
Rich-FR	0.910**	0.959**	0.754**	−0.540*	0.962**	0.850**
Rich-HS	0.899**	0.953**	0.763**	−0.472	0.949**	0.849**
Edge	0.931**	–	–	–	–	–
Elev	0.770**	0.728**	–	–	–	–
Isol	−0.377	−0.538*	−0.241	–	–	–
Shape	0.934**	0.995**	0.734**	−0.589*	–	–
Veg	0.780**	0.841**	0.731**	−0.245	0.819**	–

Rich-FR refers to richness of the 60 species of forest residents, and Rich-HS refers to richness of the 30 habitat specialists, restricted to humid pine-oak forests.

* 0.05, Significance level.

** 0.01, Significance level.

est values for C_P and s (−1.2 and 6.7 respectively). For the 30 habitat specialists, the best subset contained *Edge* as the only variable. While it accounted for less variance than the full model ($R^2 = 0.908$ compared with 0.923), adjusted R^2 was maximal (0.898) and values for both s and C_P were minimal (−2.3, 3.52 respectively), indicating that the model had higher predictive power than the overspecified full model.

The data set was further analyzed using hierarchical partitioning to assess independent contributions of each independent variable. As with the univariate findings, results for forest residents and habitat specialists were qualitatively similar. No independent variable had a significant independent effect ($R^2 > 0.482$, df = 15), the joint effect being greater than the independent effect in all cases (Fig. 3). For both analyses, *Edge* and *Shape* had the highest independent effects. Examination of the distribution of joint effects confirmed that the independent variables were closely related to one another, overwhelming independent effects of any particular independent variable on species richness.

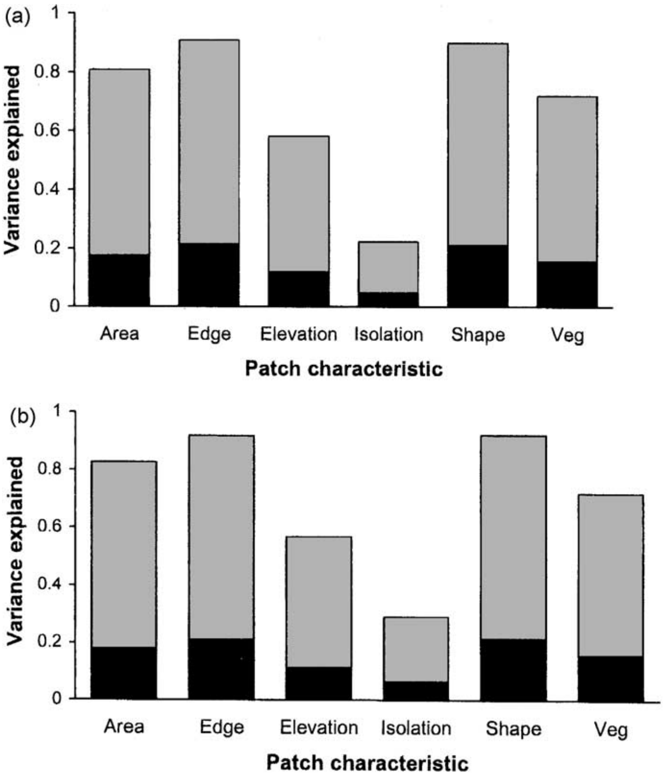

Fig. 3. Summary plots of two separate hierarchical partitions using (a), the 30 habitat specialists and (b), all 60 forest residents. The critical value at the 5% level is 0.482 for 15 degrees of freedom. Black bars signify independent effects, with grey bars for joint effects.

4.3. Area versus isolation

Of the 60 forest residents, 13 had insufficient data for analysis (recorded in five fragments or fewer) and 15 displayed random patterns with no relationship to area, isolation or interaction models (Table 3). One species (*Piranga flava*) displayed a distribution consistent with a maximum isolation pattern (Fig. 2a), occurring in all but one fragment <5.3 km from the nearest mountain range and absent from all fragments isolated by >9.0 km (Fig. 4). Thirty-one species displayed significant minimum-area distributions (Table 3), restricted to fragments larger than a particular threshold (Fig. 4). The threshold value varied from approximately 3500 ha for 16 species (including *Dendrortyx macroura*, *Troglodytes brunneicollis* and *Parula superciliosa*) to approximately 30,000 ha for three species (*Pachyramphus major*, *Vireolanius melitophrys*, and *Diglossa baritula*; Table 3). Eight other species were restricted to fragments larger than 30,000 ha but were recorded in fewer than five fragments and could not be tested. No species exhibited a distribution consistent with an interaction pattern (Fig. 2d).

4.4. Influence of autecology

The estimate of relative abundance ranged from 0.1 (recorded in one sampling period in fragments where it was observed) to 1.0 (recorded in all sampling periods in fragments where it was observed). This measure was related to patch occupancy ($r=0.74$, $n=60$, $P<0.01$), more abundant species being significantly more widespread (Fig. 5a).

The vagility index was positively related to patch occupancy ($r=0.36$, $n=60$, $P<0.01$), with species considered more vagile consistently found in more fragments (Fig. 5b). Vagility was also positively related to abundance and elevation—more vagile species tended to be more abundant and occupy broader elevational ranges (Table 5).

Elevational range varied from 1100 to 3500 m and was significantly related to patch occupancy ($r=0.32$, $n=60$, $P>0.01$), those species occupying broader elevational ranges recorded in more fragments (Fig. 5c).

Absolute measures of mass were tabulated (Table 3) and then ranked from the lightest species (*Hylocharis leucotis*, approximately 4 g) to the heaviest (*Dendrortyx macroura*, approximately 350 g). Ranked body mass was not significantly related to patch occupancy ($r=0.20$, $n=60$, $P>0.01$; Fig. 5d).

The latitudinal extent in which species are year-round residents ranged from less than one degree for *Eupherusa cyanophrys* to 81° for *Columba fasciata*. This measure of range-size was not related to patch occupancy ($r=0.22$, $n=60$, $P>0.01$; Fig. 5e), but was significantly related to body mass—heavier species occupied larger distributional ranges. (Table 5).

The number of habitats occupied throughout the species' range (Parker et al., 1996) was not significantly related to patch occupancy ($r=0.26$, $n=60$, $P>0.01$; Fig. 5f).

4.5. Habitat specificity

The 60 forest residents were classed into two groups; those recognized as habitat specialists (30) and remaining species (comprising 27 species that range into dry pine-oak forest and 3 species restricted to cloud forest; Table 3). Patch occupancy for these two groups was found to differ significantly ($t=-2.8$, $df=58$, $P<0.01$ not assuming equal variances). Examination of the area-isolation plots revealed the habitat specialists were restricted to larger patches—only three of the 30 species were recorded from patches smaller than 3000 ha (*Empidonax affinis*, *Icterus graduacauda* and *Carduelis notata*). Of the remaining humid pine-oak specialists, eight species (*Vireolanius melitophrys*, *Poecile sclateri*, *Catharus aurantiirostris*, *Turdus infuscatus*, *Ridgwayia pinicola*, *Piranga erythrocephala*, *Diglossa baritula* and *Loxia curvirostra*) were recorded only in fragments larger than 30,000 ha (Appendix). The only other species restricted to these eight largest fragments were the three cloud forest specialists (*Eupherusa cyanophrys*, *Aulacorhynchus prasinus* and *Pachyramphus major*).

5. Discussion

5.1. Nested patterns of richness

This pattern has been proposed to result from selective deterministic extinction of species (Patterson, 1984; Brown, 1986), with resilient species being widespread and sensitive species restricted to species-rich patches, although several authors suggest that it may be a more general property of communities (Cutler, 1991; Wright and Reeves, 1992). The resident avifauna of humid pine-oak forests displayed a highly nested structure, whereby assemblages of birds inhabiting less diverse sites were predictable subsets of more diverse assemblages. All matrices contained more unexpected absences than presences, both for the overall analyses and for the separate analyses of northern and southern fragments. These "hole-rich" patterns may be related to faunal relaxation (Mikkelson, 1993) or other adjustments in community structure following major disturbance. Thus, species with certain ecological attributes are more prone to extinction, leaving the same subset of resilient species in smaller patches. Hole-rich matrices may also emanate from sampling artifacts, with absences in the matrix representing missing data. This is a serious concern and may have considerable influence on studies in which standardized sampling was not used. In this study,

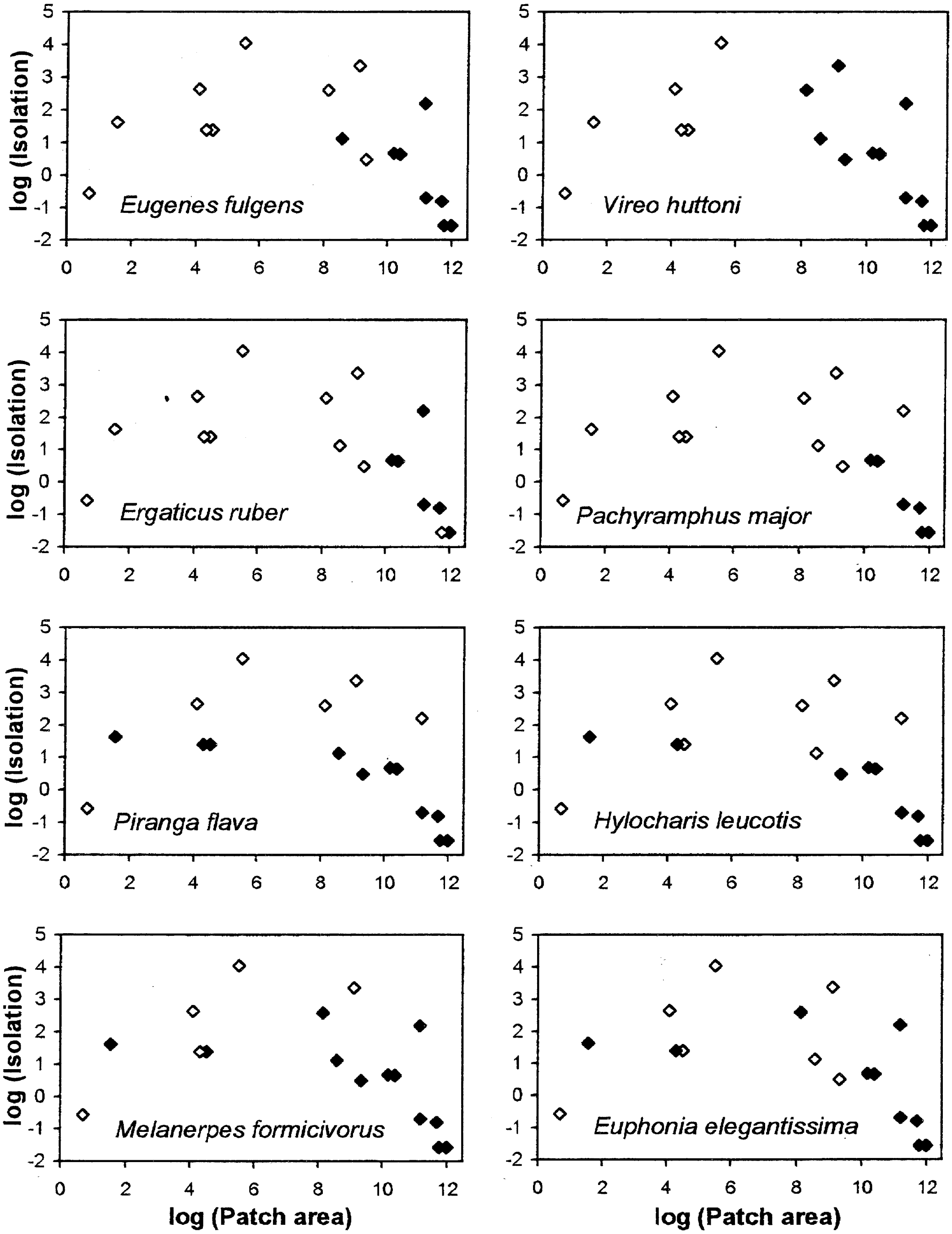

Fig. 4. Selected area-isolation plots for eight of the 60 forest residents, assigned to one of the hypothetical distributions (Fig. 2). Open diamonds are unoccupied fragments, while closed diamonds represent fragments in which the species occurs. The upper four plots display significant minimum-area patterns, with species restricted to fragments larger than a particular threshold. *Piranga flava* and *Hylocharis leucotis* both displayed distributions consistent with the maximum isolation pattern, but only *Piranga flava* was significant. The last two plots display random distributions, with species exhibiting no apparent relation to patch area or degree of isolation.

sample completeness was standardized and analyses were restricted to forest residents, thereby minimizing the potential influence of missing values. Moreover, when historic data were added, qualitative results of all analyses were the same (Watson, 1999a), further reinforcing the completeness of sampling.

Most species were restricted completely to the larger, more species rich patches, the majority of these species being habitat specialists (e.g. *Dendrortyx macroura*, *Vireolanius melitophrys*, *Ridgwayia pinicola*). There were, however, a number of species that did not conform to the overall pattern of nestedness. This group was dominated by species more typical of drier habi-

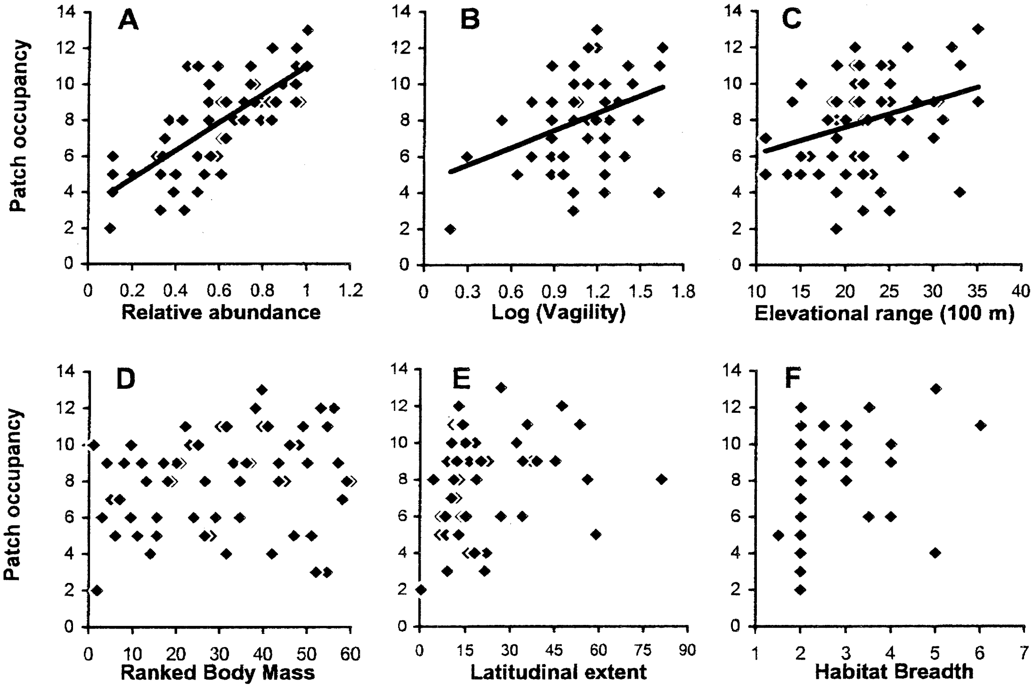

Fig. 5. Correlations of patch occupancy versus autecological indices for the 60 species of forest resident considered here. The upper three plots were significant at the 0.01 level (Table 3). (a) Relative abundance derived from frequency of occurrence in four of the largest fragments (b) Natural logarithm of the vagility index (Table 2) (c) Elevational range, taken from Parker et al. (1996) (d) Ranked body mass (e) Latitudinal extent over which the species is resident year-round (f) Habitat breadth, in terms of number of habitats occupied throughout range (after Parker et al., 1996).

tats and forest edges (e.g. *Trogon elegans*, *Contopus pertinax*), and often displayed the reverse trend, being more frequently recorded in species-poor patches. The three species restricted to cloud forest/humid evergreen forest (*Eupherusa cyanophrys, Aulacorhynchus prasinus*, *Pachyramphus major*) also departed from the overall pattern of nestedness, their distributions being influenced more by the presence of cloud forest than other patch attributes. These aspects of species-level distributional ecology are explored in more detail below.

Previous work on assemblages of birds in montane coniferous forests also found highly nested distribution patterns, but the matrix was outlier-rich, with more unexpected presences (Johnson, 1975; Cutler, 1991). By contrast, mammalian faunas in the same region were hole-rich (Brown, 1971; Brown and Gibson, 1983), the difference explained in terms of different dispersal abilities of the two groups (Cutler, 1991). Thus, birds may be similarly susceptible to local extinction, but were assumed to have greater dispersive abilities and, hence, were more likely to secondarily recolonize areas. While most bird species are theoretically capable of flying across a valley or clearing to an adjacent forest patch, it doesn't necessarily follow that they will. In the humid pine-oak forests of Oaxaca, the matrix between forest fragments is dominated by dry, thorny savanna and scrub, and there is a high degree of complementarity in both flora and resident fauna between these habitats (Goodwin, 1969; Rzedowski, 1986; Binford, 1989). While some highland species do move within this intervening matrix, it likely represents a hostile and foreign environment to most. Thus, landscape features that promote fragment connectivity may be just as important for birds and other highly mobile groups as for the mammals, reptiles and plants for which they have been primarily advocated.

Geographic location was also found to be important, as illustrated by the separate analysis of northern and southern patches. Considered separately, the nine northern sites exhibited an arrangement that was more than twice as nested as for the entire matrix (and slightly less than twice the overall value for the 30 habitat specialists). This indicates that species-poor fragments in northern Oaxaca were more closely related to their adjacent mountain ranges, than to mountains on the other side of the Oaxaca Valley. This is consistent with the suggestion that avian communities associated with the northern ranges are distinct from those in the south (Hernández-Baños et al., 1995; Watson and Peterson, 1999). Moreover, it is apparent that nestedness analysis, as with other approaches to examining spatial structuring of communities, are best tailored to the specific attributes of the study area.

5.2. Determinants of avian richness

Analyses of both the entire group of forest residents and the subset of habitat specialists showed similar qualitative patterns, the same variables having strong univariate influences. Patch-scale metrics (notably area, vegetation diversity, fractal dimension of edge and fragment shape) explained most of the variation in avian richness, while the landscape-level metric used (distance to the nearest large fragment) had considerably less influence. These results underscore the importance of patch-scale effects in explaining the distribution of diversity, in contrast to results of analyses at the regional scale (Watson and Peterson, 1999). In considering diversity patterns of humid montane forest birds throughout Mesoamerica, regional scale variables (chiefly latitude) explained most of the variation, with proximity to the two lowland isthmuses also critical (Watson and Peterson, 1999). Combining these two results (using the same classes of variables and analytical techniques), the influence of patch-scale factors appears to be scale dependent. Thus, variables including fragment shape, area and vegetation were key determinants of species richness in fragments smaller than a certain threshold value (in this case between 1000 and 3000 ha), but regional scale effects such as geographic context and latitude became more important in larger fragments (the mountain ranges discussed in Watson and Peterson, 1999).

Determining which patch-level variables are most important, however, is difficult. Indeed, I was unable to demonstrate a single significant independent effect for the six fragment attributes analyzed due to the high degree of colinearity between them. While fragment shape and edge had the highest univariate influence on the two measures of avian richness and were thus selected as constituting the ''best'' predictors, less than a quarter of the explained variance was due to independent effects. Thus, larger fragments had higher peaks, sustained more diverse vegetation types and had a more complex shape, and were found to support more diverse avian communities. Hence, the finding that larger patches support more diverse resident avifaunas is not purely a function of increased area, but reflects all of the other patch attributes that covary with area. The threshold pattern noted above may be driven by area, number of micro-habitats, patch configuration, minimum elevation, or any combination of these factors. Identifying the combination that yields the best prediction would be a simplification that ignores the close relationships between these factors.

Several authors have concluded that either area or vegetation is most important in driving patterns of diversity in a particular system (Saunders et al., 1991; Robinson et al., 1995; Simberloff, 1995; Graham and Blake, 2001; Lee et al., 2002). While there are several sound theoretical reasons why larger patches would be expected to support more species irrespective of vegetation (Holt, 1990; Mac Nally and Watson, 1997), this can only be demonstrated using standardized samples. As Loman and von Shantz (1991) stated, ''as the sample sizes usually are larger in larger areas, this [higher richnesses in larger patches] is not a very interesting finding'' (p. 177). Indeed, one could reasonably expect to find higher diversities of non-biological entities in larger patches (e.g. colors of pebble, boulder shapes) purely as a result of passive sampling. In this study, protocols were employed to avoid these shortcomings. Moreover, the patches spanned some five orders of magnitude, thereby encompassing a broad range of relevant spatial scales. If there were a meaningful, direct influence of patch area on species richness independent of other factors, I am confident that it would have been revealed. The results presented here are not sampling or statistical artifacts, but an accurate (and necessarily complex) representation of the patterns of dependence between variables such as area and habitat complexity.

5.3. Influence of isolation and fragment area

Of the 60 species examined, 31 displayed distributions consistent with the area-limitation hypothesis (Lomolino, 1986; Rosenzweig, 1995)—an important finding that underscores the sensitivity of these species to reduction in habitat area. Indeed, eight humid pine-oak forest specialists and all three cloud forest specialists were found only in forest fragments larger than 30,000 ha, an alarmingly high threshold in comparison with other studies of birds in forest fragments (Saunders et al., 1991; Walters et al., 1999; Watson et al., 2000). Given seasonal movements, dietary switches and other behavioral and developmental traits, however, resource requirements of most species are dynamic and any distributional threshold varies accordingly. Thus, while particular fragments may support a species for part of the year, there may be insufficient resources to maintain a population indefinitely. As such, the provided threshold values should be treated as a preliminary indication of areal requirements during the breeding season, and should not be viewed as critical thresholds below which species cannot survive. Those species identified as area-limited varied considerably in their autecologies, comprising similar numbers of habitat specialists and other forest residents. Comparing all 30 habitat specialists with the remaining species however, revealed the humid pine-oak forest specialists to be significantly less widespread, restricted primarily to the larger forest fragments. These findings correspond closely with regional-scale studies of highland birds in Mesoamerica, (Hernández Baños et al., 1995; Watson and Peterson, 1999) and studies of montane birds elsewhere (Vuilleumier, 1970; Johnson, 1975, 1977; Kratter, 1992; Nores, 1995) suggesting pronounced area-sensitivity may be a general attribute of montane avifaunas (Vuilleumier and Simberloff, 1980; Brown and Gibson, 1983; see also Peterson and Watson, 1998).

In contrast, isolation had remarkably little explanatory power, the distribution of only a single species (*Piranga flava*) significantly related to degree of isolation. Hence, the patch-scale and species-level analyses generated the same result—fragment attributes consistently had a major influence over distribution patterns of organisms regardless of their landscape context. Previous studies of mountain-top habitat fragments found isolation to be of minimal importance in explaining distribution patterns (Brown, 1971; Johnson, 1975; Harper et al., 1978; Wilcox et al., 1986, but see Vuilleumier, 1970; Lomolino et al., 1989) leading Brown (1971, 1995) to infer that these older systems are extinction driven, with dispersal and subsequent recolonization being rare.

Distributions of 15 species could not be explained in terms of area or isolation, however, and may be affected more by the distribution of particular microhabitats independent of fragment size or context. For instance, *Euphonia elegantissima* feeds primarily on the fruits of Loranthaceous mistletoes (Stiles and Skutch, 1989), and it was found in many small and isolated fragments, generally closely associated with fruiting mistletoe clumps. *Melanerpes formicivorus* subsists primarily on acorns (Skutch, 1969), and displays numerous behavioural specialisations to this diet. It was found in all of the largest fragments but also one of the smallest (6 ha)—in all cases fragments with stands of masting oak trees.

5.4. *Influence of autecology*

While isolation was consistently found to have little influence on distribution patterns of individual species or overall richness of fragments, it does not necessarily follow that dispersal is unimportant (in contrast to Brown, 1995). Indeed, less vagile organisms were consistently found in fewer fragments, suggesting that highly vagile species are able to disperse to suitable fragments regardless of their location, and their subsequent survival hinges upon area and other patch-scale parameters. Previous authors (Gaston and Kunin, 1997 and references therein) have noted rarer species tend to be poorer dispersers but most of this research has focused on flowering plants. While vagility has previously been implicated in determining avian distributions (Diamond, 1972; Abbott, 1978; Järvinen and Haila, 1984), this is one of the first community-level studies in which avian vagilities were estimated and related directly to distribution (Mayr and Diamond, 2001). More research is required to test the generality of this finding, explore alternative ways of estimating vagility, and examine further the interplay between distribution and vagility in patchy landscapes.

The estimate of relative abundance was also found to be associated closely with distribution—species encountered more frequently were consistently found in more fragments. This pattern has been reported from a variety of systems, but may be largely driven by sampling artifacts (Wright, 1991). Even though the abundance estimate used here was derived from less than a quarter of the study sites and a range-based measure of rarity was used, maximising the independence of the variables, the relationship may still be artificially amplified. Brown (1984) proposed a generalized explanatory theory to account for this pattern, but he cautioned that the relationship would hold only among ecologically or phylogenetically related taxa. In this case, the relationship held across 60 species spanning six orders, 20 families and a range of ecological guilds. At a more proximate scale, the observed pattern is consistent with a demographic mechanism—more abundant species by definition have larger population sizes in a given habitat fragment, affording increased resilience to extinction in the first place (Holt, 1990). According to this mechanism, more abundant species would be more widespread regardless of other ecological characteristics. This was not the case in this study—vagility and relative abundance were significantly inter-related, so evaluating their importance independently is not possible.

Elevational range was also found to be significantly related to patch occupancy, supporting the intuitive prediction that species with broader elevational tolerances are more widespread. This pattern could be driven either by increased resilience to climatic change, or by a sampling effect—species being more widespread because their preferred elevations are better represented. Given that elevational range was also closely related to vagility this latter hypothesis is more likely, with more vagile species better able to move to fragments, and subsequently more likely to find suitable elevations represented and colonise successfully.

Tying these factors together, I propose that more abundant species were originally less prone to extinction, more vagile species were better dispersers and species with broader elevational tolerances more likely to be successful colonists, resulting in all three attributes being positively related to patch occupancy. This conclusion is reinforced by anecdotal reports of humid pine-oak forest residents recorded in the southwestern United States (Heathcote and Kaufman, 1985; Stejskal and Rosenberg, 1991). While rare instances of individual birds, this information further underscores the dispersive capacity of some of these highland species, enabling them to persist in fragmented environments and move to forest fragments regardless of the degree of isolation. Rarer species were dispersal limited and less abundant, making them especially vulnerable to local extinction and less able to offset this process through subsequent recolonisation.

Other ecological traits were found to have little influence over avian distribution patterns, providing an interesting counterpoint to prevailing macroecological theory. According to Brown's general hypothesis (Brown, 1995; Brown and Gibson, 1993), maximum density reaches a peak at optimal body mass (30 g for birds), decreasing for smaller and larger species. The six species closest to 30 g ranged in relative abundance from 0.11 (*Vireolanius melitophrys*) to 0.84 (*Catharus occidentalis*), and the five most abundant species ranged from 9.5 g (*Myioborus miniatus*) to 90 g (*Cyanocitta stelleri*) showing no clear pattern whatsoever. There was no clear relationship between patch occupancy and range-size either. Indeed, for thrushes in the genus *Catharus*, the observed pattern was directly opposite to the prediction—the species with the smallest distributional range (*C. frantzii*) was recorded in the most fragments, while the species with the largest range (*C. aurantiirostris*) was the rarest.

There were however, several significant relationships between these variables: species with larger distributional ranges occupied more habitats and broader elevational ranges. These relationships are driven primarily by sampling effects—larger distributional ranges span more vegetation types and elevations—which are known from many other systems and have been discussed in detail by Stevens (1989, 1992). Note, however, that diversity gradients of highland taxa in Mesoamerica may be driven primarily by proximity to the Isthmuses of Tehuantepec and Panama (Watson and Peterson, 1999 and references therein), with latitude playing a secondary role. Interestingly, those species inhabiting greater elevational ranges tended to be larger, a pattern which may reflect physiological and energetic constraints (Brown, 1995). While some humid pine-oak species are altitudinal migrants (Winker et al., 1997), many are wholly restricted to these high elevation forests, and larger body size presumably affords greater tolerance of the colder temperatures associated with higher elevations.

5.5. *Importance of temporal scale*

Most studies of the consequences of habitat fragmentation have been conducted in relatively young landscapes, typically 60–90 years post fragmentation (Watson, 2002). Some authors (e.g. Renjifo, 1999) regard this time-scale as "long-term" and sufficient to ensure the stability of diversity patterns. In considering the generation time of forest trees, the background periodicity of disturbance regimes and the impact of stochastic factors, these anthropogenically-altered systems are still undergoing adjustments to diversity and hence may not reveal the net consequences of fragmentation. Indeed, there may not have been sufficient time to observe effects in a particular age cohort, let alone the population. This disparity in time-scales was noted by Janzen (1986), when he observed that oak trees in forest patches of northern Costa Rica were not undergoing regeneration, and that once those individuals died, the habitat patch died with them. Labeled "the living dead" this example highlights the extended time scales of many natural processes, whereby the full effects of habitat fragmentation can only be understood after several generations.

The conservative age of montane fragments in Oaxaca is 5000 years, two orders of magnitude greater than the age of most anthropogenically-created fragments discussed in the literature (Saunders et al., 1991; McGarigal and Cushman, 2002; Watson, 2002). More recent modifications to this landscape have certainly contributed to present-day distributions, but the overall arrangement of this landscape is clearly much older. Given estimates of relaxation times derived from empirical (Diamond, 1972) and theoretical (Mikkelson, 1993) approaches, it is reasonable to assume that extinctions related to re-arrangement of habitat have already occurred. Thus, the results discussed herein do not represent a transitional state between community arrangements, but a stable outcome reflecting the endpoint of the effects of fragmentation. As such, it is noteworthy that diversity patterns in this landscape could not be related to any individual factors, suggesting much of the debate on the influence of habitat versus area is irrelevant over longer time-scales. To understand distribution patterns in recently fragmented landscapes, I advocate a resource-based approach (Watson, 2001; 2002b), with long-term conservation better guided by findings from these older systems.

5.6. *Conservation implications*

Relative to other montane forests in the neotropics, avian diversity of humid pine-oak forests is exceeded only by montane evergreen forests in terms of both total number of species and species dependent on the forest as primary habitat (Stotz et al., 1996). In addition, these montane habitats are known to support a rich biota of endemic amphibians (Duellman, 1970; Wake and Lynch, 1976), mammals (Goodwin, 1969) and plants (Rzedowski, 1986), and have been recognized as a key conservation priority in Mesoamerica (Stotz et al., 1997). This diversity is in part accounted for by the regional context of these forests, at the boundary of two major biogeographic regions. Indeed, the southern range limits of many North American bird species occur in the region, and several bird families terminate in the region (e.g. Paridae, Sittidae) associated with the high elevation Mexican plateau that ends in central Oaxaca.

While all 60 forest residents examined here may be represented by three of the largest remnants (Sierra s de Yucuñacua, Juárez and Miahuatlán) this would not be representative of the true extent of diversity in the highland avifauna. Several species of pine-oak bird differ substantially within their range, such that those individuals in the northern range are diagnosably different from individuals from the south. In some cases (e.g. *Aulacorhynchus, Picoides, Cyanocitta*), these different forms are recognized as distinct subspecies (generally corresponding to valid phylogenetic species, Peterson and Navarro-Sigüenza, 1999), and both forms can be considered separately for management purposes. For some taxa, however, patterns of differentiation are less clear. Several species (e.g.*Chlorospingus ophthalmicus*) exhibit morphological variation throughout their range, and other groups (e.g. *Glaucidium, Contopus, Empidonax*) may be equally variable but have conservative external morphologies (Robbins and Stiles, 1999). It doesn't necessarily follow that the smaller fragments are therefore not as valuable for conservation. Several species, including the poorly known *Aimophila notosticta*—endemic to Oaxaca—were recorded only from the smaller patches, and small patches doubtless play an important role for many species.

In addition to the forest-dependent residents discussed here, pine-oak forests are of critical importance for neotropical migrants, supporting greater diversities of these species than any other forest type in Mexico (Hutto, 1992). A key research priority will be to examine the determinants of distribution of these migrants, testing the hypotheses generated by this research and assessing whether diversities of migrants mirror the patterns displayed by year-round residents.

The main finding of this research and the principal message for conservation is that patch-scale factors consistently influenced distribution patterns of species while landscape-scale factors had little effect. Regardless of their context, high quality fragments supported more diverse assemblages of birds, with all fragment attributes closely inter-related. Thus, no single fragment attribute was identified as a key determinant of diversity, but incorporating indirect effects and individual responses of species, larger fragments consistently supported more bird species. Thus, while landscape-attributes may have relevance in young systems, patch quality is critical over longer time frames, and should be given due recognition in long-term management plans.

Acknowledgements

I am indebted to Andrew (Town) Peterson for supporting this project and ensuring its swift completion. Discussions with Bob Holt, Mark Robbins and Bob Timm contributed greatly to the reasoning developed in this paper, and Lawrence Binford, Bette Loiselle and Maggie Watson all made constructive suggestions on earlier versions of the manuscript, greatly improving the clarity and content. Norm Slade provided statistical advice and devised the novel statistical approach used to test area/isolation plots. I am grateful to Dan Kluza, Town Peterson and Mark Robbins for scoring vagilities of the species. Partial funding for this research was provided by grants from the Frank M. Chapman Fund of the American Museum of Natural History, Tinker Foundation, Panorama Society of the Natural History Museum of The University of Kansas and the National Science Foundation (Number DEB 9801587).

Appendix

Summary of distributional records of 60 forest-dependent species in 17 naturally occurring fragments of humid pine-oak forest in Oaxaca, Mexico

Scientific Name	Class	Fragment code																	Patch
		A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	
Dendrortyx macroura	H, CF	0	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	8
Columba fasciata	PO	0	1	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	8
Hylocharis leucotis	PO	1	1	1	1	1	1	1	1	0	0	0	0	0	1	0	1	0	10
Amazilia beryllina	PO	1	1	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	6
Lampornis amethystinus	H, CF	0	1	1	1	1	1	1	1	0	1	1	0	0	0	0	0	0	9
Lampornis clemenciae	H	1	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	7
Lamprolaima rhami	H, CF	0	0	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	5
Eupherusa cyanophrys	CF	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2
Eugenes fulgens	H, CF	1	1	1	1	1	1	1	0	0	0	1	0	0	0	0	0	0	8
Trogon mexicanus	PO	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	11
Trogon elegans	PO	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	3
Aulacorynchus prasinus	CF	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	7
Melanerpes formicivorus	PO	1	1	1	1	1	1	1	1	0	1	0	1	0	0	0	1	0	11
Picoides villosus	PO	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	8
Colaptes auratus	PO	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	9
Lepidocolaptes leucogaster	PO	1	1	1	1	0	1	1	0	1	1	0	0	0	1	0	0	0	9
Lepidocolaptes affinis	H, CF	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	9
Pachyramphus major	CF	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	6
Mitrephanes phaeocercus	PO	1	1	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0	9
Contopus pertinax	PO	1	1	1	1	1	1	1	1	0	0	0	0	0	1	1	1	0	11
Empidonax affinis	H	0	0	1	1	0	1	1	0	1	1	0	0	0	1	0	1	0	8
Empidonax occidentalis	H	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	9
Vireo plumbeus	PO	1	1	0	1	1	1	1	1	1	0	0	0	0	1	0	1	0	10
Vireo huttoni	PO	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	11
Vireolanius melitophrys	H	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	6
Cyanocitta stelleri	PO	1	1	1	1	1	1	1	1	1	1	0	0	0	1	0	1	0	12
Poecile sclateri	H	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	4
Troglodytes brunneicollis	H, CF	1	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	9
Henicorhina leucophrys	H, CF	1	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	6
Myadestes occidentalis	PO	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	11
Catharus aurantiirostris	H, CF	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	4
Catharus occidentalis	H	0	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	8
Catharus frantzii	H, CF	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	9
Turdus infuscatus	H, CF	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	3
Turdus migratorius	PO	1	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	9
Ridgwayia pinicola	H	0	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	5
Melanotis caerulescens	PO	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	12
Ptilogonys cinereus	PO	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1	0	12
Peucedramus taeniatus	PO	1	1	1	1	1	1	1	0	1	0	0	1	0	0	0	0	0	9
Parula superciliosa	PO	1	1	1	1	1	1	1	0	1	1	1	0	0	0	0	0	0	10
Dendroica gracei	PO	1	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	5
Geothlypis nelsoni	H	1	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	5
Ergaticus ruber	PO	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	7
Myioborus miniatus	H, CF	1	1	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	9
Basileuterus belli	H, CF	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	8
Chlorospingus ophthalmicus	H, CF	1	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	5
Piranga flava	PO	1	1	1	1	0	1	1	1	0	0	1	1	0	1	0	1	0	11
Piranga erythrocephala	H	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	5
Euphonia elegantissima	H, CF	1	1	1	1	1	1	1	0	0	1	0	0	0	1	0	1	0	10
Diglossa baritula	H, CF	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	6
Atlapetes pileatus	H	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	11
Buarremon brunneinucha	H, CF	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	9
Pipilo ocai	H	1	0	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	8
Pipilo erythrophthalmus	PO	1	0	1	1	0	1	1	1	1	1	1	0	1	1	1	1	0	13
Junco phaeonotus	PO	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	8
Pheucticus melanocephalus	PO	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	10
Icterus graduacauda	H, CF	1	1	1	1	0	1	1	0	1	1	0	1	0	1	0	0	0	10
Loxia curvirostra	H	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	4
Carduelis notata	PO	1	1	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	6
Coccothraustes abeillei	H, CF	0	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	5
Rich-FR, total = 60		47	48	51	53	38	56	54	36	24	27	15	6	1	10	2	10	0	–
Rich-HS, total = 30		19	22	27	26	17	28	25	18	7	14	3	1	0	3	0	2	0	–

Class denotes the primary habitat occupied by each species, where CF = cloud forest, H = humid pine-oak forest and PO refers to pine-oak forests (both humid and dry). Fragment code refers to the letters defined in Fig. 1, and patch denotes patch occupancy, the total number of fragments in which each species was recorded.

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