

Landscape Heterogeneity and Diurnal Raptor Diversity in Honduras: The Role of Indigenous Shifting Cultivation¹

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ABSTRACT

I studied the relationship between diurnal raptor diversity, density, and richness, and landscape heterogeneity in continuous primary forests and forests farmed by native Amerindians in the Río Plátano Biosphere Reserve of north-eastern Honduras from January to June 1996 and 1997. I estimated landscape heterogeneity—the variability in naturally occurring and/or anthropogenic habitat mosaics—by mapping the extent and distribution of five human-modified and natural habitats in 24 1 km² survey plots. I used the Shannon index to calculate landscape heterogeneity values for the respective plots based on the proportion of total area of each habitat within each plot. Diurnal raptor surveys from canopy-emergent viewpoints in these plots resulted in 137 observations of 18 species of raptors. Four species (*Coragyps atratus*, *Ictinia plumbea*, *Leucopternis albigollis*, and *Buteo magnirostris*) differed significantly in abundance among heterogeneity classes. Raptor diversity, density, and richness all increased directly with increasing landscape heterogeneity. Landscape heterogeneity was more important in explaining differences in raptor species diversity than the presence or extent of any single habitat or combination of habitats. In contrast to previous studies, my results indicate the importance of indigenous shifting cultivation in altering the naturally occurring patterns of habitat mosaics in lowland rain forest and its effect on bird species abundance and diversity in a rain forest ecosystem.

RESUMEN

Estudí la relación entre la diversidad, densidad y la riqueza de especies de rapaces diurnas con la heterogeneidad de paisajes en bosques primarios continuos y bosques donde practican la agricultura migratoria indígenas de la Reserva de Biosfera del Río Plátano al noreste de Honduras entre los meses de enero a junio de 1996 y 1997. Evalué la heterogeneidad de paisajes—la variabilidad en mosaicos de hábitats naturales o antropogénicos—con mapas de cinco hábitats en 24 parcelas de 1 km². Usé el Índice de Shannon para calcular valores de la heterogeneidad de cada parcela, basado en la proporción de cada hábitat. Desde el dosel, hice conteos de rapaces en las 24 parcelas que resultaron en 137 observaciones de 18 especies. Cuatro especies (*Coragyps atratus*, *Ictinia plumbea*, *Leucopternis albigollis*, y *Buteo magnirostris*) difirieron significativamente en abundancia entre los grupos de heterogeneidad del paisaje. La diversidad, densidad y riqueza de especies aumentaron conjuntamente con la heterogeneidad del paisaje. La heterogeneidad del paisaje fue más importante para explicar la diversidad de rapaces que la presencia o el área de cualquier hábitat o combinación de hábitats. En contraste con estudios anteriores, mis resultados sugieron la importancia de la agricultura migratoria indígena en la alteración de mosaicos de hábitats naturales en los bosques húmedos bajos, y su efecto en la abundancia y diversidad de aves de un ecosistema forestal.

Key words: Amerindians; Honduras; landscape heterogeneity; raptor diversity; shifting cultivation; tropical moist forest.

NEOTROPICAL FORESTS ARE DYNAMIC ECOSYSTEMS in which disturbances frequently open the forest canopy (Hartshorn 1980, Foster 1990, Gentry 1990, Milton *et al.* 1994). Because canopy gaps originate from a variety of sources, there is considerable variability in gap area and age that results in a heterogeneous landscape with a variety of successional stages (Denslow 1980, Hartshorn 1980, Milton *et al.* 1994). Generally, species diversity has been found to increase with increasing landscape heterogeneity in tropical forests (Hartshorn 1980, Remsen & Parker 1983, Levey 1988, Jullien & Thiollay 1996, Brown & Hutchings 1997, Laska 1997).

Agricultural practices also create disturbances that influence the distribution and abundance of birds in the Neotropics by changing the structure and composition of vegetation (Rappole & Morton 1985, Lynch 1992, Petit *et al.* 1992, Robbins *et al.* 1992, Bierregaard & Stouffer 1997), as well as the frequency of habitat ecotones (Yahner 1988). Agricultural practices, however, are not all equal in their effects on the environment; they vary from small-scale periodic disturbances (*e.g.*, shifting cultivation practiced by Amerindian societies) to massive and permanent conversion to monocultures

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(e.g., pastures and fruit plantations). Therefore, depending on their extent and intensity, agricultural practices may either increase or decrease bird species diversity (Karr 1990, Colwell & Dodd 1995).

Amerindian peoples are often portrayed as conservators of Neotropical environments; yet with increasing population densities and entrance into cash economies, it is important to examine the impacts they have on the ecosystems they inhabit (Neitschmann 1971, Alvard 1993). Thus, the aims of this study were twofold: (1) to compare landscape heterogeneity between uninterrupted, mature lowland rain forests and forests experiencing indigenous shifting cultivation, and (2) assess differences in the raptor community between forests with and without indigenous farming.

I chose to study diurnal raptors as a subset of avian diversity in tropical forests for two reasons. First, diurnal raptors meet many criteria that may make them valuable biological indicator species (e.g., high trophic levels, low reproductive rates, and relatively large body sizes; Terborgh 1974, Karr 1977, Robinson & Wilcove 1989, Bierregaard *et al.* 1997). Also, some species suffer from deforestation and habitat fragmentation and have been extirpated in many areas as a direct result of a reduction in habitat area (e.g., Río Palenque, Ecuador [Leck 1979] and Barro Colorado Island, Panama [Karr 1982]). Second, it is possible that certain raptors are "keystone species" in tropical forests, species that, regardless of density or biomass, can exert considerable influence on the structure and organization of the community to which they belong (Paine 1966, Underwood 1986, Terborgh 1992). Therefore, the study of diurnal raptors may alert us to early signals of ecosystem decline.

MATERIALS AND METHODS

STUDY LOCATION.—The Río Plátano watershed (15°00'–16°00'N, 85°30'–84°30'W) is located in the remote Mosquitia region of northeastern Honduras. The entire drainage, from headwaters to mouth, was designated the Río Plátano Biosphere Reserve (RPBR) by the Honduran Congress and the International Committee of the International Man and the Biosphere (MAB) Program (for which UNESCO is General Secretariat; IUCN 1982). This reserve was established in part to protect pristine tropical ecosystems located within its boundaries, principally vast tracts of uninhabited lowland rain forest known to contain threatened and endangered wildlife and plant species. With an area of 525,000 ha, it is one of the largest protected

areas in Central America (Hartshorn 1992). The physiography is characterized by north–south transverse mountain ranges descending onto a broad littoral plain. Elevations range from sea level to 1356 m. Rivers and streams are abundant and are the principal routes of transportation. At the broadest level, the vegetation of the RPBR can be categorized as Tropical Moist Forest (Holdridge 1967). This designation is characterized by 2000 to 4000 mm of annual precipitation and 18 to 24°C mean annual temperature. Within the RPBR, dry (January–May) and wet (June–December) seasons occur. Primary lowland rain forests are comprised of broadleaved evergreen trees (e.g., *Swietenia macrophylla* and *Pterocarpus officinalis*) with occasional deciduous species (*Tabebuia chrysantha* and *Ceiba pendantra*). The dense canopy is typically 25–35 m high, and epiphytes are abundant.

Human habitation and farms are not uniformly distributed in the RPBR. From the mouth of the Río Plátano to 25 km upstream, there are no permanent settlements; Miskito Indians from the coast maintain scattered dwellings along the river, where they live periodically during the growing season (January–June) and near which they cultivate rice, manioc, and beans. Because all travel is by dugout canoe and daily life revolves around the river, agricultural plots are most commonly located less than 1 km from the river. Distributed among these plots, and more than 1 km from the river, undisturbed primary forests remain. Permanent human habitation is centralized around the single village of Las Marias, 25 km from the river mouth. There, 322 Pech and Miskito Indians live in 48 households (C. A. Hernandez, pers. comm.). Upper reaches of the watershed contain only uninterrupted primary forest. The overall effect of human activities, then, is to create a mosaic of farmed plots, habitats in various stages of regeneration, and primary forests along the river, all surrounded by extensive primary forest. Study sites were located in undisturbed and farmed forests in the Río Plátano watershed, with Las Marias located at the center of the study area.

LANDSCAPE HETEROGENEITY.—Based on my principal research objective of comparing habitat mosaics and raptor species diversity at a landscape level, I surveyed landscape heterogeneity in 24 1 km² plots. From January to June 1996 and 1997, I mapped five different habitats by hand on enlargements of 1:50,000 topographic maps following the approach of Jullien and Thiollay (1996). I then estimated landscape heterogeneity using the Shan-

non index: $H' = -\sum p_i \ln p_i$, where p_i is the proportion of total area of the i th habitat (Magurran 1988). The habitats mapped were: (1) CORE. Core forest area is defined as unbroken interior forest tracts 100 m or more from any edge. Core forests were identified on the basis of characters representing mature forest: tall (25–35 m) canopy, multiple canopy strata, abundant lianas, tree stems of all sizes, and the presence of large trees greater than 100 cm diameter at breast height (DBH). Temple (1986) found this core area to be a better predictor of forest-interior bird abundance than total forest area. (2) EDGE. Forested area 0–100 m from any edge. Edge forests had noticeably greater light penetration and lower humidity than core forests, with a resultant increase in shrubs and lianas. Second growth forests resulting from and usually surrounding agricultural plots were included in edge. These forests were characterized by short stature (5–10 m), a single-stratum canopy, absence of lianas, and uniform stem diameters. Forest edges are known to affect the composition of vertebrate communities (Rosenberg & Raphael 1986, Yahner 1988). (3) AG. Land area under active cultivation of any crop (manioc, beans, corn, rice, and miscellaneous bananas, in decreasing order of frequency). In some cases, I identified fields as AG even though they had been abandoned for up to one year. I did so when these fields retained characteristics of agricultural plots (*i.e.*, monocultures of self-regenerating crop plants with little to no regrowth of weeds or herbaceous plants). (4) REGEN. Land area once cleared for agriculture but since abandoned and left to regenerate. Such areas are commonly referred to as “fallows” in shifting cultivation terminology, and universally called “guamiles” in Central America. These areas had been abandoned for two to ten years (as determined by interviews with local people and personal observation). They were characterized by tall (2–3 m) and virtually impenetrable plant growth, and had not been abandoned long enough to adopt characteristics of either primary or second-growth forest (*e.g.*, a closed canopy of trees >5 m tall). Bird species diversity in the Neotropics has been reported to differ between fallows and core forest (Kricher & Davis 1992, Petit *et al.* 1992). (5) GRASS. Land area covered in tall (2–3 m) rank grasses (*Gynerium sagittatum*). This grass covered substantial areas (>10 ha) in some parts of the study area, and was especially common in low-lying areas favored for growing manioc. These areas were impenetrable and differed from REGEN in being essentially a monoculture of grass.

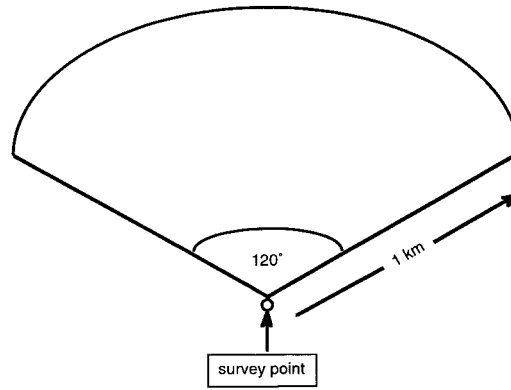


FIGURE 1. Design of an above-canopy survey plot for observing diurnal raptors in lowland tropical rain forest. Area of the plot is 1 km².

DIURNAL RAPTOR SURVEYS.—Point counts were conducted in wedge-shaped quadrats 1 km² in size from vantage points above the forest canopy (Fig. 1; Whitacre *et al.* 1992). Vantage points included one hilltop and 23 emergent trees accessed using standard arborist techniques.

Survey plots were initially divided into two gross habitat categories: undisturbed primary forests and fragmented forests partially cleared for agriculture. Also, because the locations of survey plots depended directly on the location of shifting cultivation in the study area, I made no attempt to randomize or stratify plot location. Instead, plot locations were identified based on three general criteria: plots contained a vantage point providing unobstructed views over their entirety, they were located 1 km or more from other plots surveyed the same year, and plot boundaries were 100 m or more from the Río Plátano or large streams with open canopies to reduce edge effects. Additionally, plots in primary forest were selected when they had no recent history of agriculture within their boundaries (as determined by interviews with local residents and personal observation), and were located 1 km or more from active agriculture. Fragmented forest plots contained various combinations of primary forest and modified habitats. A minimum distance of 1 km was maintained between quadrats surveyed the same year to reduce the likelihood of repeated observations of individuals of large, wide-ranging species such as vultures (Cathartidae) and hawk-eagles (principally *Spizaetus tyrannus*).

Raptors were counted during four-hour surveys that began three hours after dawn. This time period was chosen to coincide with peak raptor ac-

TABLE 1. Diurnal raptors observed in three landscape heterogeneity classes of lowland tropical rain forest, northeastern Honduras, 1996 and 1997. Number (N) and relative percentage of total of each species (%), number of plots in which each species occurred (p), and number of individuals observed (i) are given. Distributions that differ substantially from uniform are indicated in bold and by “–” or “+” for species observed less or more frequently than expected, respectively.

| Species | N ^a | % | Het 0 (N = 9) | | Het 1 (N = 6) | | Het 2 (N = 9) | |
|---|----------------|-------|------------------|-------------|------------------|------|------------------|-------------|
| | | | p | i | p | i | p | i |
| Black Vulture <i>Coragyps atratus</i> | 21.0 | 15.34 | 2 | 1.5– | 4 | 8.0 | 9 | 11.5 |
| King Vulture <i>Sarcoramphus papa</i> | 7.0 | 5.11 | 3 | 2.5 | 1 | 1.0 | 4 | 3.5 |
| Turkey Vulture <i>Cathartes aura</i> | 41.0 | 29.93 | 9 | 13.5 | 6 | 14.5 | 9 | 41.0 |
| Gray-headed Kite <i>Leptodon cayanensis</i> | 0.5 | 0.36 | | | | | 1 | 0.5 |
| Hook-billed Kite <i>Chondroheirax uncinatus</i> | 0.5 | 0.36 | | | | | 1 | 0.5 |
| Swallow-tailed Kite <i>Elanoides forficatus</i> | 4.0 | 2.92 | | | 2 | 2.0 | 1 | 2.0 |
| Plumbeous Kite <i>Ictinia plumbea</i> | 12.0 | 8.76 | 1 | 2.0– | 1 | 1.0 | 7 | 9.0+ |
| Semiplumbeous Hawk <i>Leucopternis semiplumbea</i> | 0.5 | 0.36 | 1 | 0.5 | | | | |
| White Hawk <i>Leucopternis albigollis</i> | 14.5 | 10.58 | 7 | 9.5+ | 2 | 4.0 | 2 | 1.0– |
| Great Black Hawk <i>Buteogallus urubitinga</i> | 6.0 | 4.38 | 2 | 1.5 | 1 | 1.0 | 3 | 3.5 |
| Roadside Hawk <i>Buteo magnirostris</i> | 6.0 | 4.38 | 0 | 0.0– | 2 | 2.0 | 6 | 5.0 |
| Short-tailed Hawk <i>Buteo brachyurus</i> | 2.5 | 1.82 | 1 | 0.5 | | | 1 | 2.0 |
| Black-and-white Hawk-Eagle <i>Spizastur melanoleucus</i> | 1.5 | 1.09 | 1 | 0.5 | 1 | 1.0 | | |
| Black Hawk-Eagle <i>Spizaetus tyrannus</i> | 5.5 | 4.01 | 2 | 1.0 | 2 | 1.5 | 4 | 3.0 |
| Ornate Hawk-Eagle <i>Spizaetus ornatus</i> | 1.0 | 0.73 | 1 | 1.0 | | | | |
| Laughing Falcon <i>Herpetotheres cachinnans</i> | 2.0 | 1.46 | 1 | 1.0 | 1 | 0.5 | 1 | 0.5 |
| Barred Forest-Falcon <i>Micrastur ruficollis</i> | 2.0 | 1.46 | | | | | 2 | 2.0 |
| Bat Falcon <i>Falco rufigularis</i> | 8.5 | 6.20 | 2 | 1.5 | 2 | 2.0 | 5 | 5.0 |
| Total | 137.0 | 100.0 | | 36.5 | | 37.0 | | 63.5 |

^a Half-counts of raptors resulted from averaging counts for plots surveyed twice.

tivity, based on personal observation during pilot surveys and prior studies (Iñigo 1991, Whitacre *et al.* 1992). The four-hour survey was further subdivided into 48 five-minute periods and the maximum number of raptors per species was tallied for each period. I detected raptors using both visual and aural cues, and counted any raptor detected within a plot regardless of behavior, age, or whether it was observed crossing the boundaries of the plot. I used the greatest number of birds of each species detected in any five-minute period as the datum in

subsequent analyses of raptor species diversity, richness, and density to avoid inflating raptor counts with birds observed more than once during the survey (Whitacre *et al.* 1992). The Shannon index was used to estimate raptor species diversity.

RESULTS

LANDSCAPE HETEROGENEITY.—Based on habitat maps of 24 1 km² plots, Shannon diversity values for landscape heterogeneity ranged from 0.00 for

TABLE 2. Diurnal raptor species observed in the study area but not detected during above-canopy surveys.

| Common name | Scientific name | Number of observations |
|------------------------|---------------------------------|------------------------|
| Bicolored Hawk | <i>Accipiter bicolor</i> | 1 |
| Crane Hawk | <i>Geranospiza caerulescens</i> | ≥4 |
| Black-collared Hawk | <i>Busarellus nigricollis</i> | 1 |
| Collared Forest-Falcon | <i>Micrastur semitorquatus</i> | ≥10 |
| Harpy Eagle | <i>Harpia harpyja</i> | 1 |

plots containing only core forest to 1.37 for plots containing all five habitat types. To facilitate statistical comparisons, I assigned plots to one of three heterogeneity classes based on their respective Shannon values. HET 0 (low heterogeneity): Plots in undisturbed primary forests containing no human-modified habitats received a Shannon value of $H' = 0$ ($N = 9$); by definition, such plots were 100 percent homogeneous. After consideration of these plots, Shannon values for the remaining 15 plots ranged from 0.4944 to 1.3702. I divided this range in half to form medium and high heterogeneity classes. HET 1 (medium heterogeneity): Shannon values ranged from $H' = 0.4944$ to 0.9162 ($N = 6$). HET 2 (high heterogeneity): Shannon values ranged from $H' = 0.9532$ to 1.3702 ($N = 9$).

Core forest was the most common habitat on the study area, covering 73 percent of all survey plots. Even in the most heterogeneous plot surveyed, core forest was the most common habitat covering 47 percent of the plot; in only 3 of 24 survey plots was core forest cover less than 50 percent. Anthropogenic habitats surpassed 50 percent coverage in only one plot. Results of a chi-square contingency table showed that the distribution of habitats among heterogeneity classes differed significantly from uniform (G -test: $G = 9119.02$, $df = 8$, $P = 0.001$), meaning that plots in the three heterogeneity classes differed in their habitat composition.

RAPTORS.—Twenty-four plots were surveyed for diurnal raptors, resulting in 137 observations of 18 species of raptors (Table 1). An additional 5 raptor

species were observed in the study area but not detected during raptor surveys (Table 2). Survey plots were dispersed over a 560 km² area. Average distance between plots surveyed the same year was 2.2 km in 1996 (range = 1.75–3.5 km), and 1.75 km in 1997 (1.0–4.5 km); I felt certain that these between-plot distances gave the most independent observations that were logistically possible. The distance from survey plots to the Río Plátano and/or large streams with open canopies ranged from 100 to 2750 m.

Results of a contingency table analysis for species observed more than four times indicated that the distribution of raptor species differed from uniform among landscape heterogeneity classes (G -test: $G = 34.583$, $df = 18$, $P = 0.011$; Table 1). Four species in particular departed substantially from the expected observation frequency. Black Vultures (*Coragyps atratus*), Plumbeous Kites (*Ictinia plumbea*), and Roadside Hawks (*Buteo magnirostris*), were observed less frequently in core forest than expected by chance alone. Plumbeous Kites were also observed more often in forest/cultivation habitat mosaics than expected, and White Hawks (*Leucopternis albicollis*) were observed more often than expected in core forests.

Diurnal raptor density averaged 3.89, 6.17, and 7.11 raptors for HET 0, HET 1, and HET 2 landscape heterogeneity classes, respectively (Table 3). Results of a multivariate analysis of variance (MANOVA) showed that raptor density, richness, and species diversity increased significantly with increasing landscape heterogeneity (MANOVA Wilks' lambda = 0.295, $df = 6, 38$, $F = 5.329$, $P = 0.005$). Results from preplanned linear con-

TABLE 3. Mean (\pm SE) diurnal raptor density, species richness, and species diversity for survey plots in lowland rain forest with low (Het 0), medium (Het 1), and high (Het 2) landscape heterogeneity.

| Variable | Het 0 ($N = 9$) | Het 1 ($N = 6$) | Het 2 ($N = 9$) | P |
|----------------------------|----------------------|----------------------|----------------------|--------|
| Raptor density | 3.89 \pm 0.57 | 6.17 \pm 0.69 | 7.11 \pm 0.57 | 0.0020 |
| Species richness | 2.83 \pm 0.26 | 3.83 \pm 0.31 | 5.16 \pm 0.26 | 0.0001 |
| Species diversity (H') | 0.97 \pm 0.08 | 1.19 \pm 0.10 | 1.56 \pm 0.08 | 0.0001 |

trasts showed that these three variables also differed significantly between survey plots with no or some heterogeneity (HET 0 vs. HET 1 and HET 2 classes), and between plots with medium and high heterogeneity (HET 1 vs. HET 2; data not shown).

There may have been alternative explanations for my finding higher raptor density, richness, and diversity of raptors in farmed habitats than in continuous forest plots. First, raptors may have been more observable in farmed plots within forest openings. To test this assumption, I compared the length of individual raptor observations (*i.e.*, the number of consecutive 5-min intervals that raptors were observed) in the three landscape heterogeneity classes using a contingency table analysis with a *G*-test. My logic was that if raptors were easier to detect in one habitat, the length of time they were observed should also have been longer in that habitat. Observation lengths did not differ significantly from a uniform distribution ($G = 11.593$, $df = 8$, $P = 0.170$; data not shown), indicating that observations were not longer and raptors were not more observable in open habitats. Second, raptor density, richness, and diversity may have increased in farmed plots if these plots were nearer to riverine openings than were unfarmed plots. The result of a simple linear regression of distance from survey plots to riverine openings on raptor species diversity was not significant ($R^2 = 0.12$, $F = 4.09$, $P = 0.06$).

LANDSCAPE-RAPTOR RELATIONSHIPS.—I used stepwise multiple regression to assess which habitat type(s), including landscape heterogeneity, best explained raptor species diversity (SAS 1989). Results showed that landscape heterogeneity explained 55.5 percent of raptor species diversity ($R^2 = 0.5546$, $df = 1, 22$, $F = 27.39$, $P = 0.001$; regression equation: $y = 0.497x + 0.944$). No other habitat variable met the 0.15 significance level required for entry into the regression model. I performed a second stepwise multiple regression excluding landscape heterogeneity from the model to examine which specific habitat(s), when taken as a group, best explained raptor species diversity. Percent core forest and grass cover explained 54.1 and 8.9 percent of raptor species diversity, respectively. Because stepwise procedures do not always select the most influential variables from a given data set (Wilkinson 1987), I followed the suggestion of James and McCulloch (1990); *i.e.*, I subjectively combined variables into likely meaningful groups and performed a partial regression on each group. The strongest regression was derived from the three var-

iables selected using the two stepwise regressions: landscape heterogeneity, core forest cover, and grass cover ($R^2 = 0.58$, $df = 3, 20$, $F = 11.53$, $P = 0.0001$).

DISCUSSION

LANDSCAPE HETEROGENEITY.—Shifting cultivation increased landscape heterogeneity in the study area, a result probably derived from a difference in gap size and severity of disturbance. Agricultural clearings differed in two important ways from natural forest gaps. First, agricultural gaps were likely larger, ranging from 100 m² to ca 0.5 km² in size. Size estimates from the literature for natural canopy gaps range from 87 to 125 m² in Costa Rica (Hartshorn 1978) to between 20 and 705 m² in Panama (Brokaw 1985). Hartshorn (1980) referred to "large gaps" as having an area of more than 100 m². Brokaw (1982) noted that, although there was a wide range of gap sizes on Barro Colorado Island, Panama, the majority of treefall gaps were in the 20–60 m² range. Thus, only the smallest gaps around Las Marias were in the size range reported for natural gaps elsewhere in the Neotropics.

Second, in comparison to natural gaps, clearings that resulted from shifting cultivation represented more severe disturbances of longer duration than normally occur in natural settings. Regeneration in gaps slashed and burned from the forest and subsequently farmed for two to three years differs substantially from natural gaps because natural processes of succession are prohibited or retarded by agricultural practices (Uhl *et al.* 1988, Janzen 1990).

Few objective measures of landscape heterogeneity have been reported. Jullien and Thiollay (1996) compared raptor species diversity along natural and anthropogenic landscape heterogeneity gradients in French Guiana. In natural habitats, species diversity was highest in riparian forests containing openings and successional forests associated with watercourses. Likewise, logged forests with more than 66 percent forest cover had higher species diversity than similar forests with less than 66 or nearly 100 percent forest cover. In comparison, my high landscape heterogeneity class, which had the highest raptor species diversity, averaged 67 percent core forest coverage with a range of 37 to 89 percent coverage.

DIURNAL RAPTOR.—Of the 18 raptor species observed during the study, only the White Hawk was noticeably more abundant in primary forest, and

decreasingly abundant in farmed forests. This was consistent with observations in Mexico, Guatemala, and French Guiana in which this species was found less frequently in human-modified landscapes than in primary forest and forest gaps therein. Two other species detected only in primary forest were the Ornate Hawk-Eagle and Semiplumbeous Hawk. From prior studies, we can conclude that the Ornate Hawk-Eagle is a species of primary forest, and although tolerant of forest openings, would suffer negative impacts if the landscape in the RPBR shifted from predominantly forested to principally agricultural habitats. I detected the Semiplumbeous Hawk on four other occasions, all in primary forest. The ten species in the genus *Leucopternis* exhibit an affinity for primary forest interior (Brown & Amadon 1968, Hilty & Brown 1986), and the Semiplumbeous Hawk, occurring here at the northern limit of its range, could decline with further conversion of forest to farmland. Based on our knowledge of the biology of these and other forest-dependent species observed in the study area (*e.g.*, Harpy Eagle, Bicolored Hawk, and Black-and-white Hawk-Eagle), it is reasonable to conclude that increasing deforestation of the RPBR could negatively impact the populations of bird species dependent on vast tracts of primary lowland rain forest.

In contrast, three species (Black Vulture, Plumbeous Kite, and Roadside Hawk) increased in abundance within plots having higher landscape heterogeneity. These species frequent open habitats throughout Honduras wherever anthropogenic disturbances occur (Anderson, pers. obs.). Increases in such common and widespread species does not coincide with or enhance the conservation value of the RPBR for which the reserve was specifically created.

Landscape heterogeneity had a greater effect on the diurnal raptor community than any single habitat type, including percent coverage of core forest or agriculture. Diurnal raptor species density, richness, and diversity were all greatest in survey plots with highest landscape heterogeneity. These findings were consistent with previous studies, which found greater passerine (Remsen & Parker 1983, Terborgh 1986, Robinson & Terborgh 1990) and raptor (Jullien & Thiollay 1996) diversities in more diverse habitats; however, my findings differed from studies that found similar bird species diversities between primary forests and forests experiencing shifting cultivation (Kricher & Davis 1992, Andrade & Rubio-Torgler 1994). This difference was probably due to the fact that agriculture was

relatively more intense in the area I studied. It also argues against generalizing the effects of native peoples on Neotropical ecosystems as either negligible or beneficial.

By enhancing landscape heterogeneity locally, Pech and Miskito agricultural practices may be increasing opportunities for species with a wide range of habitat preferences, foraging tactics, and prey, to coexist. In a more diversified landscape, species requiring open habitats lived in close proximity to those species found in the forest interior. Obviously, some habitats (*e.g.*, cultivated fields) would not have existed in the absence of these peoples, others (regenerating habitats and grassy fields) were more abundant than would have occurred otherwise, and some food sources (carrion from domestic livestock) increased directly because of human activities. Casual field observations also supported these conclusions: many bird species were found locally only in the vicinity of Las Marias, or found in greatly increased numbers there (*e.g.*, Cattle Egret *Bubulcus ibis*, Black Vulture, and Great-tailed Grackle *Quiscalus mexicanus*; Anderson, pers. obs.).

MANAGEMENT IMPLICATIONS.—Based on my findings, it would appear that indigenous shifting cultivation may be a useful tool for increasing biological diversity in nature. I argue against this interpretation. Biosphere reserves like the Río Plátano are internationally recognized areas created in part to protect intact ecosystems; *i.e.*, they contain all historically present components of biodiversity as well as their associated ecological processes. Most importantly, my results indicate the potential for indigenous shifting cultivation to change the structure and functioning of the rain forest ecosystem.

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