

DIVERSITY, COMMUNITY STRUCTURE, AND NICHE CHARACTERISTICS WITHIN A DIURNAL RAPTOR ASSEMBLAGE OF NORTHWESTERN PERU

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Abstract. Despite high raptor diversity and species of conservation importance, little is known about the structuring of raptor communities in tropical regions. We examined diversity across land uses, spatial-niche overlap among species, community structure, and relationships between abundance and niche position/width of diurnal raptors in Peru. Between April and December in 2008 and 2009, we surveyed raptors by distance sampling along transects, and recorded associated habitat data, in 70 randomly selected plots of 1 km² in Cerros de Amotape National Park, the Tumbes National Reserve, and its buffer areas. We recorded 563 sightings of 19 species of diurnal raptors. Abundance and richness were highest in the buffer zone and lowest in the national park. Mantel tests revealed no correlation between the species' spatial-niche overlap and body-size differences, but there was a near-significant relationship between spatial-niche overlap and dietary overlap. A canonical correspondence analysis (CCA) of raptor species and habitat variables ordinated species according to latitude, elevation, percentages of vegetation cover, and, in some cases, individual tree species. Abundance was negatively correlated with habitat-niche position (rarer species used "more extreme" habitats) and positively correlated with niche width (standard deviations of CCA axis scores). There was, however, considerable variation in the abundance–niche width relationship, and we were able to identify species with niches narrower than expected. We then calculated "niche bottlenecks" for each species. There was a strong negative relationship between degree of bottleneck and abundance, with the small rare species having particularly narrow bottlenecks.

Key words: community, neotropics, Peru, raptors, Tumbesian zone.

Diversidad, Estructura Comunitaria y Características del Nicho en un Ensamble de Rapaces Diurnas del Noroeste de Perú

Resumen. A pesar de su alta diversidad y de la presencia de especies de interés para la conservación, se sabe poco sobre la estructura de las comunidades de rapaces en las regiones tropicales. Examinamos la diversidad entre diferentes regímenes de uso de la tierra, la superposición espacial entre especies, la estructura de la comunidad y las relaciones entre abundancia y posición y amplitud de nicho en una comunidad de rapaces en Perú. Entre abril y diciembre del 2008 y 2009, utilizando el método de distancia de muestreo, evaluamos las especies de rapaces a lo largo de transectas y recolectamos información sobre sus hábitats asociados en 70 parcelas de 1 km² seleccionadas al azar en el Parque Nacional Cerros de Amotape, la Reserva Nacional de Tumbes y sus zonas de amortiguamiento. En total registramos 563 avistamientos individuales de 19 especies de rapaces diurnas. La abundancia y riqueza fueron más altas en las zonas de amortiguamiento y más bajas en el parque nacional. Pruebas de Mantel no mostraron correlación entre la superposición espacial y las diferencias de tamaño entre especies, pero hubo una relación casi significativa entre la superposición espacial y el traslape de dietas. Un análisis de correspondencia canónica (ACC) de especies de rapaces y variables de hábitat ordenó las especies de acuerdo a la latitud, elevación, porcentajes de cobertura de vegetación y, en algunos casos, especies de árboles. La abundancia estuvo negativamente correlacionada con la posición de nicho de hábitat (especies más raras usaron hábitats "más extremos") y positivamente correlacionada con la amplitud de nicho (desviaciones estándar de los valores de los ejes del ACC). Hubo, sin embargo, una variación considerable en la relación entre abundancia y amplitud de nicho, y pudimos identificar especies con nichos más estrechos de lo esperado. Luego calculamos "cuellos de botella en los nichos" para cada especie. Hubo una fuerte correlación negativa entre la magnitud del cuello de botella y la abundancia y las especies raras y pequeñas tuvieron cuellos de botella particularmente estrechos.

INTRODUCTION

Tropical ecosystems are the most diverse in the world (Wilson 1988), with 90% of all raptor species occurring wholly or partially in the tropics (Kennedy 1986). With around 34 species,

the forests of extreme northwest Peru hold a particularly rich assemblage of raptors (Piana et al. 2010), including the endangered Gray-backed Hawk (*Pseudastur occidentalis*). Thiollay (1994) considered this region a priority for raptor conservation

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because of the high diversity of raptors and the occurrence of several endemics. As elsewhere in South America, the drier forests of Tumbes are particularly threatened—in western Ecuador and northwestern Peru less than 5% of forest cover remains (Best and Kessler 1995). Birds of prey are difficult to study, and the status and distribution of many species remain poorly known (Bildstein et al. 1998). As top predators, raptors usually occur at low density and occupy large territories and therefore may be sensitive to habitat degradation (Bierregard 1998, Watson 1998). Thiollay (1998) considered habitat loss, degradation, and fragmentation as the main issues in raptor conservation in tropical Asia.

Although several studies have addressed tropical raptors, these have concentrated on the abundance, habitat associations, and ecology of individual species (Whitacre and Thorstrom 1992); there have been few attempts to describe raptor community composition (Thiollay 1996, 2007, Carrete et al. 2009). Studies attempting to identify factors that segregate sympatric raptors have generally been oriented toward dietary structuring of communities (Iriarte et al. 1990), although there is evidence that vegetation cover and structure (Preston 1990) and availability of nesting and perching sites are also factors that segregate (or aggregate) raptor species in the landscape (Janes 1985). Few attempts have been made to characterize and compare species by habitat-niche dimensions such as niche position, width, and overlap (an exception is Thiollay 1993). In this paper, we deal with the ideas of the Grinnellian or Hutchinsonian niche (the habitats within which a species is found, or the multi-dimensional “hypervolume” within which it is found) rather than the Eltonian niche (how a species fits into a community). Niche position can be defined as the typicality of the conditions used by a species (Gregory and Gaston 2000) and, in our study, reflects how extreme or “average” are the habitats a species uses relative to those available in the landscape. Niche width can be defined as the range of conditions used by a species (Gregory and Gaston 2000, Marsden and Whiffin 2003) and, in our study, reflects the proportion of the gradient of variability in a composite of measures of the habitat the species uses. Niche overlap is the degree to which two or more species share niches (Pianka 1974), that is, the proportion of all geographical areas, habitat components, or resources shared by two taxa. In this study we compare spatial niche overlap, or the proportion of sites in which pairs of raptor species were recorded compared to those used by just one of the pair. These measures are seen as being critical drivers of biotic community make-up (Hofer et al. 2004) and have important implications for conservation biology (Devictor et al. 2010). For example, niche position is usually found to have a strong effect on abundance (Seagle and McCracken 1986, Marsden and Whiffin 2003) with extreme niche positions being associated with low abundance, which is itself associated with high extinction risk (Pimm 1988). Niche width is generally not thought to have a strong influence on abundance

(Gaston et al. 1997), but more important may be niches particularly narrow along certain dimensions. For example, if a species has a broad diet and uses a wide range of habitats for foraging, yet has an extremely specialized breeding habitat (it has a narrow niche in breeding habitat), then it may be particularly vulnerable to relatively small anthropogenic habitat changes if they occur on the dimension on which its niche is narrowest. We term this narrow niche a “niche bottleneck,” and in this paper we compare the width of a species’ habitat niche across several habitat gradients to determine how severe any niche bottleneck might be.

Our aim was to examine the make-up of the diurnal raptor assemblage in Tumbes, northwestern Peru, in terms of abundance, spatial niche overlap across species, and the main environmental drivers of assemblage patterns. We then look at the relationships between abundance and niche characteristics to determine if some species may be particularly susceptible to declines or local extinction due to their specialization in particular habitats or their intolerance of the anthropogenic environmental changes underway in the area. We include an investigation into the extent to which individual species’ habitat niches might be constricted on particular habitat gradients and whether such niche bottlenecks have an influence on local abundance.

METHODS

STUDY AREA

Located in the centre of the Tumbesian Endemic Zone, the North Western Biosphere Reserve is a set of three adjacent protected areas, Cerros de Amotape National Park (CANP), the Tumbes National Reserve (TNR), and El Angolo Hunting Preserve. Together they preserve 230 000 ha of dry, semi-deciduous, and deciduous forests, the largest tract of these forest types still remaining in the whole Tumbesian endemic region (Best and Kessler 1995). These protected areas are Important Bird Areas from which at least 34 diurnal raptors have been reported (Angulo 2009, Piana et al. 2010). CANP is a strictly protected area within which no direct use of natural resources is allowed. However, because of poorly implemented control policies the park is used for free-range cattle grazing and hunting. TNR is a national protected area where direct use of natural resources is allowed as long as these uses are compatible with the objectives of the reserve and its management plans. In the sections we surveyed, these activities included low-intensity timber extraction, hunting, cattle grazing, and conversion of forest to pastures. According to the Peruvian Law No. 26834, buffer areas are not part of the protected areas yet activities there should be compatible with the objectives of the protected areas adjacent to them. Despite this, human-induced activities in the buffer areas we studied ranged from forest clearing for agriculture and pastures, free-range cattle grazing, hunting,

commercial and subsistence logging, extraction of non-timber forest products (e.g., collection of fruits, parrots). During field work we never encountered any representatives of the park or reserve administration in the buffer zone.

We selected a study area of 25 × 25 km (62 500 ha) in the northern part of the North Western Biosphere Reserve, the center of this square lying over the El Caucho Research Station (Fig. 1). The study area encompassed the northern sector of the CANP and the TNR, from the small town of El Tutumo (3° 45' S) in the park's buffer area to Quebrada El Ebano (4° S) and from the small town of Belen (80° 30' W) to the Tumbes river on the border with Ecuador (80° 45' W, eastern limit of the TNR).

The study area includes four main habitat types within the seasonally dry tropical forests (Linares-Palomino 2006). Classification of these habitats is based on Aguirre et al. (2006), although we divided the deciduous forest further into two habitat types. The habitats considered were dry savanna (30–100 m above sea level), where algarrobo (*Prosopis pallida*) and faique (*Acacia macracantha*) trees dominated the vegetation; dry deciduous forest (100–300 m), where madero (*Tabebuia bilbergi*) trees dominated and some ceibo (*Ceiba trichistrandra*) and pasallo (*Eriotheca ruizii*) trees occurred; deciduous forest (300–600 m), where guásimo (*Guazuma ulmifolia*) dominated the lower strata and ceibo the upper strata,

and semi-deciduous forest (>600 m), with Fernán Sanchez (*Triplaris cumingiana*), guaruma (*Cecropia littoralis*), polopolo (*Choclospermun vitifolium*), and ceibo. Precipitation in the study area is approximately 520 mm per year and is markedly seasonal with a rainy season from January to April (85% of annual precipitation). Average yearly temperature is 26°C, with night temperatures higher in lower areas. During El Niño precipitation in Tumbes department can be many times higher than in average years, and the average temperature can increase by 2° C (CDC-UNALM 1992).

RAPTOR SURVEYS AND HABITAT RECORDINGS

We recorded data on raptors and their habitats over two field seasons, April–December of 2008 and 2009. Such long periods in the field were necessary for us to cover the large areas and to accumulate sufficient raptor records. Long field seasons may introduce biases due to seasonality, but we surveyed only outside of the local wet season. All raptor species included were resident in the area. Breeding is most likely during the wet season (Vargas 1995), and we noted no transportation of nesting materials, active nests, or prey supply to nestlings during the field work.

We established 70 plots of 1 × 1 km in the 25 × 25-km study area (11.2% of the total area). Plots were allocated

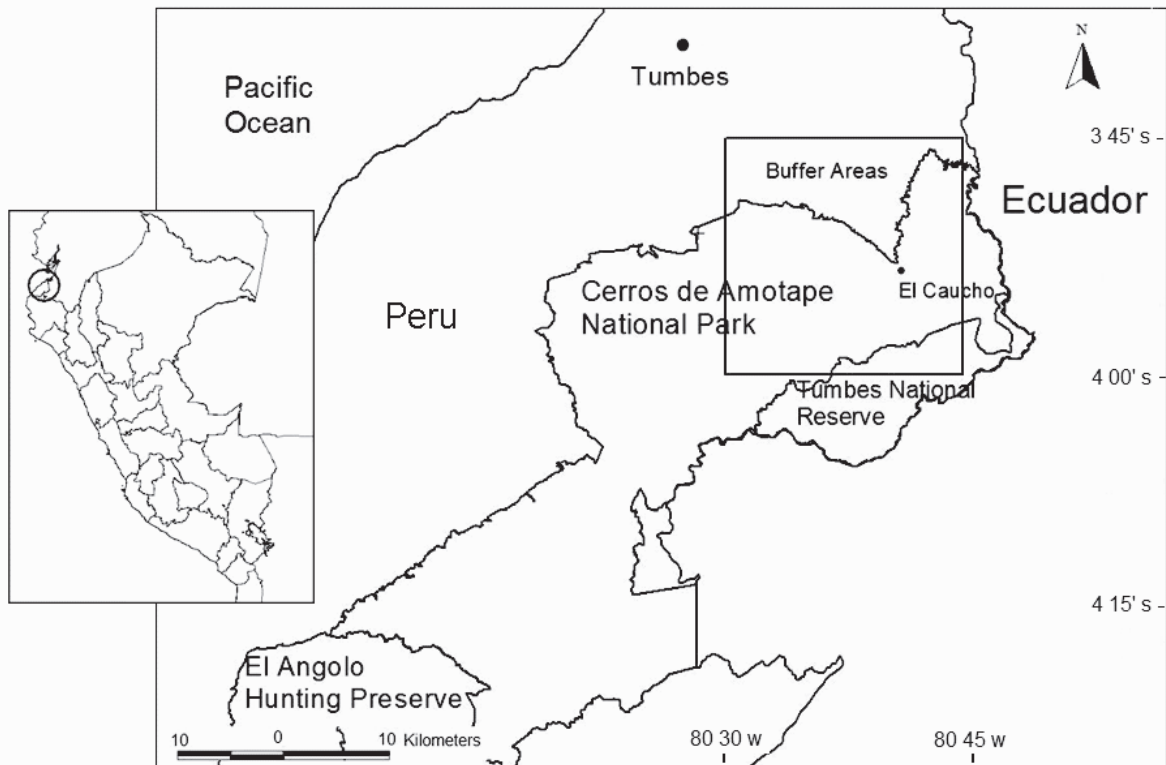


FIGURE 1. Study area in northwestern Peru.

randomly without stratification within all areas of the study site except the TNR. A few plots were too remote to allow safe access so for these we substituted plots up to 2 km closer to existing trails (Thiollay 1993). We chose plots so that no two fell in adjacent squares. Six 1-km² plots were randomly positioned in the reserve for an assessment of the effects of intense cattle grazing. We used existing trails as transects or cut new ones; in each square, transects were 1.8 km long, ideally 0.7 km long, followed by a segment 0.4 km long perpendicular to the first, then another segment of 0.7 km parallel with the first. We maintained a walking speed of 1 km hr⁻¹. Transects were walked only once in the morning, 90 min after sunrise, sometimes later if rain or fog reduced raptors' detectability/activity (Thiollay 1989).

We walked only one transect per day. We accept that time spent surveying within the 1-km² squares was low (around 2 hr on the formal survey). This may give rise to problems with defining true absences from squares, especially if raptors were more easily detected in some habitats than in others (Buckland et al. 2001). In our examinations of niche positions and widths, we might expect bias to be fairly consistent across species.

We recorded all diurnal raptors heard or seen perched or flying along each transect, identifying them to species, age, sex, and color morph. We recorded the horizontal distance to each bird with a laser rangefinder. Additionally, we noted characteristics of individuals (absence of feathers due to molt on flying birds) and excluded from the counts birds we suspected to have been detected previously. We acknowledge, however, that some individuals may have been double-counted (we suggest that the importance of this is not so great, as the main currency of our bird data is bird occurrence within plots rather than numbers).

We took habitat measurements at eight points, 200 m apart, along each transect. To avoid possible biases derived from sampling along edges, we made the measurements 15 m from the trail inside the forest. We recorded the elevation, latitude, and longitude with a GPS and measured the gradient with a clinometer. Although the study area is not large, the coordinates are important, as they allow identification of geographical relationships within the raptor community (for example, the north tends to be wetter than the south). There was no significant correlation between elevation and latitude or longitude ($r_{sMax} = 0.12$, $P_{Min} = 0.33$), so the geographical variables are not simply surrogates for relief.

We visually estimated the canopy height, height of upper vegetation strata (the height at which the mid point of the uppermost vegetation continuum was located), and percentage cover at different four vegetation strata (0–1 m, 1–5 m, 5–15 m, and 15–25 m above ground), the last in increments of 5% within a 10-m-radius circle above the recorder. We then averaged these values across the eight points along each transect, to some degree lessening issues of inaccuracy or unusual readings at individual points. We selected, identified,

and measured the diameter at breast height (dbh) of the two largest trees within 15 m of the plot's central point if they were one of the following species: algarrobo, faique, madero, ceibo, guásimo, or polopolo (see Study Area for details of these trees' ecological significance).

We detected 19 species of raptors but analyzed only 14 (those species noted in seven or more plots): the Turkey Vulture (*Cathartes aura*), Black Vulture (*Coragyps atratus*), King Vulture (*Sarcoramphus papa*), Bicolored Hawk (*Accipiter bicolor*), Crane Hawk (*Geranospiza caerulescens*), Great Black-Hawk (*Buteogallus urubitinga*), Harris's Hawk (*Parabuteo unicinctus*), Gray-backed Hawk (*Pseudastur occidentalis*), Short-tailed Hawk (*Buteo brachyurus*), Zone-tailed Hawk (*Buteo albonotatus*), Black Hawk-Eagle (*Spizaetus tyrannus*), Laughing Falcon (*Herpethoteres cachinnans*), Crested Caracara (*Caracara cheriway*), and Bat Falcon (*Falco rufigularis*). Species not included (all resident in the study area) were the Swallow-tailed Kite (*Elanoides forficatus*), Savanna Hawk (*Buteogallus meridionalis*), Roadside Hawk (*Rupornis magnirostris*), Collared Forest-Falcon (*Micrastur semitorquatus*), and American Kestrel (*Falco sparverius*).

STATISTICAL ANALYSES

We expressed raptor abundance in two ways. The first was a simple rate of encounter of both flying and perched birds expressed as the number of individuals of each species recorded along the 1.8 km of transect within each square. The second was an indication of density derived through distance sampling (Buckland et al. 2001, 2008) with Distance 6.0 (Thomas et al. 2010). To maximize sample size for individual species, we included in the analysis, data from both perched and flying birds, so our derived densities are more than likely overestimates of the birds' true density (Marsden 1999). Our method does, however, attempt to account for differences in detectability across species and habitats. We used the Multiple Covariates Distance sampling engine of Distance 6.0 with land-use type as a covariate for the commoner species and species as a covariate for the rarer species. There was a significant positive correlation between a species' encounter rate and density estimate ($r = +0.83$, $df = 12$, $P < 0.001$).

We tested for differences in encounter rates and species richness (number of species recorded within each km²) across habitat types and land uses with Kruskal–Wallis ANOVAs. We calculated spatial niche overlap between species' occupancy of a square with the symmetric equation formula proposed by Pianka (1973)

$$O_{ij} = \frac{\sum_{i=1}^n P_{ij} P_{ik}}{\sqrt{\left(\sum_{j=1}^n P_{ij}^2\right) \left(\sum_{k=1}^n P_{ik}^2\right)}}$$

where p_{ij} and p_{ik} are the proportions of all records of the j th and k th raptor species within the i th square, with values ranging from 0 (no overlap) to 1 (complete overlap); for this we used the number of plots in which a species was recorded. We assessed relationships between degree of spatial niche overlap between pairs of species and body-size differences (Marquez et al. 2005) and dietary overlap between those pairs of species by Mantel tests with the software PAST (Hammer et al. 2001). Dietary-overlap data were taken from the Global Raptor Information Network (2010) database and were expressed as the number of dietary items (from a list of nine categories: insects, crustaceans, fish, amphibians, reptiles, birds, terrestrial mammals, bats, carrion) shared by each pair of species. Significance level was set at 0.05.

We used canonical correspondence analysis (CCA) in PAST (Hammer et al. 2001) to ordinate raptor species along the main community and environmental axes. CCA is an ordination method that incorporates habitat variables into the analysis so the axes of the final ordination are a linear combination of environmental variables and species data (ter Braak 1986, Henderson and Seaby 2008). In CCA, explanatory variables are represented as vectors pointing to higher values of that variable; their relative lengths are directly proportional to their importance in influencing community structure (ter Braak 1986, Grand and Cushman 2003). We included only the 14 species recorded in $>7 \text{ km}^2$. Environmental variables entered were means of the variables recorded at each habitat plot along each transect (thus were averages within each km^2). Counts of tree species recorded >49 times were included (species were ceibo, polopolo, guásimo, algarrobo, faique, and madero).

We calculated values of habitat-niche position for each species by summing the absolute deviations of each species' centroid from the origin on each of the four main CCA axes.

Niche widths were obtained from the standard deviations of the presence of species in each plot and canonical values for the first four axes (Carnes and Slade 1982) with SPSS 16.0 (SPSS 2007). We considered canonical values per axis as the dependent variable.

RESULTS

RAPTOR ABUNDANCE/RICHNESS AND SPATIAL DISTRIBUTION

We recorded 563 sightings of 19 raptor species along transects but included only species with more than seven records (see Methods) in subsequent analyses of species abundance, spatial niche overlap, and niche position, widths, and bottlenecks. The community was dominated by two vultures, the Turkey Vulture (148 records) and Black Vulture (139 records), along with Harris's Hawk (55 records), the Laughing Falcon (44 records), and the endangered Gray-backed Hawk (34 records). In all, these five species contributed 75% of all raptors recorded. Of the Accipitridae and Falconidae, Harris's Hawk was detected in 32 plots, the Laughing Falcon in 30, and the Gray-backed Hawk in 17.

Encounter rates and species richness did not differ across the four habitat types (Kruskal–Wallis nonparametric ANOVA) but did differ (with vultures both included and excluded) across the three land-use regimes: CANP, TNR, and buffer areas. Encounter rates and species richness tended to be highest in the buffer zone and lowest in the national park (Table 1).

Spatial niche overlap between pairs of species is presented in Table 2. There was no significant correlation between measures of spatial niche overlap between species and the differences in their body masses (Mantel test; $r = +0.04$, $P = 0.32$). There was, however, a nearly significant positive

TABLE 1. Encounter rates (median number of individuals encountered per km^2 ; interquartile range in parentheses) and species richness (median number species recorded per km^2 ; interquartile range in parentheses) of raptors in various habitats and land uses. Dual analyses included or excluded the dominant vulture species, the Turkey Vulture and Black Vulture.^a

	n^b	Vultures included		Vultures excluded	
		Encounter rate	Richness	Encounter rate	Richness
Habitat type					
Dry savanna	9	9 (4–14)	4 (2–5)	2 (2–4)	2 (1–3)
Dry deciduous	26	6.5 (4–13)	4 (2–5)	3.5 (2–6)	2 (2–4)
Deciduous	17	7 (3–13)	4 (2–6)	4 (2–7)	3 (2–4)
Semi-deciduous	18	5 (2–8)	3.5 (2–4)	3 (2–4)	2.5 (1–4)
Difference (H)		3.9 ns	1.5 ns	4.7 ns	3.7 ns
Land use					
National park	32	4.5 (2–9)	3 (2–4)	3 (2–5)	2 (1–4)
National reserve	6	7 (4–12)	4 (2–5)	4 (2–6)	2.5 (1–4)
Buffer zone	32	16.5 (12–27)	6.5 (4–9)	4 (2–6)	2.5 (1–4)
Difference (H)		13.1**	9.2*	8.3*	5.0 ns

^aLevels of significance: * $P < 0.05$; ** $P < 0.005$; ns, not significant.

^bNumber of sample squares in each habitat type/land use.

TABLE 2. Measures of spatial niche overlap (Pianka 1973) between 14 abundant raptors in Tumbes, northwestern Peru.

	Black Vulture	King Vulture	Bicolored Hawk	Crane Hawk	Great Black-Hawk	Harris's Hawk	Gray-backed Hawk	Short-tailed Hawk	Zone-tailed Hawk	Black Hawk-Eagle	Laughing Falcon	Crested Caracara	Bat Falcon
Turkey Vulture	0.68	0.20	0.12	0.20	0.34	0.81	0.29	0.38	0.44	0.20	0.30	0.33	0.32
Black Vulture		0.33	0.02	0.10	0.35	0.63	0.30	0.47	0.38	0.28	0.20	0.34	0.26
King Vulture			0.11	0.00	0.33	0.13	0.28	0.20	0.03	0.24	0.24	0.09	0.19
Bicolored Hawk				0.07	0.16	0.18	0.00	0.00	0.07	0.08	0.15	0.00	0.00
Crane Hawk					0.00	0.11	0.14	0.19	0.00	0.10	0.04	0.00	0.00
Great Black-Hawk						0.52	0.29	0.42	0.25	0.27	0.19	0.13	0.23
Harris's Hawk							0.22	0.42	0.27	0.31	0.38	0.60	0.33
Gray-backed Hawk								0.38	0.39	0.26	0.28	0.06	0.42
Short-tailed Hawk									0.34	0.36	0.24	0.20	0.21
Zone-tailed Hawk										0.10	0.36	0.00	0.17
Black Hawk-Eagle											0.25	0.00	0.07
Laughing Falcon												0.05	0.21
Crested Caracara													0.00

correlation between spatial niche overlap and degree of dietary overlap (Mantel test; $r = +0.17$, $P = 0.09$).

RAPTOR COMMUNITY AND VEGETATION ORDINATION

The four most important CCA axes together accounted for 70.4% of overall variation in the raptor and environmental data. Figure 2 shows correlations between individual environmental variables and numbers of key tree species recorded within plots and scores on axes 1 and 2. Elevation, latitude, tree sizes (dbh and height), percentage of vegetation cover between 5 and 15 m, and numbers of tree species such as guásimo and polopolo were among the most powerful variables for distinguishing the species (Fig. 2, 3).

A few species form outliers on one or more axes (Table 3). The Black Hawk-Eagle had a very high positive score on axis 1 (an association with large trees at higher altitudes), while the Crested Caracara had a high negative score. The Bicolored Hawk had an extreme positive score on axis 2 (an association with large trees and sparse ground cover) and an extreme negative score on axis 3 (an association with lower-elevation forest with dense lower strata). Several species, namely, the Turkey Vulture, Black Vulture, Harris's Hawk, Gray-backed Hawk, Short-tailed Hawk, and Laughing Falcon, have unremarkable scores on most or all axes, indicating that they tend to occupy average habitats. In contrast, the Bicolored Hawk appears to have extreme/unusual habitat positions on several axes.

NICHE CHARACTERISTICS

Density estimates (derived by distance sampling and averaged across all samples within the study area), niche width, niche position, and bottlenecks are presented for each species in Table 4. As expected, there was a significant negative correlation between species density and habitat niche position ($r_s = -0.64$; $P = 0.02$)—common species had centroids usually close to the origin on the four CCA axes.

Abundance (density) was positively correlated with niche width ($r_s = +0.72$; $P < 0.01$), although there was considerable variation in the abundance–niche width relationship for individual species (Fig. 4). The density estimated for the Black Vulture was only one-third of that for the Turkey Vulture, yet the two species had similar niche widths. Of the rare species, the King Vulture, Zone-tailed Hawk, Crested Caracara, and Bat Falcon had unusually narrow niches, the Bicolored Hawk and Crane Hawk relatively wide habitat niches.

The most important bottlenecks in niche width (those axes where individual species had their narrowest niche) were on axes 1 and 2. There was a significant positive relationship between degree of bottleneck and overall niche position ($r_s = +0.59$; $P = 0.03$) and a negative relationship with abundance ($r_s = -0.56$; $P = 0.04$). Again, there was variation across species in the abundance–bottleneck relationship (Fig. 4), with the small rare species (Bicolored Hawk, Crane Hawk, and Bat Falcon) having particularly narrow bottlenecks and the Turkey Vulture, Black Vulture, Harris's Hawk, Gray-backed

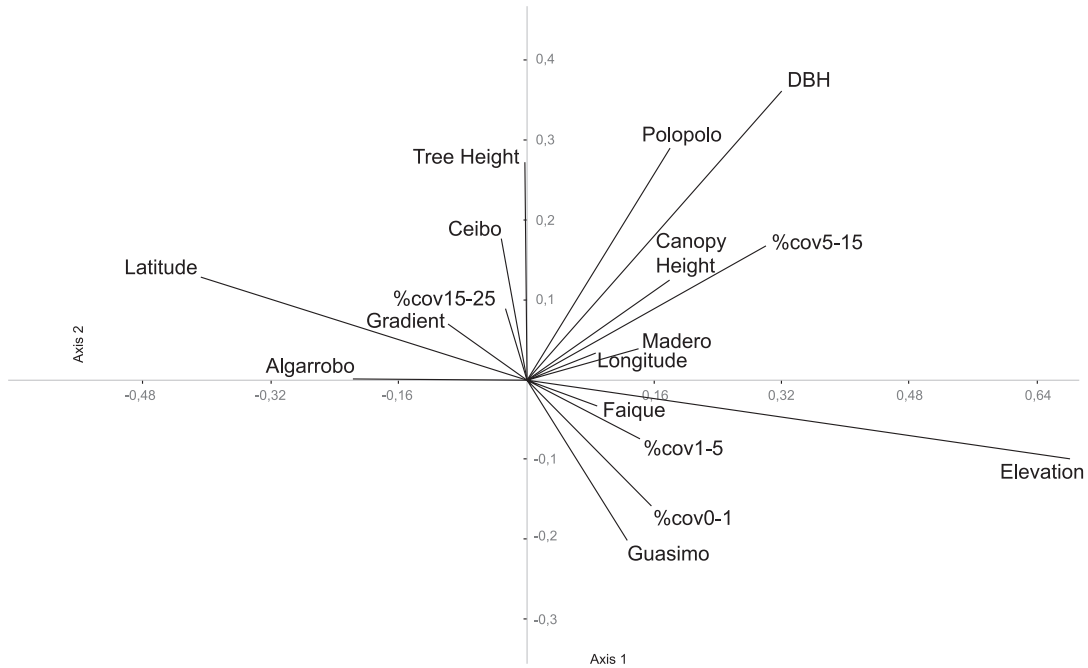


FIGURE 2. Ordination of habitat variables on the first two canonical axes of CCA. Algarrobo, faique, madero, ceibo, guásimo, and polopolo are the numbers of each tree species recorded within the km² (see Study Area for details of these trees' ecological significance). Axis 1: increasing altitude with greater prevalence of large, tall trees and fuller mid-level cover in south. Axis 2: large trees with sparse ground cover and absence of guásimo trees.

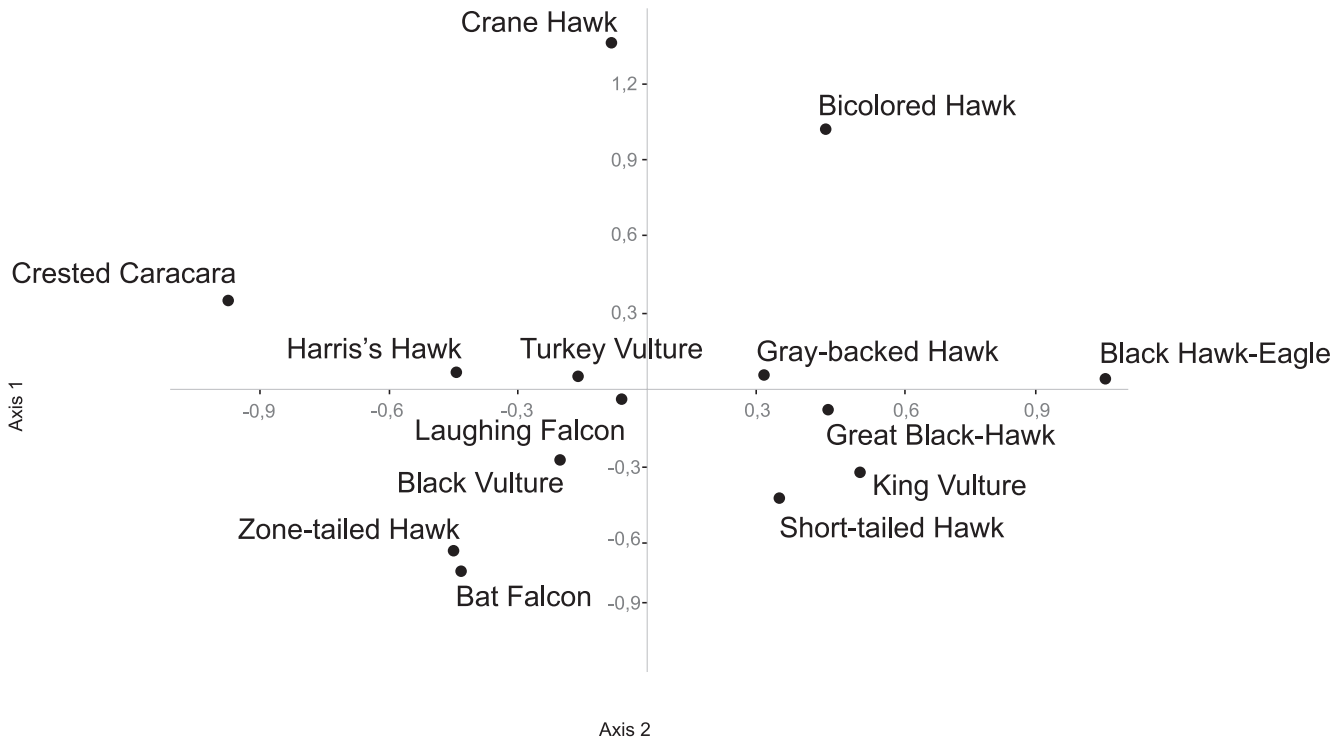


FIGURE 3. Ordination of raptor species on the two first axes of CCA.

TABLE 3. Centroid positions for each raptor species on each of the four main CCA axes. Values < 0.10 are not shown. For interpretations of axes 1 and 2, see Fig. 2. Axis 3: higher areas south of study site with open low strata and large numbers of ceibo trees. Axis 4: relatively flat areas with dense low strata where madero is present and polopolo is absent.

Species	Axis 1	Axis 2	Axis 3	Axis 4
Turkey Vulture	-0.15			
Black Vulture	-0.27	-0.27		+0.25
King Vulture	+0.54	-0.33	-0.21	+0.40
Bicolored Hawk	+0.49	+1.07	-1.10	+0.88
Crane Hawk	-0.12	+1.33		-0.45
Great Black-Hawk	+0.49		+0.15	
Harris's Hawk	-0.42			-0.22
Gray-backed Hawk	+0.34		+0.28	
Short-tailed Hawk	+0.35	-0.43	+0.45	-0.40
Zone-tailed Hawk	-0.44	-0.65	-0.85	-0.55
Black Hawk-Eagle	+1.29		+0.29	-0.11
Laughing Falcon			-0.21	-0.30
Crested Caracara	-1.07	+0.35	+0.97	+0.32
Bat Falcon	-0.42	-0.70	-0.36	+0.26

Hawk, Short-tailed Hawk, and Crested Caracara showing little constriction on any CCA axis.

DISCUSSION

COMMUNITY ASSEMBLAGE

We were able to separate species in terms of their niche positions and specifically in terms of their associations with environmental variables within the study area. Species preferring habitats with large trees (e.g., Bicolored Hawk) separated from birds that preferred dry forests (e.g., Crested

Caracara) and species preferring borders (e.g., Laughing Falcon). Some inferences regarding habitat preferences can be made between community members that share similar morphometric characters: the Bicolored Hawk and Crane Hawk, both species with long tails, long tarsi, and small body mass (but with different diets; see Thorstrom and Quixhán 2000, Sutter et al. 2001) were associated with very high scores on axis 2 (forest with large trees but sparse ground cover). The Black Hawk-Eagle, another forest specialist with a long tail (Thiollay 2007), was associated with increasing elevation and was relatively common in high-canopy semi-deciduous forests, while the morphologically similar Harris's Hawk was associated with drier habitats in the lowlands where algarrobo trees dominated. The Gray-backed Hawk and Laughing Falcon, similar in body mass, body length, and diet (Vargas 1995, Valdez 1996), were relatively abundant in borders but segregated geographically and by elevation, percentage of vegetation cover from 5 to 15 m, and canopy height.

NICHE RELATIONSHIPS

There was a wide range of variation in habitat niche width among species, and most species appear to be generalists in the use of space. We acknowledge that our inclusion of aerial individuals was not ideal for two reasons. First, it may inflate density estimates for the species, although in this paper we discuss not absolute density but species-specific densities relative to each other, corrected for differences in detectability with the use of distance sampling (e.g., Buckland et al. 2001). Second, our inclusion of aerial birds means that individuals we recorded over a particular square did not necessarily belong to it since they may have been flying over rather than using the area for hunting. Several studies (Seagle and McCracken

TABLE 4. Density estimates (95% confidence intervals), niche position, width, and bottleneck for raptors in Tumbes, Peru. Niche bottleneck was calculated as deviation of the minimum niche width on any single axis from the mean niche width (on all four axes) divided by this mean. Thus large values indicate a narrow minimum niche width. Also shown is the axis on which niche width was narrowest.

Species	Density (individuals km ⁻²)	Niche position	Niche width	Niche bottleneck (axis)
Turkey Vulture	2.4 (1.6–3.6)	0.61	3.14	0.22 (1)
Black Vulture	0.78 (0.49–1.3)	1.42	1.95	0.12 (1)
King Vulture	0.14 (0.07–0.27)	2.24	0.63	0.38 (1)
Bicolored Hawk	0.13 (0.06–0.30)	7.27	1.93	0.75 (1)
Crane Hawk	0.49 (0.23–0.04)	2.99	7.50	0.54 (1)
Great Black-Hawk	0.36 (0.20–0.67)	1.56	1.60	0.31 (2)
Harris's Hawk	0.85 (0.57–1.3)	0.76	2.10	0.10 (1)
Gray-backed Hawk	0.29 (0.17–0.50)	1.89	2.63	0.24 (1)
Short-tailed Hawk	0.11 (0.06–0.21)	2.88	1.00	0.19 (3)
Zone-tailed Hawk	0.04 (0.02–0.09)	3.45	0.29	0.45 (2)
Black Hawk-Eagle	0.12 (0.07–0.20)	2.70	1.43	0.38 (2)
Laughing Falcon	0.33 (0.23–0.48)	1.29	2.82	0.34 (1)
Crested Caracara	0.31 (0.14–0.70)	3.46	0.10	0.27 (2)
Bat Falcon	0.08 (0.03–0.17)	2.21	0.10	0.72 (2)

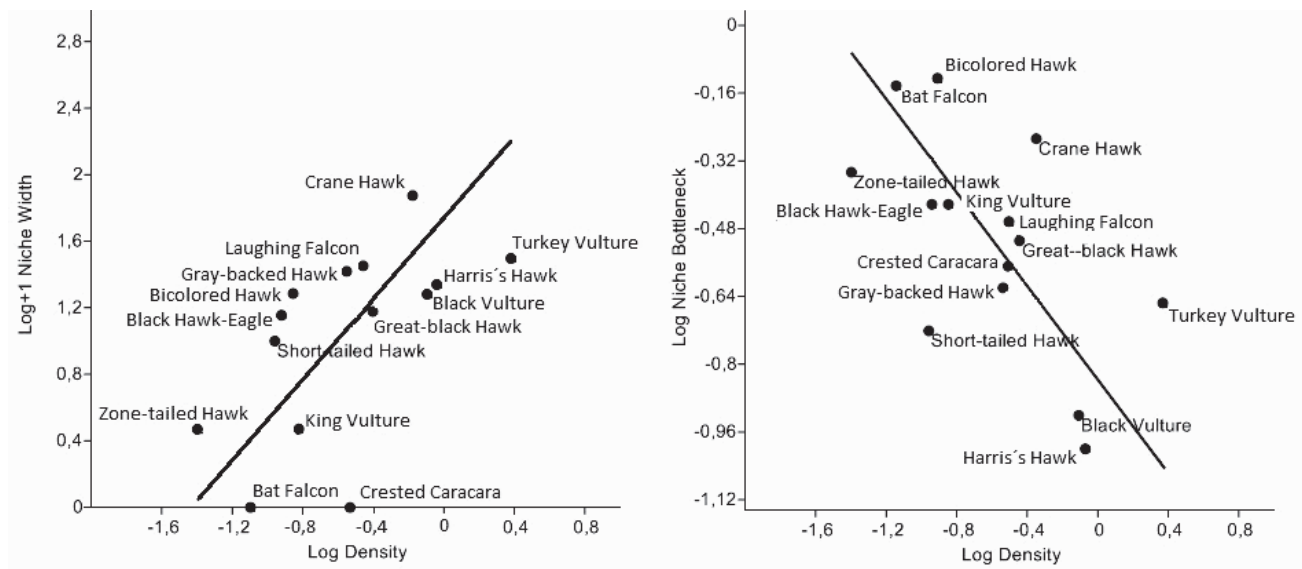


FIGURE 4. Scatterplot of the relationships between log-transformed species densities and log +1 species' habitat niche width and log-transformed species' bottlenecks. Densities were estimated by distance sampling and are averaged across all 70 1-km² squares within the study area.

1986, Gregory and Gaston 2000, Marsden and Whiffin 2003) have found no relationship between bird abundance and niche width (none of the above focused on raptors). In our study we found a significant positive relationship between a species' habitat niche width and abundance. Analysis of data from Table 2 in Thiollay's (1993) study of raptors in India also reveals a positive significant relationship between habitat niche width and species abundance ($r_s = 0.76$; $P = 0.002$), indicating that, in these two raptor communities, species that are able to function in a wider range of habitats are likely to be more abundant overall (Table 4).

Spatial niche overlap (Table 2) indicates how two species shared geographical space, with high values indicating more affinities in the use of spatial resources (Pianka 1974). In our study, species that were usually detected at borders and in degraded areas showed greater niche overlap; whereas forest-interior species showed less niche overlap. Mantel tests revealed no correlation in spatial niche overlap between species and body-size differences, but there was a nearly significant relationship between spatial niche overlap and dietary overlap.

CONSERVATION IMPLICATIONS

There were significant differences in species diversity and abundance of raptors within the three different land-use regimes in the study area. Raptors were more diverse and abundant in the buffer areas, followed by the reserve and the park, despite the last being under the highest level of protection (SPDA 2004). In extreme northwest Peru protection of forested areas outside the TNR and the CANP can help preserve habitats that are fundamental to maintaining this highly

diverse raptor community and the species they support. If properly managed, the recently created Tutumo–Matapalo Conservation Area, in the buffer area north of the CANP, can help to achieve this.

Kruger and Radford (2008) identified body weight, clutch size, and habitat niche width as the three most important variables that predict extinction risk among the Accipitridae. Therefore, in our study, species with higher values of habitat niche width (Crane Hawk, Turkey Vulture, and Laughing Falcon) might be of least conservation concern. Among the Accipitridae, the Great Black-Hawk and Black Hawk-Eagle had the highest body mass, the Gray-backed Hawk the lowest reproductive rate (0.8 fledged young per nest; Vargas 1995). The Black Hawk-Eagle had a narrower habitat niche and a higher niche position than the Great Black-Hawk and, within the community, is probably the most susceptible to habitat loss, particularly of semi-deciduous forest that in extreme northwest Peru occurs only above 600 m in the CANP and has been largely destroyed in adjacent Ecuador (Dodson and Gentry 1991, Best and Kessler 1995). The deciduous forests inside the CANP are probably the largest and more continuous tracts of this habitat still remaining in the whole Tumbesian zone and may be crucial for the species' persistence in this endemic bird area.

Niche bottlenecks show the greatest constriction of a species' niche width on any of the axes (Table 3). There was a very strong positive relationship between bottleneck width and abundance, with the small rare species, the Bicolored Hawk, Crane Hawk, and Bat Falcon, having particularly narrow bottlenecks. This has important implications for conservation management. If we can identify the axis on which a

species has its narrowest niche, then we can use this information to guide habitat management for that species (e.g., Botham et al. 2011). Specifically, we can increase the proportion of habitat within the study area that falls within the range of values (e.g., a range of canopy-closure values or the numbers of a preferred tree species) that the species uses. Habitat management that increases land cover within the species' (realized) niche may be more important on the bottleneck axis than on other habitat axes because the species has a narrower range of tolerance on that niche axis. For example, with the Bicolored Hawk, managing habitat so more areas fall within its niche position on axis 1 may be most beneficial to it—and this corresponds to increases in higher-altitude forest that has large trees and fuller mid-level vegetation cover.

Almost all species we studied are wide ranging, occurring over much of the neotropics. In Peru, these species are widespread east of the Andes but are also present in Tumbes. The only range-restricted species, the endangered Gray-backed Hawk (BirdLife International 2011), was the fifth most often recorded species but had only the eighth highest density estimate (Table 4). This species had an “average” niche position and the fourth widest habitat niche with little niche constriction. In Ecuador the species has been recorded in primary and secondary forests, forest borders, and adjacent agricultural areas and pastures (Vargas 1995, Freile et al. 2004), supporting the idea that it has a wide habitat niche. Despite this, the species' population has, apparently, been in continual decline in Ecuador because of forest destruction for agriculture and cattle ranching (Vargas 1995, BirdLife International 2011). Although it is now evident that the Gray-backed Hawk can use degraded areas, it is not known whether it can breed there, so future research is needed to clarify this.

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