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Effects of habitat degradation on the abundance, richness and diversity of raptors across Neotropical biomes

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ABSTRACT

Population growth and human development result in biodiversity loss and biological homogenization not only in developed countries, but increasingly in the less developed countries as well. In those countries, where urbanization and agricultural intensification occur at a faster rate than in developed countries, habitat degradation appears to be the leading cause of wildlife loss. During the breeding seasons of 2002-2005 we conducted road surveys across five biomes of Argentina to detect variations in raptor community attributes as potential indicators of broad scale habitat degradation. Abundance of individuals, richness and diversity of species were calculated to assess the effects of habitat transformation and patch size on these community attributes. Raptor communities strongly varied in relation to habitat transformations, with lower abundance of individuals, richness and diversity of species in more transformed landscapes. Small patches of natural vegetation and locations in which natural and cultivated lands where interspersed showed lower richness and diversity of raptors than large patches. Fragmentation was the main cause of reductions in abundance of individuals. Although the relative contribution of our two estimates of habitat degradation to abundance, richness and diversity of raptors varied among biomes, these community attributes proved useful as predictors of habitat degradation. This was especially true in habitats where raptor communities are more complex although overall patterns remained constant across biomes, from forests to deserts. Taking into account current trends of habitat transformation (drastic increments in monocultures, urban areas, and habitat patchiness), the conservation of raptor communities in these biomes could be seriously compromised. In terms of species-specific responses of raptors to habitat degradation, a rapid process of homogenization can be expected, resulting in only a few winner species within a general scenario of losers.

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BIOLOGICAL CONSERVATION

1. Introduction

Population growth and human development are two major driving forces behind biodiversity loss not only in developed countries, but increasingly in the less developed countries as well (Savard et al., 2000; McKinney, 2006). In these regions, usually corresponding to biodiversity hotspots (Jha and Bawa, 2006), processes of urbanization and agricultural intensification are occurring faster than in developed countries where landscapes have been largely transformed by human activities over more than 10,000 years (Le Honerou, 1981). This slow rate of transformation might be responsible for the adaptation of many vertebrate species to different semi-natural habitats created by humans (e.g., Bignal and McCracken, 1996; Blanco et al., 1998; Carrete and Donázar, 2005), contrasting with that occurring in many developing countries where rapid habitat degradation appears to be the leading cause of wildlife extinction (BirdLife International, 2000).

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Growing concern about the effects of wide-scale anthropogenic changes to ecosystems has led to a need for monitoring methods to detect variations in biological integrity over large geographic areas. A common tool for monitoring biological integrity is the use of indicator species (Margules and Pressey, 2000). Ideal indicator species include those that are sensitive to the management regime applied, common, widespread, and easy to monitor (Lambeck, 1997). Some bird taxa such as raptors may be appropriate indicators for monitoring changes at an ecosystem scale because they are at the top of food chains, occurring across a broad gradient of anthropogenic disturbance, from pristine wilderness to metropolitan areas, and because individual species are often associated with particular habitat types (e.g., Tella et al., 1998; Sánchez-Zapata et al., 2003; Carrete and Donázar, 2005). Moreover, in some biological systems these top predators are tightly associated with high biodiversity values (Sergio et al., 2008) such that simulated networks of protected sites constructed on the basis of raptors were more efficient for conserving biodiversity than networks based on lower trophic level species, thus justifying their use as flagship

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or umbrella species (Sergio et al., 2006). Nevertheless, the adaptation of some raptors to human-altered environments (Bird et al., 1996; Anderson, 2001; Panasci and Whitacre, 2002) makes their widespread potential as indicators of environmental degradation controversial (Rodríguez-Estrella et al., 1998).

We present here an initial assessment of the effects of recent habitat changes occurring in different Argentinean biomes on raptor communities, looking for potential large-scale indicators of environmental alterations. Our main prediction is that the relative abundance, richness, and diversity of raptors should decrease along gradients of habitat transformation and fragmentation, making them reliable indicators of habitat degradation. Taking into account that not only life history and behaviour but also abundances, habitat selection patterns, and conservation threats of most Neotropical raptor species are very poorly known (del Hoyo et al., 1994; Bierregaard, 1998; Trejo, 2007), we also examined the responses of single species to habitat degradation to disentangle their individual contribution to community patterns. We expected stronger negative responses among supposedly habitat-restrictive species than among generalist raptors. For these purposes, we relied on two rough approaches that allowed us to cover very large areas, (1) roadside counts, a method that despite many limitations (Fuller and Mosher, 1981; Millsap and LeFranc, 1988) has been successfully used to examine relative abundances and habitat preferences of raptors in many large, poorly known regions (e.g., Sánchez-Zapata et al., 2003), and (2) estimates of habitat degradation measured in situ, to yield simple but reliable results comparable among the very different biomes surveyed.

2. Study areas

Field work covered five Neotropical biomes sampled in Argentina, namely: (1) Paraná forest, (2) Espinal, (3) Pampas, (4) Patagonian forest, and (5) Monte desert (Fig. 1).

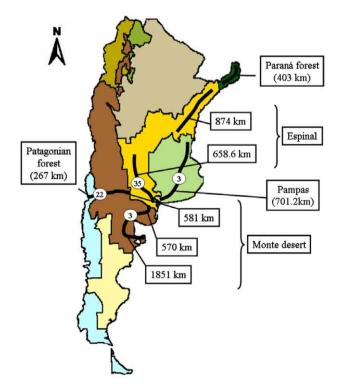


Fig. 1. Main biomes and study areas in Argentina following Cabrera (1976). Lines represent approximately the main national roads (names in circles) where counts were conducted (km surveyed in brackets).

2.1. Paraná forest

Paraná/Paraiba interior forest, spreading from Southeast Brazil and Paraguay to Northern Argentina, represents the largest and best protected portions of the Brazilian Atlantic semi-deciduous rainforest, an ecosystem strongly transformed and fragmented by human activity. There, timber extraction, agriculture and hunting are continuous threats to biodiversity. At present, vegetation is represented by approximately 17,211 km² of well conserved semi-deciduous rainforests, although thousands of 0.01–1 km² remnants surrounded by pastures and agriculture represent the dominant biological scenario (Brown et al., 2006).

2.2. Espinal

This region is a mosaic of ecosystems that combines xerophile woods, palm savannas and flood low lands. Human activities have profoundly changed the composition of the vegetation communities either by destroying the herbaceous layer through cattle-raising or by burning the forest for agriculture. Commercial exploitation of plant species has led to a decline in their abundance, and its continued practice threatens to permanently change the vegetative structure of the region (Brown et al., 2006).

2.3. Pampas

This biome occupies the extensive plains of eastern Argentina. The natural vegetation in the area is composed of grasslands and xeric woodland, with various endemic animals that are threatened by habitat destruction and degradation. This is one of the most heavily populated areas of Argentina and has been extensively used for agriculture and cattle-grazing, the two most severe threats for the region (Brown et al., 2006).

2.4. Patagonian forest

These mountain forests traverse the Southern Andes, bounded on the east by grasslands and to the west by the Pacific Ocean. They represent a unique assemblage of ancient species, both floral and faunal, which today persist as relicts of Gondwanaland. The main threats to these temperate forests include invasion by exotic animal species (e.g., red deer *Cervus elaphus*, wild boars *Sus scrofa*, minks *Mustela vison*, and several species of trout Salmoniformes) and the replacement of the species-rich native forests by monocultures of exotic trees, pressure from tourism, logging for commercial purposes and firewood (Brown et al., 2006).

2.5. Monte desert

This is a warm scrub desert extending along the eastern foothills of the Andes to the Patagonian steppe. Human populations occupy oases in valleys and other locations close to rivers, so some sections of this ecoregion are intensively altered but others are not. The Monte desert is experiencing seriously damaging effects due to human activities, especially overgrazing by sheep and cattle, clear cutting for fuel, and land clearing for agriculture, mining and oil exploration (Brown et al., 2006).

3. Methods

3.1. Species surveyed, road counts, and raptor community structure

Surveys covered diurnal raptors in its broadest sense, including typical birds of prey (Families *Accipitridae* and *Falconidae*) as well as New World vultures (Family *Cathartidae*) (see del Hoyo et al.,

1994; Bierregaard, 1998). Roadside surveys were conducted during the month of December (i.e., breeding season) of the period 2002– 2005, following the methodology widely used for raptors (e.g., Fuller and Mosher, 1981; Donázar et al., 1993; Villafuerte et al., 1998; Sánchez-Zapata et al., 2003; Seoane et al., 2003; Blanco and Montoya, 2004). Counts were done by two experienced observers (the driver and another person), from 2 h after sunrise to 1–2 h before sunset, avoiding adverse weather conditions such as intense heat, rain or fog. Average driving speed was 50–70 km/h. In a few cases it was necessary to stop the vehicle to identify the birds, but we did not record new individuals observed during these stops. Surveys were performed only once for each road transect to avoid pseudoreplication and double counting.

Abundance (number of individuals) was estimated as the total number of individuals counted across transects. Richness was obtained as the total number of species present, while diversity was measured by means of the Shannon–Wiener index.

3.2. Habitat variables

Habitat destruction has different forms, such as fragmentation of natural areas into small patches, or transformation into different habitat types. Thus, we estimated habitat fragmentation by measuring (in km) the longitudinal size of each habitat patch crossed during road surveys. These patches were also categorized within four main groups representing an increasing degree of transformation, namely: (1) natural habitats, (2) natural habitat mixed with cultivated lands, (3) cultivated lands, and (4) urbanized areas. Although these measures may seem crude estimates of habitat transformation, they may be more representative of the actual state of a patch than information available from satellite or GIS maps when transformations are operating in real time (Sánchez-Zapata et al., 2003). Variability in grazing pressure was not included in our habitat sampling, since we focused on broad habitat degradation categories.

3.3. Analytical procedure

We used generalized linear models (GLM) to assess the effects of habitat transformation and patch size on abundance of raptors (both at the community and species levels), and richness and diversity of species in the five biomes surveyed. We modelled abundance and richness (link function: logarithm, and error distribution: Poisson), and diversity (log-transformed; link function: identity, and error distribution: normal) through the GENMOD procedure of the program SAS V8 (SAS Institute Inc., 2004). Abundance, richness, and diversity were calculated for each single patch (n = 391) crossed by our road surveys, constituting the sample units for statistical analyses. Degree of transformation was incorporated in models as a fixed factor with four levels while patch size was included in both its linear and quadratic forms as a covariate. Abundance, richness and diversity were not corrected a priori for patch size because one of our aims was to test this effect. However, the effects of habitat transformations were qualitatively similar when these parameters were corrected a priori for patch size (results not shown).

Following Carrete et al. (2007) we used a deviance partitioning analysis to separate the pure effects of habitat transformation and fragmentation as well as the combined variability of their joint effects. We assumed that the deviance explained by a model is a good measure of the variability in the data set explained by the variables included. Thus, we performed a series of models (habitat fragmentation model, habitat transformation model, and habitat fragmentation + habitat transformation model) to isolate all the components needed for partitioning through simple equation systems.

Table 1

Overall survey characteristics and attributes of raptor communities in five biomes of Argentina.

	Survey (km)	Patches (n)	Raptors			
			Abundance (individuals/km)	Overall richness	Overall diversity	
Paraná forest	403	49	0.47	12	1.71	
Espinal	1532.4	179	0.57	21	2.08	
Pampas	701.2	50	1.61	15	1.30	
Patagonian forest	267	29	0.47	11	2.00	
Monte desert	3002	84	0.23	12	1.66	

4. Results

4.1. Differences among biomes in habitat conservation and raptor communities

We performed more than 5900 km of road counts in five different biomes distributed from Northern to Southern Argentina (Fig. 1; Table 1). Although the most common landscape crossed by our linear surveys was classified as natural (4425.3 km, 75%), counts were performed in habitats with differing degrees of transformation (Fig. 2). Many kilometres of our work traversed areas where natural and agricultural lands were interspersed (845.7 km, 14%), while others crossed completely cultivated areas (333.6 km, 6%). As we used national roads, we often passed through villages and towns (301 km, 5%).

Natural vegetation dominated in most biomes (Patagonian forest: 85%; Espinal: 69%, and Monte desert: 88%), except in the Paraná forest where a mixture of natural vegetation and cultures was the most common habitat type (65%, Fig. 2) and in the Pampas, where almost everything referred to as natural lands are actually semi-natural pastures used for cattle-grazing (see Section 5). Accordingly, the largest patches were those classified as natural vegetation in all biomes except in the Paraná forest (Fig. 2). Highly transformed habitats such as monocultures or urban lands covered more than 10% of the surveyed surface of the Pampas, the Paraná forest, and the Espinal.

Overall, we recorded 2672 diurnal raptors belonging to 29 species of the families *Cathartidae* (n = 4), *Accipitridae* (n = 17), and *Falconidae* (n = 8; Table 2). Abundance of individuals varied among

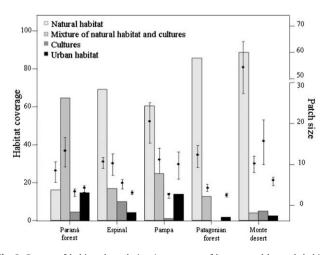


Fig. 2. Degree of habitat degradation (percentage of km covered by each habitat type along road surveys, and average length of habitat patches, in km) in the five biomes studied.

the five biomes surveyed (Table 1). The highest values were registered in the Pampas (1.61 individuals/km) while the lowest were observed in the Monte desert (0.23 individuals/km). The other habitats showed abundances ranging from 0.47 to 0.57 individuals/km. Richness of species was highest in the Espinal (21 species recorded), and lowest in the Patagonian forest (11 species). In accordance, the highest diversity of species was also recorded in the Espinal (2.08), while the least diverse community was registered in the Pampas (1.30).

4.2. Effects of habitat degradation on raptor communities

Both habitat transformation and fragmentation simultaneously reduced the abundance (transformation: $\chi^2 = 116.66$; p < 0.0001, fragmentation: $\chi^2 = 866.89$; p < 0.0001), richness (transformation: $\chi^2 = 47$; p < 0.0001, fragmentation: $\chi^2 = 47.32$; p < 0.0001), and diversity of raptors (transformation: $\chi^2 = 53.23$; p < 0.0001, fragmentation: $\chi^2 = 22.64$; p < 0.0001), while controlling for significant differences among biomes (p < 0.0001) in GLMs.

The structure of raptor communities strongly varied in relation to habitat transformations. Abundance of individuals tended to decrease in more transformed areas, except in the Monte desert where highest abundance was found in cultivated lands (Fig. 3). Although differences were not always statistically significant (Table 3), richness and diversity of species were also higher in natural or mixed habitats, showing a marked decline in more transformed landscapes (Fig. 3). After controlling for habitat transformation in GLMs, abundance, richness and diversity of raptors were positively associated to patch size (habitat fragmentation) in all surveyed

Table 2

Species and number of individuals	observed	during	road	counts	performed	in f	ive
different biomes of Argentina.							

Family Cathartidae	
Andean condor (Vultur gryphus)	1
Black vulture (Coragyps atratus)	149
Lesser yellow-headed vulture (Cathartes burrovianus)	4
Turkey vulture (Cathartes aura)	309
Vultures (<i>Cathartes</i> spp.) ^a	19
Family Accipitridae	
Black-chested buzzard-eagle (Geranoetus melanoleucus)	18
Black-and-white hawk-eagle (Spizastur melanoleucus) ^b	1
Crowned eagle (Harpyhaliaetus coronatus)	1
American swallow-tailed kite (Elanoides forficatus)	1
White-tailed kite (Elanus leucurus)	18
Plumbeus kite (Ictinia plumbea)	52
Snail kite (Rostrhamus sociabilis)	433
Long-winged harrier (Circus buffoni)	9
Cinereous harrier (Circus cinereus)	13
Bicoloured hawk (Accipiter chilensis)	1
Roadside hawk (Buteo magnirostris)	24
White-tailed hawk (Buteo albicaudatus)	9
Swainson's hawk (Buteo swainsoni)	14
Variable hawk (Buteo polyosoma)	39
Short-tailed hawk (Buteo brachyurus)	1
Black-collared hawk (Busarellus nigricollis)	3
Savanna hawk (Buteogallus meridionalis)	17
Unidentified hawks ^a	130
Family Falconidae	
Chimango caracara (Milvago chimango)	1082
Yellow-headed caracara (Milvago chimachima)	4
Southern crested-caracara (<i>Caracara plancus</i>)	120
Barred forest-falcon (Micrastur ruficollis) ^b	2
Spot-winged falconet (Spiziapteryx circumcinctus) ^b	2
Aplomado falcon (Falco femoralis)	2
American kestrel (Falco sparverius)	197
Peregrine falcon (Falco peregrinus)	2

^a Data used for modelling abundance but not richness and diversity.

^b Observed out of systematic roadside counts and thus not included in analyses.

biomes (Table 3, Fig. 3). However, some responses were quadratic while others were just linear.

The deviance partitioning analyses showed that habitat fragmentation was more important in explaining changes in abundance and richness of raptors than habitat transformation (Wilcoxon paired ranks test for abundance: z = -2.02, p = 0.043; Fig. 4, and richness: z = -1.75, p = 0.08). Although non-significant, there was also a trend across biomes for a preponderance of pure effects of fragmentation over transformation on diversity (z = 0.94, p = 0.35, Fig. 4). The pure effects of both variables were always more explicative than their joint effects (Wilcoxon paired ranks test for abundance, richness, and diversity: z = -2.02, p = 0.043; Fig. 4).

4.3. Effects of habitat degradation on raptor species

Median abundances of the 12 most common raptor species in relation to habitat transformation and fragmentation are shown in Fig. 5. In five cases, models did not converge because of data distribution among biomes, habitat and patch size categories. Except for roadside hawks and black vultures which were not significantly sensitive to fragmentation (p > 0.1148), GLM performed for the other species showed that their abundances were simultaneously affected by our two estimates of habitat degradation (transformation: *p*-range = 0.0044–0.0001 and fragmentation: *p*-range = 0.0083–0.0001), even when controlling for biome effects in those species present in more than one biome (*p*-range: 0.0452-0.0001). Responses toward the natural-urban gradient were, however, strongly variable (Fig. 5). Eight out of 12 species (turkey vulture, Southern crested-caracara, roadside hawk, plumbeus kite, black-chested buzzard-eagle, snail kite, variable hawk, and savanna hawk) showed lower abundances the larger the habitat transformation, while abundances of three species (black vulture, white-tailed kite, and American kestrel) peaked at intermediate stages, and one species (chimango caracara) showed its largest abundances in urbanized and cultivated landscapes.

5. Discussion

Carnivores and raptors are often used as reliable sentinel or indicator species owing to their position at the top of the food web and to a number of life history traits (low density or low fecundity) that make them particularly vulnerable to human-induced alterations of their supporting ecosystems (Sergio et al., 2008). Consistent with this idea of higher sensitivity, much evidence suggests that they are usually the first to go extinct or to be seriously affected in a system after anthropogenic perturbations such as contamination (Newton, 1979; Duffy, 2002), or modification of landscape structure and composition (Chamberlain et al., 2000; Crooks, 2002; Carrete et al., 2007). In the latter case, however, the efficacy of top predators as indicators of landscape degradation and management practices may be less general and more conditional on the life-history of particular species, primarily their specialist/generalist habits regarding habitat use (Rodríguez-Estrella et al., 1998).

Neotropical biomes in general, and Argentinean landscapes in particular, are subjected to widespread alteration by humans, mainly because of their use for agriculture, timber exploitation, extensive livestock production, and urban development (Brown et al., 2006). However, consequences of the resulting urban-rural gradients have been scarcely explored, even when they can have potentially serious effects on biodiversity (e.g., Moilanen and Cabeza, 2002). Here, we show how large-scale habitat degradation, mainly associated with extreme poverty or rapid development, can alter some attributes of wild animal communities. Our results

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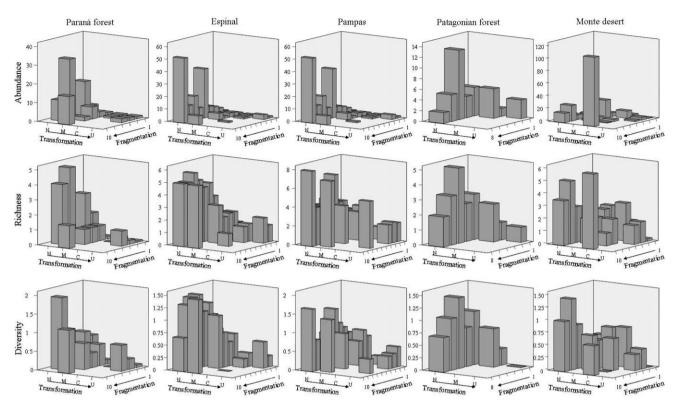


Fig. 3. Relationship between habitat transformation and abundance (individuals/km), richness (species/km) and diversity (*H'*) of raptors in five biomes of Argentina. Figure shows average values (±sd) obtained by using the 391 habitat patches as sample units. N: natural habitats, M: natural habitats mixed with cultivated lands, C: cultivated lands, and U: urbanized areas.

Table 3

Effects of habitat transformation and patch size on abundance, richness and diversity of raptors in five biomes of Argentina. In brackets, response to patch size, +: linear positive, ++: quadratic positive.

	Habitat type	Habitat transformation	Patch size
Abundance	Paraná forest Espinal Pampas Patagonian forest Monte desert	$\chi^{2} = 50.38; p < 0.0001$ $\chi^{2} = 164.28; p < 0.0001$ $\chi^{2} = 159.29; p < 0.0001$ $\chi^{2} = 5.60; p = 0.0610^{*}$ $\chi^{2} = 188.67; p < 0.0001$	$\begin{split} \chi^2 &= 71.39; \ p < 0.0001 \ (++) \\ \chi^2 &= 199.39; \ p < 0.0001 \ (++) \\ \chi^2 &= 218.89; \ p < 0.0001 \ (++) \\ \chi^2 &= 10.80; \ p = 0.0010 \ (++) \\ \chi^2 &= 12.13; \ p = 0.0005 \ (++) \end{split}$
Richness	Paraná forest Espinal Pampas Patagonian forest Monte desert	$\chi^{2} = 18.42; p = 0.0004$ $\chi^{2} = 16.82; p = 0.0008$ $\chi^{2} = 4.31; p = 0.2302$ $\chi^{2} = 0.50; p = 0.7794$ $\chi^{2} = 7.68; p = 0.0530^{*}$	$\begin{split} \chi^2 &= 17.11; \ p = 0.0071 \ (++) \\ \chi^2 &= 25.80; \ p < 0.0001 \ (++) \\ \chi^2 &= 15.38; \ p < 0.0001 \ (+) \\ \chi^2 &= 5.99; \ p = 0.0144 \ (++) \\ \chi^2 &= 17.86; \ p < 0.0001 \ (+) \end{split}$
Diversity	Paraná forest Espinal Pampas Patagonian forest Monte desert	$\chi^2 = 10.62; p = 0.0140$ $\chi^2 = 21.62; p < 0.0001$ $\chi^2 = 15.06; p = 0.0018$ $\chi^2 = 1.29; p = 0.5255$ $\chi^2 = 6.93; p = 0.0741^*$	$\begin{split} \chi^2 &= 7.49; \ p = 0.0062 \ (++) \\ \chi^2 &= 26.71; \ p < 0.0001 \ (++) \\ \chi^2 &= 5.96; \ p = 0.0146 \ (+) \\ \chi^2 &= 6.68; \ p = 0.0097 \ (++) \\ \chi^2 &= 6.34; \ p = 0.0118 \ (++) \end{split}$

* Models marginally significant (p < 0.08).

showed that those habitats with low degrees of transformation (i.e., natural or mixed habitats) have the richest and most diverse communities of raptors. Moreover, when they become fragmented, small patches support less abundant and rich raptor assemblages than large ones. Importantly, these patterns remain constant across biomes, from forests to deserts.

5.1. Roadside raptor surveys: are they reliable tools to track the response of raptor communities to large-scale habitat degradation?

Roadside surveys have been extensively used to obtain information on the distribution and relative abundance of raptors at several temporal and spatial scales (e.g., Fuller and Mosher, 1981; Donázar et al., 1993; Villafuerte et al., 1998; Meunier et al., 2000), especially in large, poorly known areas where information on the biology and ecology of species is scarce (see review in Ellis et al., 1990; Bierregaard, 1998). Fewer attempts have been made, however, to relate roadside raptor surveys to large-scale habitat transformations (Sánchez-Zapata et al., 2003; Seoane et al., 2003). Our results support the suitability of this kind of survey to accurately assess rough variations in the attributes of raptor communities in several Neotropical biomes. Moreover, presence–absence data and counts obtained with roadside surveys, which are largely used to create and test models of species distribution

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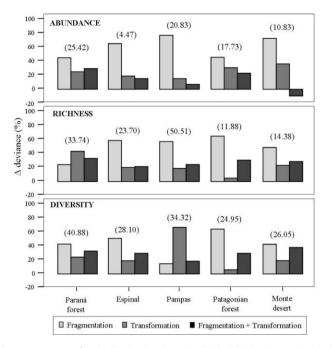


Fig. 4. Percentage of variability in abundance (individuals/km), richness (species/km) and diversity (*H*') of raptors explained by the pure and joint effects of habitat fragmentation (measured as patch size) and habitat transformation in five biomes of Argentina. In brackets, total deviance explained by multivariate models.

(Fielding and Bell, 1997; Manel et al., 2001), calculate incidence functions for metapopulation studies (Hanski, 1997), and facilitate optimal reserve selection (Pressey et al., 1996; Margules and Pressey, 2000; Gaston et al., 2002), can also offer a potentially low-cost and rapid method to track the conservation status of most raptor communities.

It is worth noting that several sources of bias inherent to the roadside transect method can influence our results (Fuller and Mosher, 1981; Millsap and LeFranc, 1988; Meunier et al., 2000). Perching sites close to roads (e.g., power lines and telephone poles) as well as prey availability (road kills) may increase the attractiveness of roadsides to raptors (Meunier et al., 2000), while disturbance from roads may alter habitat use by more sensitive species (Speziale et al., 2008). Moreover, habitat composition between roadsides and surrounding areas may also affect, positively or negatively, the abundance estimation of raptors obtained through roadside counts (Keller and Scallan, 1999). However, these potential biases pose a problem when attempting to calculate absolute densities for large areas or to elaborate predictive spatial models based on roadside census (Kadmon et al., 2004), but not when using their results as relative estimates (Reese et al., 2005). Indeed, estimates of relative abundances of raptors through road surveys are highly correlated with their actual abundances when territorial mapping is simultaneously conducted (Villafuerte et al., 1998). Experimental work also showed that roadside survey counts uncorrected for distance at which raptors are observed yield accurate and precise data in large areas of open and semi-open

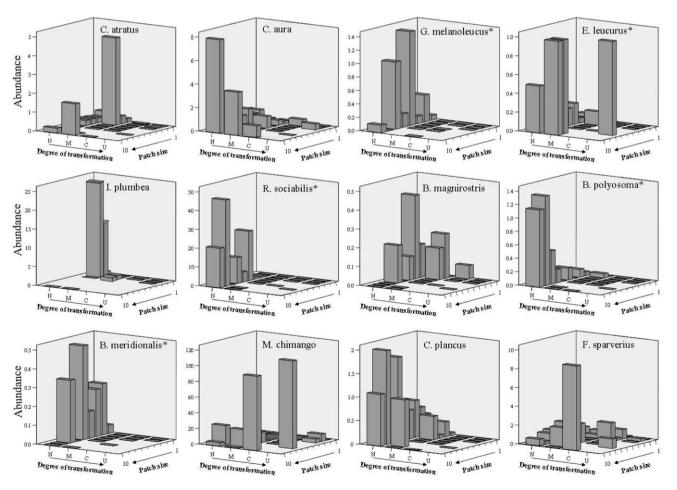


Fig. 5. Mean abundance of the 12 most common raptor species surveyed in relation to habitat transformation (N: natural habitats, M: natural habitats mixed with cultivated lands, C: cultivated lands, and U: urbanized areas) and fragmentation. Sample sizes are given in Table 1. Asterisks indicate species for which statistical models did not converge (see Section 4).

vegetation (Millsap and LeFranc, 1988), and reflected actual densities even for species showing scavenging behaviour (Villafuerte et al., 1998). The Monte desert and the Pampas are dominated by open to nearly open habitats, and thus detectability should not have significantly affected our results. In fact, we detected nearly all species potentially present in those areas, their relative abundances (Table 1) corresponding strongly with their supposed population status in the Neotropics (del Hoyo et al., 1994). A different picture emerges for other biomes. Raptors are notoriously difficult to survey in habitats such as the Paraná forest, and very time-consuming, distinct techniques are needed to avoid biases of density estimates (Thiollay, 1989). Not surprisingly, we detected only about half of the species potentially inhabiting the Paraná forest (del Hoyo et al., 1994). Some of the unrecorded species are near extinction (e.g., the Harpy eagle) or extremely rare due to the very large areas of forest required to maintain their breeding territories. while others may have been undetected due to the elusive behaviour of most forest-dwelling Neotropical raptors (Thiollay, 1989). These facts have surely led to an underestimate of abundance, and most certainly of the richness and diversity of this raptor community compared with the other four biomes (Table 1). It is worth noting, however, that a recent study using a large number of sampling points in the Paraná forest led a composition of raptor species very similar to the reported in our study (Zurita and Bellocq, 2007). In any case, the lower detectability of raptors in large, undisturbed forest patches render our results conservative regarding the effects of habitat transformation and fragmentation (Table 3 and Fig. 3), which are the main focus of this paper. On the other hand, the Espinal was a savanna-like forest, and species detectability was thus relatively high. Indeed, except for the most elusive species (e.g., the spot-winged falconer Spiziapteryx circumcinctus), the other diurnal raptors were all detected in our surveys. Finally, the Patagonian forest represents a particular case of extremely low bird density and richness (Lencinas et al., 2005), and our rough sampling method was as (or much more) effective in counting raptors than more sophisticated methods such as point sampling (for comparison of abundances and species detection see Lencinas et al., 2005).

5.2. Community vs. species-specific responses to habitat degradation

Raptors have been largely used as indicators of habitat quality (e.g., Sánchez-Zapata et al., 2003; Carrete and Donázar, 2005) or biodiversity conservation (Sergio et al., 2006), as well as to design optimal conservation areas (Burnham et al., 1990; Thiollay, 1989; Sergio et al., 2006; for an extensive review on the relationship between raptors and biodiversity, see Sergio et al., 2008). However, when a raptor community contains a large number of generalist species that may adapt to human-modified habitats (Swihart et al., 2003), raptor abundance can lose its tendency to reflect habitat degradation (Rodríguez-Estrella et al., 1998) thus making its use as an environmental indicators controversial.

Studies of bird communities have reported different results on the relationship between species richness and diversity and habitat transformation (Hill and Hamer, 2004). Some argue that these parameters generally decrease with agricultural intensification (Chamberlain et al., 2000) and urbanization (Clergeau et al., 1998; Cam et al., 2000), whereas others show that both species richness and diversity peaked at moderate levels of development (Blair, 1996; Anderson, 2001). We found that, in general, abundance, richness and diversity of raptors were negatively affected by habitat transformation. Moreover, fragmentation also reduced these parameters (often as a quadratic response), with small patches supporting raptor communities lower in abundance (see also Zurita and Bellocq, 2007), richness and diversity than large ones. This is especially true in forested habitats, where raptor communities are generally more complex (Thiollay, 1989). There, the decline in species richness or diversity could arise from the local extinction of specialist species with large home range size, aversion to the conditions found at habitat edges, or low habitat versa-tility (Meffe and Carroll, 1997). On the other hand slight changes in some ecosystems such as arid lands may result in increased structural elements, high water and nutrient inputs, and steep productivity gradients that may increase their carrying capacity and, therefore, their capability to support higher abundances and richness of species (Morrison and Bolger, 2002; Bolger, 2002; Crooks et al., 2004). Nonetheless, the general tendency for a reduction in abundance of individuals, and richness and diversity of species in highly transformed and fragmented habitats allow us to support their use as fairly good indicators of large-scale habitat changes.

Species-specific responses toward habitat degradation could be largely variable, and context-dependent (Sergio et al., 2008), being profoundly affected by carrying capacity, food web complexity. prey refuges, and human action (Schmitz et al., 2000; Bowyer et al., 2005; Ray, 2005). In our study, we found that some species considered as generalists and poor indicators of environmental changes in other areas such as turkey vultures or Southern crested-caracaras in the desert of Baja California (Rodríguez-Estrella et al., 1998), behaved differently, with larger abundances in more natural habitat types. Although we found the abundance of most species decreased with habitat degradation, the abundance of a few of them peaked at intermediate stages and numbers of chimango caracara, the most abundant species across our sampled biomes (Table 2), were larger in the more transformed habitats. Thus, the use of community parameters such as richness or diversity can be more conservative than overall abundance when monitoring changes in landscape modification because of the low species redundancy of predator communities (Woodroffe and Ginsberg, 2005) and because of the direct link between their richness and diversity and ecosystem-level conservation (Sergio et al., 2006).

5.3. Conservation of Argentinean biomes and their raptor communities

Neotropical biomes are among the least studied of the world. and their ratios of conservation research to land area designated as a conservation priority are negative when compared to those biomes of North America and Europe (Lawler et al., 2006). Here, we show how raptor communities occupying some Neotropical biomes are eroded as habitat becomes degraded through agricultural intensification and urbanization. Moreover, reduction in the size of patches entails an additional impoverishment of their raptor communities. The low percentage of deviance explained by some models suggests that habitat characteristics other than those coarsely measured in this study are also affecting raptor community parameters. Nonetheless, our results stress that the current trend of rapid changes in these habitats should be halted to avoid an impoverishment of their raptor communities. In this sense, it is essential to preserve large patches of habitats as similar to the original habitat of the region as possible. These areas would be contained within a mixed matrix where natural or semi-natural vegetation are interspersed with extensive cultures to allow the maintenance of many less restricted species. To the contrary, extensive monocultures, which are of little value to raptors as well as most native fauna (Fernández et al., 2003; Brown et al., 2006; Filloy and Bellocq, 2007), should be avoided. In particular, surface area designated to soya cultures is dramatically increasing in Argentina (mean rate of 91.5% for the period 1998-2007; Argentinean Agriculture, Livestock, Fishing and Food Secretariat), affecting mostly tropical and subtropical dry forests and temperate grasslands and savannas (Grau and Aide, 2008). Soya production was originally devoted to cattle and human food consumption in China and Europe but now is increasingly addressed to the worldwide

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demand of biofuels (Grau and Aide, 2008). Therefore, it is the top exported product and the most widely planted crop in Argentina, which is the third-largest soybean producer of the world after the United States and Brazil, and the leading exporter of soybean oil. In 2008, a total of 15.2 M hectares of land was used for soybean cultivation, which is over half of the entire area devoted to agriculture in Argentina (http://ipsnews.net/news.asp?idnews=32959). As a consequence, the country is experiencing dramatic degradation involving the most intense deforestation in its history due to the replacement of forests with this crop. From the period 1998-2002 to 2002-2006, deforestation rate increased by ca. 35% (National Directorate of Forests, Argentina). Also associated with these mainly transgenic soya crops are the increasing use of agrochemicals, fertilizers and herbicides (from just 1.10 ml of the herbicide glyphosate in 1990 to 150 ml used in 2003), the growth of massive transportation infrastructure, increasing soil degradation and socioeconomic problems. Of increasing concern, soya expansion represents a recent and powerful threat to biodiversity not only in Argentina, but also in other countries of Latin America such as Brazil, Paraguay and Bolivia (Grau and Aide, 2008). While ecological impacts of soybean crop expansion have been still scarcely examined (Scharlemann, 2008), our results show negative effects of extensive monocultures on Neotropical raptor communities and stress the urgent need of pursuing biofuel production practices compatible with biodiversity conservation (Groom et al., 2008).

Even when natural or semi-natural vegetation is still the dominant form of land use, our data reveal that human activities are degrading, with differing intensity, many biomes of Argentina. This is especially true in areas such as the Paraná forest, an ecoregion of the South American Atlantic forest which in the past covered the Atlantic coast of Brazil, the western part of Paraguay and north-eastern Argentina, and which has now been reduced to 7% of its original size. Considered a biodiversity hotspot containing most of Brazil's threatened species (Myers et al., 2000; Marini and García, 2005), the largest part of this original formation is currently restricted to Argentina (Holz and Placci, 2003), where disperse urbanization, subsistence agriculture and monospecific plantations of exotic trees (mainly *Pinus* and *Eucaliptus*) are fragmenting and transforming it outside of protected areas (Brown et al., 2006; Izquierdo et al., 2008). Another troubling example is the Pampas. Although in our survey we considered most of this biome as represented by natural vegetation, it actually comprises grasslands devoted to extensive grazing activities from the beginning of colonization by Europeans (Baldi and Paruelo 2008), which now are highly grazed by domestic herbivores (e.g., in 2001 more than 22.5 million of domestic animals grazed these pastures in the Buenos Aires Province; INDEC, 2001). Overall, these rangelands bear a close resemblance to the original vegetation (Baldi et al., 2006), so their maintenance could be useful for the conservation of native fauna, as has occurred in many lowintensity managed landscapes in Europe (Tella et al., 1998; Benton et al., 2003; Carrete and Donázar, 2005). Nonetheless, grassland cover has suffered a significant reduction in recent decades, being substituted by annual crops and eucalyptus afforestation (Baldi and Paruelo, 2008). Tall trees are novel in the Pampas and their introduction has added structural complexity to the region, allowing the expansion of suitable habitat for some raptor species such as the Swainson's (Sarasola and Negro, 2006) or the Roadside hawks (authors' unpublished data). Fortunately, other biomes such as the Monte desert appear to be undergoing a less intensive transformation. In any case, of greatest concern is the fact that natural landscapes are subject to increasing pressure and, regrettably, only protected areas appear to be free of risk. These areas amount to only 6.8% of the country, and some regions such as the Espinal or the Pampas are very scarcely represented (Brown et al., 2006).

Species vary in their ability to adapt to the often drastic changes along the rural–urban gradient. Consequently, there is an increase

in the compositional similarity among communities due to the expansion of cosmopolitan species (also called winning species), and a contraction of rare, often endemic, native species (also called losing species) (McKinney and Lockwood, 1999). This process of biotic homogenization can be considered an unprecedented form of global change and one of the most important forms of biological impoverishment world-wide (Olden et al., 2004). It can be driven by invasion of species into new areas (winning species), extinction of resident species (losing species), or a combination of invasions and extinctions (Olden et al., 2004). Our findings show that under current conditions of rapid habitat changes, most raptor species exhibit negative trends along rural-urban gradients (losers), while just one (the chimango caracara) can be considered as a clear winner species. Although more information on species-specific responses at finer landscape scales (e.g., Ursúa et al., 2005; Filloy and Bellocq, 2007) is needed, present results and future perspectives of habitat degradation, which predict larger increments in monocultures and urbanized areas (Grau and Aide, 2008), are a concern for the long-term conservation of raptor communities in Argentinean biomes.

Finally, rapid biodiversity assessment and conservation planning require the use of easily quantifiable surrogates of biodiversity. In this sense, our results show that tracking some easily measurable attributes of raptor communities through road surveys can be helpful in assessing large-scale habitat conservation status. Although we did not test the effectiveness of these taxa for finescale management, the close association between raptors and other biodiversity components (Sergio et al., 2006) highlight their usefulness in large-scale maintenance of natural habitats. Moreover, taking into account difficulties of using species data for large-scale conservation, our correlations between the attributes of raptor communities and habitat degradation support the usefulness of some environmental surrogates of biodiversity such as land-use maps for prioritising areas for investment and conservation focus (e.g., Pressey et al., 1996; Margules and Pressey, 2000).

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