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Densities and habitat preferences of Andean cloud-forest birds in pristine and degraded habitats in north-eastern Ecuador

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Summary

The montane cloud-forests of the north-central Andes and the montane grassland and transitional elfin forest of the central Andean páramo contain a high diversity of bird species including several restricted range and uncommon species. Little is known of how densities of Andean cloud-forest species are affected by habitat degradation. Bird densities within pristine and degraded habitats at the Guandera Biological Reserve, Carchi province, Ecuador were recorded over a 10-week period. Densities were calculated for 48 species; where densities could be compared, 69% of species occurred at a higher density in pristine habitats. Pristine forest had the highest species richness with 72 species and páramo contained 44 species. In total, 26% of pristine forest species were only found in pristine forest, 39% of páramo species only in páramo, 13% of farmland species only in farmland and there were no exclusively secondary scrub species; 47% of species found in pristine forest, and 50% found in páramo were found in both secondary scrub and farmland. Restricted range species recorded at Guandera included the Carunculated Caracara *Phalcobenus carunculatus*, Black-thighed Puffleg *Eriocnemis derbyi*, Chestnut-bellied Cotinga *Doliornis remseni*, Crescent-faced Antpitta *Grallaricula lineifrons*, Masked Mountain-tanager *Buthraupis wetmorei* and Black-backed Bush-tanager *Urothraupis stolzmanni*. Three further species that occurred at Guandera of relatively local occurrence were the Grey-breasted Mountain Toucan *Andigena hypoglauca*, Golden-breasted Puffleg *Eriocnemis mosquera* and Mountain Avocetbill *Opisthoprora euryptera*. Of these nine species at least five used degraded habitats, while three occurred only in pristine treeline habitats.

Introduction

The Andes of South America contain several areas of bird endemism (Collar *et al.* 1994, Stattersfield *et al.* 1998). Two of these endemic bird areas (EBAs) are the montane cloud-forests of the north-central Andes and the montane grassland and transitional elfin forest of the central Andean páramo (Wege and Long 1995, Stattersfield et *al* .1998). The north-central Andes contain at least eight restricted range species and the central Andean páramo at least 10 (Wege and Long 1995, Stattersfield *et al.* 1998). These endemic bird areas have been subject to widespread and severe deforestation in this and recent centuries. The transitional

areas between the cloud-forest and the páramo are also threatened by frequent burning, grazing and conversion to agriculture such as potato cultivation (Collar *et al.* 1992, Wege and Long 1995, Collar *et al.* 1997). Consequently all of the restricted range species in the north-central Andes are considered threatened or near-threatened, and half the species of the central Andean páramo are globally threatened (Collar *et al.* 1992, Collar *et al.* 1994, Wege and Long 1995).

Although Andean endemic species are all vulnerable because of their restricted ranges, some species will be more at threat from habitat modification than others. Identification of those endemic species that cannot survive as viable populations within secondary or degraded habitats is crucial to determine which species should be considered as a conservation priority. The upper temperate zone of the northern Andes of Ecuador encompasses two endemic bird areas, but there is little quantitative data on bird habitat use there (Fjeldså and Krabbe 1990, Bloch *et al.* 1991, Robbins *et al.* 1994a). In this paper we present data on bird densities within the newly established Guandera Biological Reserve in the north-east of Ecuador. The reserve conserves part of the last inter-Andean valley forest in northern Ecuador, and includes a large area of páramo. Parts of the reserve have been cleared and it is surrounded on its lower slopes by farmland. The reserve therefore provides a mosaic of pristine and degraded habitats in which to measure the effects of habitat change on bird density.

Methods and study area

Between 8 and 14 observers surveyed the Guandera Biological Reserve (0° 36′ N, 77°41′ W: GPS data) from 17 July to 11 September 1997. The area surveyed was approximately 650 ha. This area includes all of the 400 ha forested area of the Guandera reserve, a large part of the páramo of the reserve, and a boundary region of farmland around the reserve. The height surveyed ranged from 3,000 to 4,100 m.

Habitat data

Plants were identified using Gentry (1993), Cuamacás and Tipaz (1995), Palacios and Tipaz (1996) and from specimens at the Herbario Internacional QCA at the Pontificia Universidad Católica del Ecuador. Habitats within the survey area were defined using ten 100-m^2 quadrats in habitats of dense vegetation, and ten quadrats of 400 m^2 in habitats of sparser vegetation, randomly placed along the bird census transects (see below) through each of the major habitat types. Vegetation measurements were taken as described below using the methods in Kent and Coker (1992), Bonham (1989) and Bibby *et al.* (1992).

1. Canopy height was estimated by eye to be in one of four height classes; 0–5, 5–10, 10–15 and >15 m. One estimation was made per quadrat and the modal class was taken as representative.
2. Tree/shrub canopy cover was estimated as a percentage by eye. Four estimates were taken per quadrat and the results expressed as a mean for the whole habitat.
3. Relative density of tree/shrub species was calculated as (number of indi-

viduals of the species in sample ×100)/(number of individuals in sample). The sample was taken as the total of all the trees/shrubs present in the ten quadrats surveyed in the habitat. Trees were defined as having a diameter at breast height of ≥10 cm.

4. Ground-cover was estimated from four subquadrats from each 100 m^2 quadrat, using a 1-m^2 quadrat frame with cross-wires at 25-cm intervals. The cross-wire intersections were used to point sample the ground vegetation, giving 100 point samples for each 100-m^2 quadrat. Ground-cover for each species was then calculated as (number of points covering the species ×100)/(number of points sampled). The results were expressed as a mean for the whole habitat.
5. Variation in the degree of visual obstruction in each habitat was measured in order to determine how the detectability of birds would differ between the habitats. Visibility was measured as the distance at which a 25-cm^2 yellow square became invisible from a randomly selected point, at a height of 1.5 m. Distances for eight fixed compass bearings were taken for each point and the mean visibility at that point was calculated. Ten points were sampled in each habitat and the overall mean visibility for each habitat is given in Table 1.

Habitat type

Primary forest on slope Diverse montane forest found at altitudes of less than about 3,300 m. Canopy height >15 m extended to 25–30 m. Average canopy cover was 65%. The relative density of tree species was: Melastomataceae (mainly *Miconia* sp.) 21%, *Ocotea* (Lauraceae) 20%, *Weinmannia* (*W. pinninata, W. brachystachya, W. rollotii*) (Cunoniaceae) 19%, *Symplocus alpinus* (Symplocaceae) 12%, *Clusia flaviflora* (Clusiaceae) 8%. The remainder was made *inter alia* of *Hedyosmum* (Chloranthaceae), *Brunellia* (Brunelliaceae), *Clethra* (Clethraceae), *Oreopanax* and *Schefflera* (Araliaceae) and *Palicourea* (Rubiaceae). The ground-cover was dense and tangled, sometimes forming a subcanopy 1–2 m high. Total ground-cover was about 70% (leaf litter 30%), comprising: *Boehmeria* (Urticaceae) 30%, *Anthurium* (Araceae) 13%, *Pilea* (Urticaceae) 8% , other species 19%.

Primary "Guandera" forest High montane forest at approximately 3,500 m altitude, occurring immediately before transitional and elfin zones and dominated by two tree species. Canopy height was 10–15 m and canopy cover was 70%. The relative density of tree species was: *Clusia flaviflora* 78% (called Guandera locally), and *Ilex* sp. (Aquifoliaceae) 22%. The understorey and ground-cover was relatively open, and was composed of bromeliads 27%, mosses 11%, and *Blechnum* sp. or spp. 8% (Blechnaceae), with 50% of the ground being kept free of vegetation by the dense *Clusia* leaf litter.

Primary forest at páramo edge Elfin treeline forest at altitudes of approximately 3,500–3,700 m. Canopy height was between 5 and 10 m, and the average canopy cover was 60%. The relative density of tree species was: *Ilex* sp. 50%, *Weinmannia brachystachya* 32% and *Clusia flaviflora* 9%, with the remainder being made up of *Diplostephium* (Asteraceae) and *Miconia*. There was a tangled understorey of *Miconia*, Ericaceae and *Desfontainia spinosa* (Loganiaceae). The forest was inter-

spersed with islands of open páramo-like vegetation in wetter areas, with *Blechnum* tree ferns occurring on forest edges.

Páramo High altitude grassland above the treeline at approximately 3,700 m, dominated by bunch grasses and with characteristic *Espeletia* (Asteraceae) with about 20 individuals/100 m^2, and *Puya* (Bromeliaceae) with about four individuals/100 m^2. Islands of shrubby vegetation similar in composition to páramo edge forest occurred at lower altitudes. Scattered pools and marshy areas were also present.

Secondary scrub on ridges A secondary habitat, that consisted of dense shrubby vegetation, with the canopy usually between 0 and 5 m, although extending up to around 10 m due to isolated stands of trees. Average shrub canopy cover was 70%. The relative density of woody species was: *Weinmannia brachystachya* 27%, *Blechnum* sp. 26%, *Diplostephium* sp. 22%, Ericaceae 10%. The remainder was made up of Melastomataceae, *Brunellia*, *Clusia*, Araliaceae and *Ilex*. Ground-cover consisted of grasses and mosses, especially *Sphagnum* (Sphagnaceae).

Secondary scrub after clearance Diverse secondary scrub resulting from relatively recent forest clearances, with a variable canopy height of usually between 0 and 10 m, although extending to >10 m where stands of trees had been left. Average tree canopy cover was 10%. The total ground-cover by the shrub canopy was 60%. The relative density of woody species was: Asteraceae (numerous species) 31%, *Weinmannia* spp. 16%, *Brunellia* 12%, Melastomataceae 12%, Ericaceae 8%. The remainder was made up of *Ocotea*, *Schefflera*, *Oreopanax*, *Chusquea* (Poaceae), *Clusia* and *Monnina* (Polygalaceae). Ground-cover was of grasses.

Farmland A very heterogeneous habitat, at altitudes of up to 3,000 m, adjacent to montane forest. A mixture of rough pasture, often with heavy infestation of *Rumex* (Polygonaceae) and arable fields (mainly potato), bounded by thick, florally diverse hedges. Isolated trees were also present, sometimes with dense growths of the parasite *Aetanthus* (Loranthaceae).

Density data

The density of birds in each habitat was calculated using the distance/transect method (Buckland *et al.* 1993). Transects were marked out through each habitat and their total length was measured using a GPS receiver to the nearest 10 m where possible. In areas of poor satellite reception distances were measured using a 100-m tape measure to the nearest 10 m. Transects were walked each day between 06h30 and 09h00 to minimize the effects of time of day on bird detectability, (e.g. see Poulsen 1993, Poulsen and Krabbe 1998). Transects were walked by 1–3 observers, with the number and identity of observers being varied for each day of a transect to equalize any effects of variation in observer ability. During each transect all birds seen, their species and perpendicular distance to the transect line were recorded. Birds that were heard only were not recorded (it is impossible to judge distances accurately using only auditory cues). Transects

Table 1. Mean unobstructed visibilities within different habitats

	Visibility (m)	
	Mean	Standard error
Ridge scrub	4.4	0.8
Guandera forest	10.1	1.4
Slope forest	4.4	0.4
Edge páramo forest	6.3	0.7
Cleared scrub	9.6	2.0
Farmland	34.0	4.0
Páramo	51.5	5.6

were repeated from 10 to 13 times over the 8-week survey period in order to obtain sufficient encounters to calculate densities.

Densities were calculated using the DISTANCE programs (Laake *et al.* 1993) for repeated transects. Detectability curves and densities were calculated for each habitat separately because of differences in visibility between the habitats (see Table 1). Records of birds at a distance of more than 100 m were ignored when calculating densities to minimize problems of reduced precision in observers judging long distances accurately. Densities for a species for the three primary forest habitats (slope, "Guandera" and páramo edge), and for the two secondary scrub habitats were combined to give a mean density for a species for primary forest and secondary scrub respectively.

Diversity data

Birds were also recorded opportunistically by field observation (sightings and vocalizations), mist-netting and by later identification of sound-recordings made at Guandera. A bird was considered only to use a habitat if it was recorded during transects through the habitat, or opportunistically three or more times from a habitat. In total, there were 44 separate days of observational survey making a total of 422 observer days at Guandera. Mist-nets were mainly used in areas of dense vegetation with the aim to catch skulking species that are otherwise difficult to record. Mist-netting was carried out on 17 days; an average of 30.0 $m^2 h^1$ of netting were used for a total of 41.9 hours. All birds were released unharmed after capture.

Results

Densities within one or more habitats could be calculated for 48 species (Table 2). Where densities could be compared, 69% of species occurred at a higher density in pristine habitats (using 27 species where densities were available for both a pristine and a degraded habitat, and five species that probably only occurred within one habitat type). Overall 98 species were recorded during transects and a further 20 species were recorded opportunistically three or more times within any one habitat. A few new species were being added to the total for most habitats as transect effort increased at the end of the survey (Figure 1). Also several other nocturnal or difficult to detect species such as White-throated Screech-owl

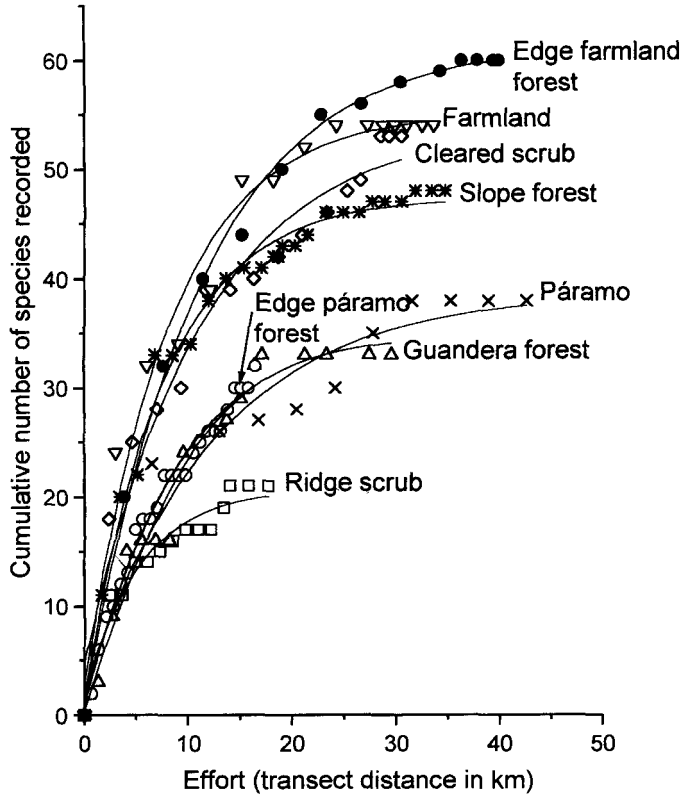

Figure 1. The cumulative numbers of species recorded per kilometre of transect in different habitats of the Guandera reserve.

Otus albogularis, Ocellated Tapaculo *Acropternis orthonyx* and Flammulated Treehunter *Thripadectus flammulatus* were recorded only by vocalizations or from mist-net captures. This suggests that all habitats were under sampled to some degree. However, the slow rate of addition of new species for increased transect effort in all habitats except edge páramo forest suggests that the majority of species were recorded (Figure 1).

Several of the species that were recorded at Guandera are classified as having restricted ranges. These included the Black-thighed Puffleg *Eriocnemis derbyi*, Chestnut-bellied Cotinga *Doliornis remseni*, Crescent-faced Antpitta *Grallaricula lineifrons*, Masked Mountain-tanager *Buthraupis wetmorei* and Black-backed Bush-tanager *Urothraupis stolzmanni*. Three further species that occurred at Guandera are of relatively local occurrence; these were the Grey-breasted Mountain Toucan *Andigena hypoglauca*, Golden-breasted Puffleg *Eriocnemis mosquera* and Mountain Avocetbill *Opisthoprora euryptera*. The Black-thighed Puffleg occurred at highest densities in pristine forest (150 per km^2) although it was also common in secondary scrub (60 per km^2) and farmland (20 per km^2). The Golden-breasted Puffleg, however, occurred at highest densities in secondary scrub (160 per km^2) with only up to about 30 per km^2 in pristine habitats. Pristine forest was the most important habitat for Chestnut-bellied Cotinga, Masked Mountain-tanager and

Black-backed Bush-tanager: these species were only recorded in primary habitats. The Mountain Avocetbill, Grey-breasted Mountain Toucan and Crescent-faced Antpitta were recorded in both pristine and secondary habitats. The Mountain Avocetbill was recorded almost entirely from secondary scrub, but would have had a low detectability in primary forest due to visual identification difficulties, so it may have been overlooked there. The Grey-breasted Mountain Toucan occurred at low densities in primary forest (four per km^2) but was recorded in secondary scrub and farmland (where, according to local people, it was attracted to fruiting trees in gardens). The Crescent-faced Antpitta was recorded singing from primary forest and secondary forest where the canopy had regrown to five or more metres. The species is, however, practically undetectable unless singing.

The species totals for the four main types of habitats (in terms of human effects) were primary forest 72, páramo 44, secondary scrub 65 and farmland 61 (Figure 2). In total, 26% (19 of 72) of pristine forest species were only found in pristine forest, 39% (17 of 44) of páramo species only in páramo, 13% (8 of 61) of farmland species only in farmland and there were no exclusively secondary scrub species. Eleven species (9%) were found in all habitats: Andean Guan *Penelope montagnii*, Mountain Velvetbreast *Lafresnaya lafresnayi*, Tyrian Metaltail *Metallura tyrianthina*, Pearled Treerunner *Margarornis squamiger*, White-throated Tyrannulet *Mecocerculus leucophrys*, Great thrush *Turdus fuscater*, Spectacled Whitestart *Myioborus melanocephalus*, Masked Flowerpiercer *Diglossopis cyanea*, Glossy Flowerpiercer *Diglossa lafresnayii*, Black Flowerpiercer *Diglossa humeralis* and Rufous-collared Sparrow *Zonotrichia capensis*. It should be noted that the páramo areas that were sampled were mostly adjacent to the treeline accounting for the records of typical forest species such as Andean Guan and Pearled Treerunner there. Of the two primary habitats, 47% (34 of 72) of species found in pristine forest, and 50% (22 of 44) found in páramo were found in both secondary scrub and farmland (Figure 2). In general, scrub after clearing (degraded forest) had fewer species than primary forest, and those species occurred at lower density (Figure 3). Primary forest and secondary scrub had similar visibility indices (see Table 1) so that any comparison of density and diversity between the two habitats is likely to be equally biased because of detectability.

Discussion

Primary forest and páramo were the most important habitat for a discrete range of species (30%) including several of the restricted range species of particular conservation interest. The majority of treeline forest and páramo species are clearly adaptable to habitat degradation and occur in reasonable densities in secondary scrub and even farmland adjacent to primary habitat. Of the 72 primary forest species, 72% occurred in secondary scrub and 47% occurred in both secondary and farmland habitats, and for the 44 páramo species, 56% occurred in secondary scrub and 50% occurred in both secondary and farmland habitats (Figure 2). The similarity in species richness of primary and secondary forest at Guandera was partly a consequence of secondary habitats being intermediate in character between primary forest and more open habitats. High species richness has often been reported in habitats containing elements of two or more vegetation types (Connell 1978, Ralph 1985, Johns 1991). However, much of the divers-

Table 2. Densities of birds and transect lengths in the four main habitat types at Guandera. Species that were most abundant in primary habitats are in bold, and those most abundant in secondary habitats are in italics

		Density per hectare or number of sightings			
		Primary forest	Secondary scrub	Farmland	Páramo
Total distance of transects (Km)		84.5	42.1	33.7	42.3
Maximum unrepeated length of transect (Km)		7.6	2.6	3.0	6.5
Curve-billed Tinamou	*Nothoprocta curvirostris*			$n = 2$	
Sharp-shinned Hawk	*Accipiter striatus*		$n = 4$	$n = 3$	
White-throated Hawk	*Buteo albigula*	$n = 1$	$n = 2$		
Carunculated Caracara	*Phalcoboenus carunculatus*		$n = 1$		
American Kestrel	*Falco sparverius*			$n = 1$	
Andean Guan	*Penelope montagnii*	0.4 (0.2–1.2)		0.2 (0.1–0.4)	$n = 2$
Noble Snipe	*Gallinago nobilis*				0.2 (0.1–0.7)
Andean Snipe	*Gallinago jamesoni*				$n = 3$
Band-tailed Pigeon	*Columba fasciata*	0.3 (0.1–0.9)	0.2 (0.1–0.4)	0.4 (0.1–1.3)	
Eared Dove	*Zenaida auriculata*				0.04 (0.01–0.1)
White-capped Parrot	*Pionus seniloides*	$n = 16$	$n = 9$	$n = 18$	
Andean Pygmy-owl	*Glaucidium jardinii*	$n = 1$			
Rufous-bellied Nighthawk	*Lurocalis rufiventris*	$n = 1$			
Band-winged Nightjar	*Caprimulgus longirostris*				$n = 4$
Sparkling Violetear	*Colibri coruscans*			$n = 1$	
Shining Sunbeam	*Aglaeactis cupripennis*				0.3 (0.1–1.0)
Mountain Velvetbreast	*Lafresnaya lafresnayi*	0.3 (0.1–0.5)	0.2 (0.1–0.4)	$n = 1$	
Great Sapphirewing	*Pterophanes cyanopterus*	$n = 2$	$n = 4$		0.5 (0.2–1.1)
Buff-winged Starfrontlet	*Coeligena lutetiae*	1.4 (1.0–2.1)	0.8 (0.4–1.7)	0.6 (0.2–1.3)	$n = 1$
Sword-billed Hummingbird	*Ensifera ensifera*		$n = 3$	$n = 4$	
Golden-breasted Puffleg	*Eriocnemis mosquera*	0.2 (0.1–0.6)	1.3 (0.7–2.4)	0.1 (0.1–0.4)	
Black-thighed Puffleg	*Eriocnemis derbyi*	0.9 (0.2–2.6)	0.6 (0.3–1.2)	0.2 (0.1–0.5)	
Purple-backed Thornbill	*Rhamphomicron microrhyncum*	0.9 (0.3–2.5)	0.8 (0.4–1.6)		
Tyrian Metaltail	*Metallura tyrianthina*	0.7 (0.3–2.1)	1.3 (0.8–2.1)	0.5 (0.3–0.8)	$n = 3$
Rainbow-bearded Thornbill	*Chalcostigma herrani*				0.5 (0.2–1.1)
Blue-mantled Thornbill	*Chalcostigma stanleyi*				$n = 1$

		Density per hectare or number of sightings			
		Primary forest	Secondary scrub	Farmland	Páramo
Masked Trogon	*Trogon personatus*	0.1 (0.1–0.3)			
Grey-breasted Mountain Toucan	*Andigena hypoglauca*	0.04 (0.01–0.1)	$n = 1$		
Bar-bellied Woodpecker	*Veniliornis nigriceps*	$n = 1$	$n = 1$		
Crimson-mantled Woodpecker	*Piculus rivolii*		$n = 1$	$n = 2$	
Elegant Spinetail	*Synallaxis elegantior*				$n = 1$
Rufous Spinetail	*Synallaxis unirufa*		$n = 1$	$n = 1$	
White-browed Spinetail	*Hellmayrea gularis*	$n = 2$			
White-chinned Thistletail	*Schizoeaca fuliginosa*	$n = 2$	$n = 4$		$n = 3$
Many-striped Canestero	*Asthenes flammulata*				$n = 1$
Pearled Treerunner	*Margarornis squamiger*	0.5 (0.2–1.6)	0.2 (0.1–0.3)	0.2 (0.1–0.9)	
Streaked Tuftedcheek	*Pseudocolaptes boissonneautii*	0.1 (0.0–20.4)		$n = 1$	
Rufous Antpitta	*Grallaria rufula*	$n = 2$			
Tawny Antpitta	*Grallaria quitensis*	$n = 1$			0.3 (0.1–0.9)
Undulated Antpitta	*Grallaria squamigera*	$n = 1$			
Andean Tapaculo	*Scytalopus magellanicus*	$n = 1$		$n = 2$	
Red-crested Cotinga	*Ampelion rufaxilla*	0.04 (0.02–0.08)	0.4 (0.2–0.8)		
Chestnut-bellied Cotinga	*Doliornis remseni*	$n = 1$			
Agile Tit-tyrant	*Anairetes agilis*	$n = 2$	$n = 3$	$n = 3$	
Tufted Tit-tyrant	*Anairetes parulus*	$n = 1$			
White-throated Tyrannulet	*Mecocerculus leucophrys*	0.3 (0.1–0.6)	0.3 (0.1–0.6)	$n = 2$	0.1 (0.03–0.2)
White-banded Tyrannulet	*Mecocerculus stictopterus*	0.4 (0.2–1.1)	0.1 (0.04–0.4)	$n = 2$	
Black-capped Tyrannulet	*Phyllomyias nigrocapillus*	$n = 4$		$n = 4$	
Cinnamon Flycatcher	*Pyrrhomyias cinnamomea*	$n = 4$			
Rufous-headed Pygmy-tyrant	*Pseudotriccus ruficeps*	$n = 4$			
Brown-backed Chat-tyrant	*Ochthoeca fumicolor*		0.6 (0.2–1.3)		0.1 (0.02–0.6)
Rufous-breasted Chat-tyrant	*Ochthoeca rufipectoralis*	0.5 (0.2–0.9)	$n = 3$	$n = 4$	
Slaty-backed Chat-tyrant	*Ochthoeca cinnamomeiventris*	$n = 2$			
Crowned Chat-tyrant	*Ochthoeca frontalis*	$n = 1$	$n = 2$		
Red-rumped Bush-tyrant	*Cnemarcus erythropygius*				$n = 2$
Streak-throated Bush-tyrant	*Myiotheretes striaticollis*				$n = 2$
Smoky Bush-tyrant	*Myiotheretes fumigatus*	$n = 1$	$n = 1$		
Pale-footed Swallow	*Notiochelidon flavipes*	$n = 46$	$n = 2$	$n = 28$	$n = 2$

Table 2. *cont.*

		Density per hectare or number of sightings			
		Primary forest	Secondary scrub	Farmland	Páramo
Brown-bellied Swallow	*Notiochelidon murina*	$n = 2$	$n = 3$	$n = 8$	$n = 2$
Turquoise Jay	*Cyanolyca turcosa*	$n = 3$		$n = 5$	$n = 1$
White-capped Dipper	*Cinclus leucocephalus*	$n = 1$			
Rufous Wren	*Cinnycerthia unirufa*	$n = 8$	$n = 1$	$n = 3$	
Mountain Wren	*Troglodytes solstitialis*	0.6 (0.2–2.2)	0.1 (0.04–0.5)	$n = 2$	
Grass Wren	*Cistothorus platensis*		$n = 2$	0.6 (0.2–2.1)	0.4 (0.2–0.8)
Great Thrush	*Turdus fuscater*	1.8 (1.2–3.1)		6.2 (4.8–7.8)	0.4 (0.2–0.8)
Paramo Pipit	*Anthus bogotensis*				0.2 (0.1–0.6)
Spectacled Whitestart	*Myioborus melanocephalus*	2.2 (1.4–3.5)	0.5 (0.3–0.8)	0.8 (0.4–1.9)	$n = 4$
Citrine Warbler	*Basileuterus luteoviridis*	0.1 (0.04–0.3)	$n = 2$		
Black-crested Warbler	*Basileuterus nigrocristatus*	1.1 (0.1–7.5)	$n = 1$	$n = 3$	
Cinerous Conebill	*Conirostrum cinereum*			$n = 2$	
Blue-backed Conebill	*Conirostrum sitticolor*	0.2 (0.1–0.8)	0.2 (0.1–0.6)	$n = 3$	
Masked Flowerpiercer	*Diglossopis cyanea*	0.4 (0.1–0.8)	0.2 (0.04–0.7)	0.1 (0.04–0.4)	$n = 1$
Black Flowerpiercer	*Diglossa humeralis*	$n = 3$	0.4 (0.1–1.5)	0.2 (0.1–0.4)	$n = 2$
Glossy Flowerpiercer	*Diglossa lafresnayii*	0.3 (0.1–1.0)	1.1 (0.6–1.9)	$n = 1$	0.3 (0.2–0.6)
White-sided Flowerpiercer	*Diglossa albilatera*	0.1 (0.03–0.3)	$n = 3$	$n = 1$	$n = 1$
Hooded Mountain-tanager	*Buthraupis montana*	0.6 (0.2–3.4)	0.3 (0.04–0.9)	0.5 (0.3–1.0)	
Black-chested Mountain-tanager	*Buthraupis eximia*	$n = 3$		$n = 2$	
Buff-breasted Mountain-tanager	*Dubusia taeniata*	$n = 2$			
Grass-green Tanager	*Chlorornis riefferii*	$n = 4$			
Lacrimose Mountain-tanager	*Anisognathus lacrymosus*	0.6 (0.3–1.4)	0.2 (0.1–0.5)	$n = 1$	
Scarlet-bellied Mountain-tanager	*Anisognathus igniventris*	0.6 (0.5–1.3)	0.4 (0.2–0.8)	0.2 (0.1–0.4)	$n = 1$
White-capped Tanager	*Sericosspyha albocristata*	$n = 4$			
Golden-crowned Tanager	*Iridosornis rufivertex*	$n = 7$	0.3 (0.1–0.8)		
Common Bush-tanager	*Chlorospingus ophthalmicus*	$n = 3$			
Black-backed Bush-tanager	*Urothraupis stolzmanni*	$n = 1$			$n = 3$
Black-headed Hemispingus	*Hemispingus verticalis*	$n = 8$	$n = 3$		
Superciliaried Hemispingus	*Hemispingus superciliaris*	0.3 (0.1–1.1)		$n = 4$	
Black-capped Hemispingus	*Hemispingus atropileus*	$n = 1$			

		Density per hectare or number of sightings			
		Primary forest	Secondary scrub	Farmland	Páramo
Pale-naped Brush-finch	*Atlapetes pallidinucha*	$n = 8$	0.4 (0.2–0.9)	$n = 1$	
Rufous-naped Brush-finch	*Atlapetes rufinucha*	0.2 (0.1–0.6)	$n = 4$	0.4 (0.1–1.0)	
Stripe-headed Brush-finch	*Buarremon torquatus*	1.5 (0.6–3.7)	$n = 2$	$n = 2$	
Slaty Brush-finch	*Atlapetes schistaceus*	0.3 (0.1–1.4)	0.4 (0.1–0.9)		
Paramo Seedeater	*Catamenia homochroa*	$n = 3$	$n = 3$	0.6 (0.1–3.5)	0.5 (0.2–1.4)
Plain-coloured Seedeater	*Catamenia inornata*	0.3 (0.1–1.3)	0.4 (0.1–1.3)	0.9 (0.4–1.8)	1.3 (0.5–3.8)
Plumbeous Sierra-finch	*Phrygilus unicolor*				0.1 (0.03–0.2)
Andean Siskin	*Carduelis spinescens*			$n = 4$	1.9 (0.4–8.3)
Hooded Siskin	*Carduelis magellanica*	$n = 2$	$n = 2$		
Rufous-collared Sparrow	*Zonotrichia capensis*	2.9 (1.5–5.6)	0.8 (0.3–1.9)	9.0 (5.813.9)	0.6 (0.2–1.3)

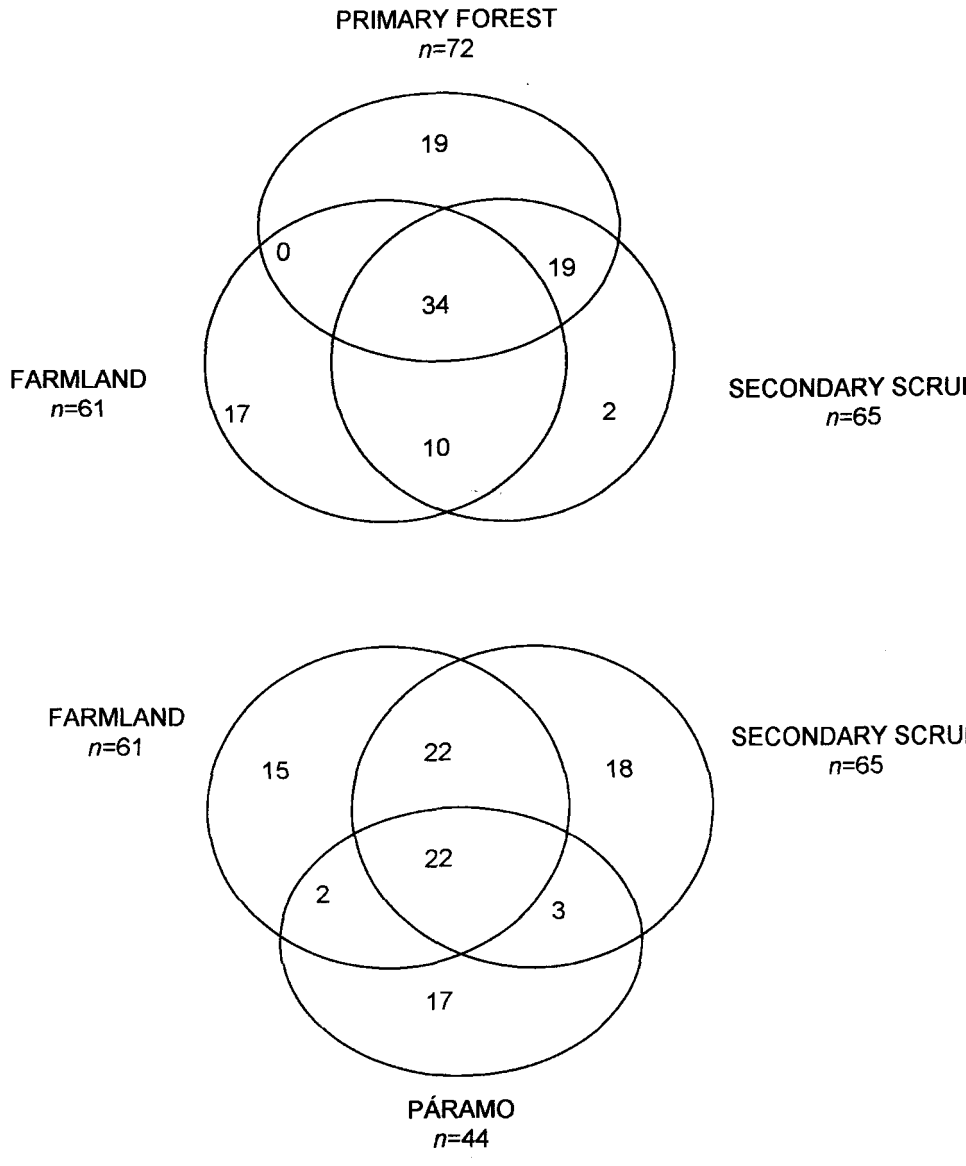

Figure 2. The number of species found in each of the four main habitats (with respect to human influence) and how they are distributed across habitats.

ity in secondary habitats at Guandera was due to the presence of many of the primary forest species there, rather than the presence of new opportunistic species. Only 18% of species in secondary forest did not occur in primary forest.

The adaptability of a large component of the avifauna to degraded habitats may be due to the natural temporal and spatial variation in treeline habitats that has preselected for flexibility in habitat use. Treeline forest is naturally fragmented due to the interaction between slope, aspect and altitude that allows patches of forest to establish beyond the main treeline. Fragmentation also occurs

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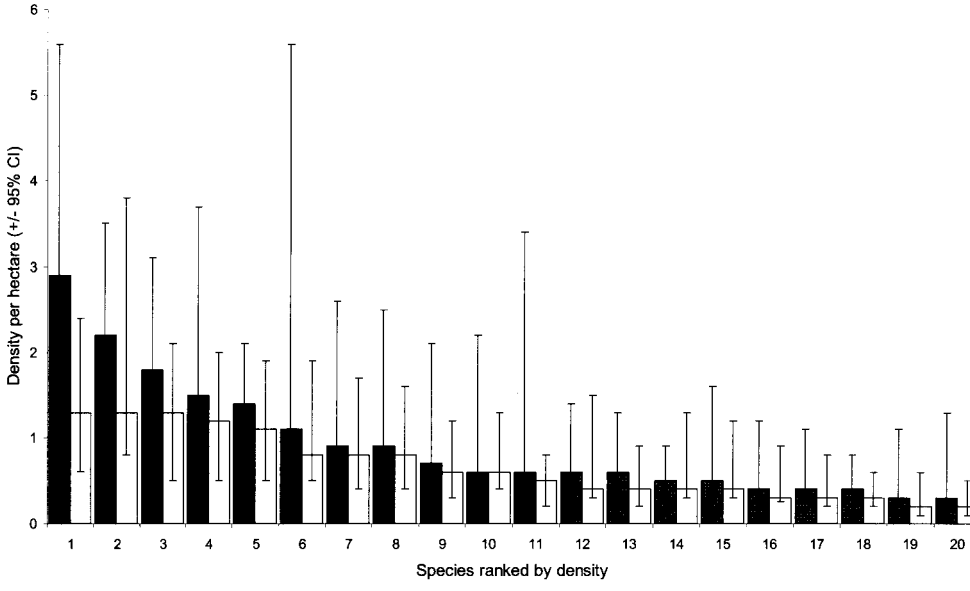

Figure 3. The relative densities (±95% confidence intervals) per hectare of the most abundant 20 species within primary forest (grey bars) and secondary scrub (pale bars). Data and species are from Table 2.

due to the effects of landslides and páramo fires. The central Andean valley in Carchi province has cloud-forest on its western and eastern slopes, and the eastern slope forest (of which the Guandera reserve is a part) is only separated from the western forested slope of the Andes by a few kilometres. There may therefore be an advantage for mobility particularly for frugivorous species to exploit the likely differing seasonal patterns of food abundance in the different areas of forest. Higher altitude species do seem to move more easily between forest fragments than lowland species (Poulsen 1994). It can be equally argued, however, that the apparent adaptability of many of the treeline species is because only mobile species can deal with the temporal and spatial variation in the habitats there. This is partly supported by the increase with altitude in the proportion of the total species list that is composed of frugivorous species such as mountain-tanagers and nectarivorous species such as hummingbirds, that exploit resources that are typically widely dispersed and ephemeral (Terborgh *et al.* 1990). The characteristic mixed flocks of neotropical forests are also much less stable at high altitude (Poulsen 1994, 1996).

Although many of the treeline bird species appear able to exist in reasonable densities in secondary habitats, it is the small number of restricted range and rare species that are of particular conservation interest. Black-thighed Puffleg is a central Andean endemic (Wege and Long 1995, Stattersfield *et al.* 1998), and Golden-breasted Puffleg has a similar restricted range (Fjeldså and Krabbe 1990). Black-thighed Puffleg occurred at highest densities in primary forest but occurred at reasonably high densities in secondary scrub, and even into farmland where there were remaining patches of natural vegetation or trees. Golden-breasted Puffleg actually occurred in highest densities in secondary scrub, but

were almost never found in farmland. Other species' density data from this survey are limited because of the low encounter rates of the rarer species and so further conclusions are tentative. Pristine forest was apparently most important for the Chestnut-bellied Cotinga, Masked Mountain-tanager and Black-backed Bush-tanager, all restricted range species (Wege and Long 1995, Stattersfield *et al.* 1998). All three species, however, are edge páramo forest specialists and so may be able to cope well with fragmented habitat. Even with extensive deforestation, forest patches frequently remain in very steep areas and isolated gullies (pers. obs.) and these may be used by the species. This is probably true at least for the Chestnut-bellied Cotinga which appears to exploit the secondary vegetation of landslides (Robbins *et al.* 1994a, b). The Crescent-faced Antpitta is a restricted range species (Wege and Long 1995, Stattersfield *et al.* 1998) which occurred at Guandera in both primary and secondary forest: it appears at least partly able to use secondary habitats in other areas (Robbins *et al.* 1994a). The Grey-breasted Mountain Toucan is a near-threatened species (Collar *et al.* 1992) and used primary and secondary forest at Guandera and also isolated stands of trees within farmland. The Mountain Avocetbill is a relatively unrecorded species known currently from a few Andean sites (Fjeldså and Krabbe 1990, Krabbe *et al.* 1997) and occurred in cleared scrub and secondary forest habitats at Guandera. The Carunculated Caracara, another restricted range species (Wege and Long 1995, Stattersfield *et al.* 1998), occurred at very low densities at Guandera (probably 1 or 2 pairs) and was observed over both páramo and farmland. To summarize, of the nine species of particular conservation interest at Guandera, at least five used degraded habitats, while three occurred in pristine habitats that may be naturally fragmented, and that may be retained even with extensive deforestation.

There are major problems of detectability within any study that attempts to compare density and diversity between pristine habitats that are typically dense, with degraded habitats where the vegetation has been cleared. Within a dense habitat more effort is needed to record all of the bird species present (Figure 1). There will also be fewer encounters so that fewer species' densities can be calculated compared with a more open habitat. One of the major assumptions of the distance method is that all birds at zero metres are detected (Buckland *et al.* 1993). This assumption is clearly violated to a greater degree in dense habitats where the transect line is not visible ahead, compared with open habitats, where birds are more likely to be seen moving away from the observer. The net result of all the biases due to detectability are that species diversity, the number of calculable densities and the actual densities calculated will all be lower in a dense, pristine habitat relative to an open, degraded habitat. The total bias will be reduced as the duration and the intensity of the study continues, but even with an intensive survey as at Guandera, the importance of pristine habitats for birds will be underestimated. The general conclusion of this study, of the greater importance of pristine habitats for Andean birds, can be considered reasonably robust, however, because of the direction of the bias.

A major confounding factor in making conclusions from this study is the mosaic nature of the pristine and degraded habitats, and the potential effects of sink and source populations. For example, farmland at Guandera may only have had reasonable densities of Black-thighed Puffleg because adjacent primary

forest was at carrying capacity forcing surplus birds into suboptimal habitat. If the forest is then removed, Black-thighed Pufflegs may not be able to maintain the farmland population. Another problem is that density itself may be a misleading indicator of habitat quality because of competitive interactions (van Horne 1983). Nevertheless, the remaining area of forest at Guandera, sandwiched between farmland and the páramo, was only 400 ha (although the forest continues intermittently for several hundred kilometres along the ridge line). The diversity of species at Guandera is also relatively high for a high-altitude site (Robbins *et al.* 1994a, Poulsen and Krabbe 1997). The small size of the remaining forest at Guandera, its diversity and the density of birds there, even in secondary habitats, suggests that the remaining inter-Andean forest in north-eastern Ecuador even when substantially degraded is still an important habitat for Andean birds. More study is needed, though, to confirm the possible resilience of the bird species to its continued fragmentation, and to identify the inevitable limits of this adaptation.

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