Distribution and habitat use of Neotropical migrant landbirds in the Amazon basin and Andes

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Summary

We documented the geographical distributions and habitat selection of Neotropical migrants in South America along a successional gradient in the lowlands of Amazonian Peru, and along elevational gradients in the Andes of south-eastern Peru and of eastern and western Ecuador. Most of the 30 species of northern migrants that regularly winter in South America appear to be concentrated in the western edge of the Amazon basin and on the lower slopes (<2,000 m) of the Andes. Migrants in a lowland site were documented more often in early successional habitats than in primary forest, and no species were confined to mature forest habitats. The number of species and relative abundance of migrants in primary forest, however, increased with elevation up to about 1,200 m and decreased above that elevation. Several species (*Contopus borealis*, *Dendroica cerulea* and *Wilsonia canadensis*) were largely confined to primary forest in the 1,000–2,000 m elevational zones in both Peru and Ecuador. Migrants on the western slope of the Ecuadorean Andes included several species that primarily winter further north. In general, the species richness of migrants and residents was inversely correlated, both on a biogeographical and a local scale. Migratory birds are most likely to be adversely affected by deforestation of the lower slopes of the Andes, which is proceeding at a rapid pace. The impact of human alterations of Amazonian forests will be greater on resident than on migratory birds. The loss of mid-successional lowland forests, however, might have a negative effect on several species.

Introduction

In the rapidly growing literature on the ecology and conservation of Neotropical migrant landbirds (e.g. Keast and Morton 1980, Terborgh 1989, Hagan and Johnston 1992, Finch and Stangel 1993), species that winter in South America have received comparatively little attention (Stotz *et al.* 1992). Of the 30 species of Neotropical migrant landbirds that winter regularly in Amazonian South America (Fitzpatrick 1980, Robinson *et al.* 1988, Stotz *et al.* 1992), none has been studied in detail, even though some are of great conservation concern (e.g. Cerulean Warbler *Dendroica cerulea*: Robbins *et al.* 1992b). Robinson *et al.* (1988) noted that Neotropical migrants were mostly found in early successional habitats in the Amazonian lowlands, but were commonly found in primary forest in the eastern Andes (see also Robbins *et al.* 1992b). These results are in general agreement with other studies showing low diversity and abundance of Neotropical migrants in primary lowland forest in Amazonia (e.g. Pearson 1980,

Bierregaard 1990, Terborgh *et al.* 1990, Stotz *et al.* 1992, J.W.F. unpubl. data). Data from other studies of Andean forests are scarce but generally show that migrants use both primary and secondary forests (e.g. Chipley 1976, Terborgh 1989).

The purpose of this paper is to expand on the preliminary analysis of Robinson *et al.* (1988) by: (1) presenting data on the wintering distributions of Neotropical migrants in South America; (2) describing geographical replacements among closely related species; and (3) quantifying the habitat use of migrants along lowland successional gradients and elevational gradients in the Andes of Peru and Ecuador. We confirm that migrants concentrate in early and mid-successional habitats in the Amazonian lowlands, but occupy both primary and secondary forests in the middle elevations of the Andes. We then compare these results with overall patterns of species richness in these communities and with the much more extensive data from Central America (e.g. Lynch 1989, 1992, Greenberg 1992, Petit *et al.* 1992, Rappole *et al.* 1992, Robbins *et al.* 1992a).

Study area and methods

Geographical distributions

Wintering distributions for species reported here were mapped from published checklists, recent unpublished data from various fieldworkers, and unpublished records from specimens housed at the Field Museum of Natural History and the Louisiana State University Museum of Natural Science.

Amazonian lowlands. Habitat use of migrants was quantified in the vicinity of the Cocha Cashu Biological Station (11°55′S 77°18′W) on the Manu River about 90 km upriver from the mouth. This area is in the Manu National Park, department of Madre de Dios, Peru. The bird community of this site has been described in detail in Terborgh *et al.* (1984, 1990), Terborgh (1985), Robinson *et al.* (1990), and Robinson and Terborgh (1990). The vegetation of this community has also been described in detail in Foster *et al.* (1986) and Terborgh and Petren (1991). The successional dynamics of rivers in this region create a complex mosaic of successional and backwater habitats (Salo *et al.* 1986), which contributes greatly to the high species richness of this area (Parker 1982, Remsen and Parker 1983, Terborgh *et al.* 1984, Terborgh 1985, Robinson *et al.* 1990).

We quantified the habitat use of migrants in the following successional stages from Terborgh's (1985) classification. (1) Beaches are exposed along the Manu River during the dry season (June–October). (2) *Tessaria*, a composite tree, and cane (*Gynerium*) dominate the earliest successional stage on the insides of meander loops. (3) Mid-successional forests constitute a diverse array of successional stages of increasing tree species richness and structural complexity with age (Terborgh and Petren 1991). (4) Mature floodplain forest only forms in areas that escape being recycled by the meandering rivers for a very long time (probably 300 years or longer: Terborgh and Petren 1991). This forest is extremely diverse and structurally complex, and has been censused intensively (Terborgh *et al.* 1990). (5) *Terra firme* or upland forest is above the level of the

floodplain and consists of a heterogeneous mixture of mature forest, bamboo patches, and steep ravines. Terborgh and Petren (1991) estimate that *terra firme* forest covers roughly 70% of the western Amazon basin. (6) Oxbow lakes form when a meander loop of the Manu River becomes pinched off from the rest of the river. Cocha Cashu, the oxbow lake we studied, has a marshy border with shrubs invading the drier sections of the marsh and figs growing along the edge (Bolster and Robinson 1990).

Peruvian Andes. We worked at three primary forest sites in the upper tropical zone of the Andean foothills (600–1,400 m) and one at 2,700 m in the upper subtropical zone. The upper tropical zone sites had a maximum canopy height of 35 m, and the upper subtropical site consisted of primary elfin cloud-forest. All sites were located in the Cosñipata Valley in the departments of Cusco and Madre de Dios, south-eastern Peru (c. 11°S 78°W). Data from 400–1,400 m were gathered in the general vicinity of the towns of Pilcopata, Atalaya and Shintuya. Camps and study sites in these locations in the foothills were amidst undisturbed, humid pre-montane rainforest.

Ecuadorean Andes. Work was conducted by J.T. in February 1986 on both the eastern and western slopes of the Andes in the Parque Nacional Sangay (1,400 m, east slope), Puyo–Tena road (600 m), Hacienda San Vincente near the town of Mindo (1,500 m, west slope), Tinalandia (760 m, west slope), the Río Palenque (225 m, west slope), Río Coca (380 m, east slope), Salto de Coca (1,330 m, east slope), and Volcán Reventador (1,600 m). Habitats censused include primary and secondary forests (road edges and overgrown pastures) at all sites.

Methods

Two census methods were used to quantify habitat use of Neotropical migrants. (1) Visual censuses were conducted in specific habitats. Observers walked through habitats counting every bird observed, a method used by Pearson (1980) and Robinson *et al.* (1988). The percentage of Neotropical migrants in each sample (a minimum of 50 birds per sample) and the number of each species of migrant were calculated. Because we already reported data from the percentages of all migrants in each habitat at our Peruvian sites (Robinson *et al.* 1988), our emphasis in this paper will be on the distributions of each species. Results from the Ecuadorean transects, however, have not been published elsewhere. Visual counts tend to be biased towards canopy-dwelling species (Robinson *et al.* 1988), unlike mist-net samples. We did not record singing birds, to avoid biasing our detections in favour of territorial resident species. We made no attempt to quantify absolute abundance or population densities of migrants in any habitat. For visual censuses, we only used counts conducted from November through February in each habitat.

Additional flock counts were made in transects in the eastern Andes. Because these results have already been published in Robbins *et al.* (1992b), however, we mention them only briefly.

Mist-net censuses were conducted in November–February in habitats at various successional stages of the lowlands of the Manu National Park, along the elevational gradient in the Peruvian Andes and at 1,500 m in the western Andes of Ecuador. Mist-nets (12-m, with 36-mm mesh) were strung end to end in lines of 10–40 nets and opened from dawn to dusk on 2–4 consecutive days. We calculated the numbers of individuals of each species captured and the percentages of migrants in each sample. Because mist-net samples are strongly affected by vertical habitat structure and interspecific differences in movement patterns, we use these data only as general indices of the presence of migrants in particular habitats and elevational stages. We assume, however, that very large (five-fold) differences in proportional captures in mist-nets are correlated with differences in abundance. We used only data from net lines from November through February to maximize the numbers of migrants in samples. For the Manu National Park, we combined data from all years, 1973–1985, in our samples from each successional stage. For netting results in the Peruvian Andes, an effort was made to capture a minimum of 300 individual birds per sample. In the lowlands, each sample was smaller, but cumulative samples from all years contained up to 1,000 individuals sampled in some habitats.

Results

Geographical distributions

Thirty landbird species regularly winter in significant numbers in the Amazon and central Andes south of Colombia (Appendix 1). Two other species, *Empidonax virescens* and *Vermivora chrysoptera*, were recorded in our Ecuadorean sample (see below), but mostly winter farther north. The 30 species fall mostly into two broad ecological categories: foliage-gleaning insectivores (19 species) and aerial insectivores (nine species; Appendix 1). Many of the foliage gleaners and at least one aerial insectivore (*Tyrannus tyrannus*) also consume significant amounts of fruit on the wintering grounds (Morton 1971, Fitzpatrick 1980). Foliage-gleaning insectivores are predominantly species that breed in eastern North America and migrate along the Caribbean coast of Mexico and Central America, whereas the aerial foragers show more widespread North American distributions (Figure 1).

Besides the Osprey *Pandion haliaetus*, an aquatic feeder, only a single raptor (*Buteo platypterus*) commonly winters in the area, although two others (*B. swainsoni* and *Ictinia mississippiensis*) pass through along the Andean foothills in transit to the south (Davis 1989, Terborgh *et al.* 1989). Winter distributions of foliage gleaners and aerial foragers show a distinct tendency to be concentrated toward the western edge of the Amazon basin and eastern Andes (Figure 1). Even those few species that occur across much of the Amazon basin are considerably more common in the west and north. The central and eastern Amazonian lowlands are almost devoid of migrants from North America.

Geographical segregation

Fitzpatrick (1980) showed that closely related migrant tyrannid flycatchers are distributed in winter as mosaics of largely allopatric or parapatric ranges across
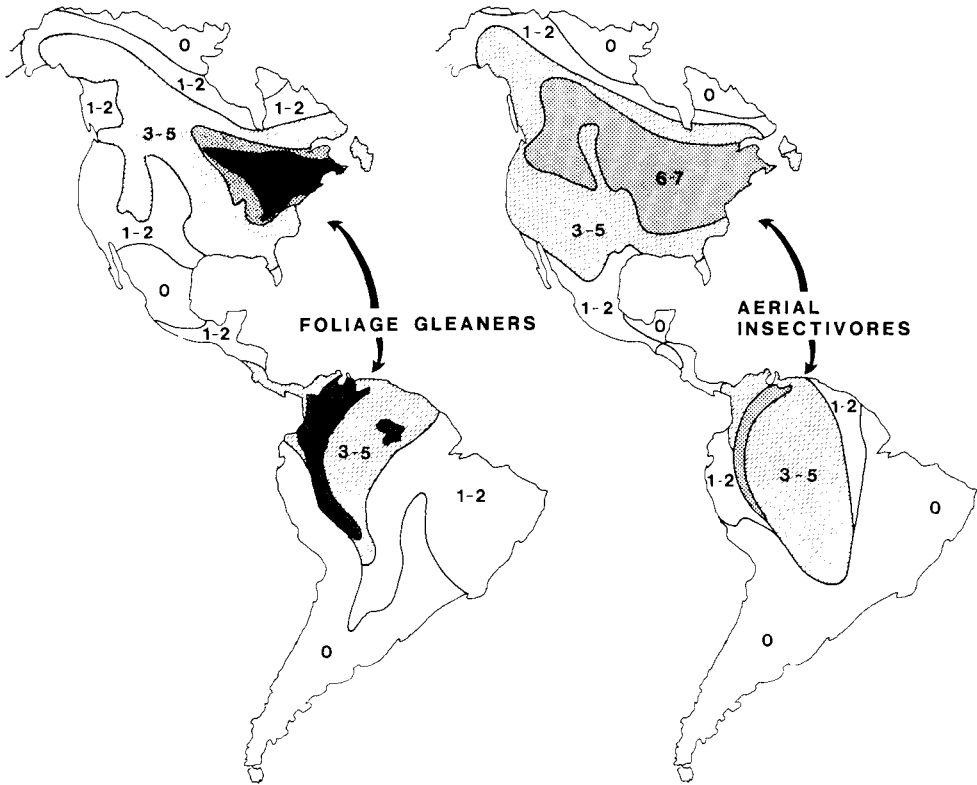
Figure 1. Breeding and wintering distributions of bird species whose predominant winter distributions fall in the Amazon drainage. Isopleths and shading depict geographic patterns of species richness for foliage gleaners (18 species) and aerial-insect feeders (9 species). Black, 11–13 species; dark stippling, 8–10 species; figures for remaining shades are shown on maps.

the Neotropics. Additional groups of foliage-gleaning species that include Amazonian winterers show this tendency as well, especially thrushes (*Catharus* spp.) and several groups of wood warblers (*Oporornis* spp., *Wilsonia* spp., *Dendroica* spp.) (Chipley 1980). The Amazon basin generally harbours the southernmost species in each of several genera or species groups, such that any one locality typically contains only one species from each group (Fitzpatrick 1980).

Geographical replacement among closely related migrants on their wintering grounds is more conspicuous among the foliage-gleaning species than among the aerial foragers. Among the species foraging on aerial insects, only two species pairs show substantial geographical segregation. Segregation among *Tyrannus* kingbirds was mapped in Fitzpatrick (1980). In addition, Western and Eastern Wood-pewees *Contopus sordidulus* and *C. virens* both winter in the forested Andes. Reliable records of *C. sordidulus* are scarce, especially south of Colombia; all records are from elevations above 1,200 m. Records of *C. virens* are widespread south to Peru and Bolivia, and indicate a substantial lowland population in the western Amazon basin (see below). *Contopus borealis* overlaps

Table 1. Number of Neotropical migrants netted and observed in the major habitats present in the vicinity of the Cocha Cashu Biological Station. All counts made from 1 to 30 November 1984–1986

Species	Tessaria/Cane		Mid-successional forest		Mature floodplain		Terra firme	
	Net	Visual	Net	Visual	Net	Visual	Net	Visual
Coccyzus erythropthalmus	0	+	0	0	0	0	0	0
C. americanus	0	+	0	+	0	+	0	0
Contopus borealis	0	0	0	+	0	0	0	0
C. virens	1	0	1	11	0	2	0	1
Empidonax alnorum	24	1	2	0	0	0	0	0
Myiodynastes luteiventris	0	2	0	9	0	0	0	0
Tyrannus tyrannus[a]	1	6(44)	0	1(17)	0	0	0	0
Catharus ustulatus	2	3	1	4	8	+	4	1
Piranga rubra	0	0	0	+	0	+	0	0
P. olivacea	0	0	0	+	0	+	0	+
Oporornis agilis	2	0	0	0	0	0	0	0
Vireo olivaceus	0	0	0	1	0	0	0	0
V. flavoviridis	1	0	0	4	0	0	0	1
Dolichonyx oryzivora	1	3	0	0	0	0	0	0
Total migrants	32	15	4	30	8	2	4	4
Total sample	182	121	123	342	669	312	364	322
% Migrants	17.6	12.4	3.3	8.9	1.2	0.6	1.1	1.2
Captures/ 100 net-days	133.3		6.7		1.4		1.4	

A "+" sign indicates that the bird has been observed in this habitat, but not during the sample.
[a] This species occurs in flocks; the number given is the number of flocks observed, the number in parentheses refers to the number of birds present in flocks.

C. virens throughout its wintering and breeding ranges, but tends to be found at higher elevations (see below).

Geographical and elevational segregation also occurs among the three southernmost-wintering species of *Dendroica* warblers. All three species (*D. fusca*, *D. cerulea*, and *D. striata*) winter in mixed-species flocks in the forest canopy or subcanopy of South America (Robbins *et al.* 1992b). Of 21 migratory species in this large North American genus, only *D. striata* regularly occurs in the forests of the lowland Amazon, predominantly north of the Amazon River (Pearson 1980). Along the Andean foothills, at elevations between 650 and 1,150 m, only *D. cerulea* is encountered. Above 1,200 m *D. cerulea* is abruptly replaced by *D. fusca*, which occupies cloud-forests of middle and upper elevations nearly to 3,000 m (see Robbins *et al.* 1992b).

Habitat preferences in the lowlands

As described elsewhere (Robinson *et al.* 1988), both northern and austral migrants (as well as intratropical migrants) show a pronounced preference for open, brushy, and early successional habitats rather than tall, mature forest (Table 1; see also Bierregaard 1990 for data from Manaus, Brazil). Because species richness is higher in mature forest and lower in successional vegetation
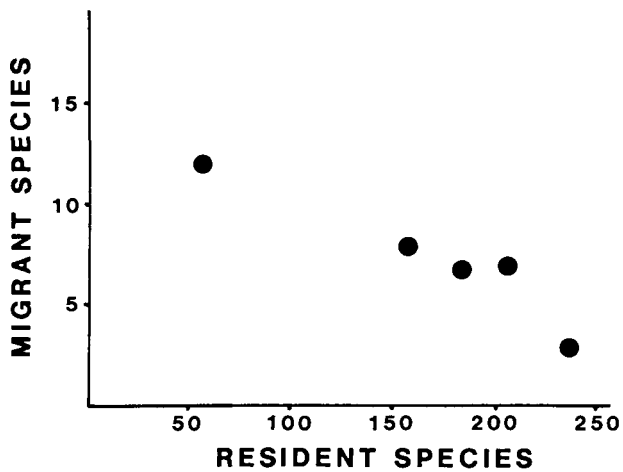
Figure 2. Species richness measures of migrant versus resident bird communities in south-eastern Peru, based on censuses of five tropical habitats conducted from October to December.

(Terborgh 1985, Terborgh *et al.* 1990), there is an inverse correlation between migrant and resident species richness (Figure 2). Among Neotropical migrants, only *Contopus virens* (large forest treefalls and bamboo patches), *Catharus ustulatus, Vireo flavoviridis* and *Piranga olivacea* were regularly observed or captured inside mature forest (Table 1). The capture rate of migrants in the earliest successional stages (*Tessaria* and cane) was nearly two orders of magnitude higher than in mature floodplain and *terra firme* forest, which together cover most of western Amazonia (Terborgh and Petren 1991). Mist-net samples, however, may be biased toward detecting migrants in early successional habitats because they sample the entire community in low, shrubby habitats whereas they only sample understorey birds in mature forest (Robinson and Terborgh 1990). For this reason, differences in capture rates should be treated with caution. Lake-margin samples (Robinson *et al.* 1988) also show high populations of *Myiodynastes luteiventris* and *Tyrannus tyrannus*, which forage mostly in lauraceous trees (Fitzpatrick 1980, S.K.R. unpubl. data). Four of our six lowland records of *Contopus borealis* were from the lake margin.

Several species were only recorded in the earliest successional stages (Table 1). *Dolichonyx oryzivora* was found only in marshes and in beach grasses. *Empidonax alnorum* was abundant in *Tessaria* and appeared to be territorial; individuals sang, occasionally chased each other, and at least two banded individuals were still present at their site of capture two weeks later (S.K.R. unpubl. data). *Tyrannus tyrannus* was often the most abundant bird during its southward migration. On 22 October 1982, 5,200 were counted passing over and foraging along the edge of Cocha Cashu (S.K.R. pers. obs.). By December, however, only a few small flocks (less than 50 individuals per flock) remained in the Cocha Cashu area.
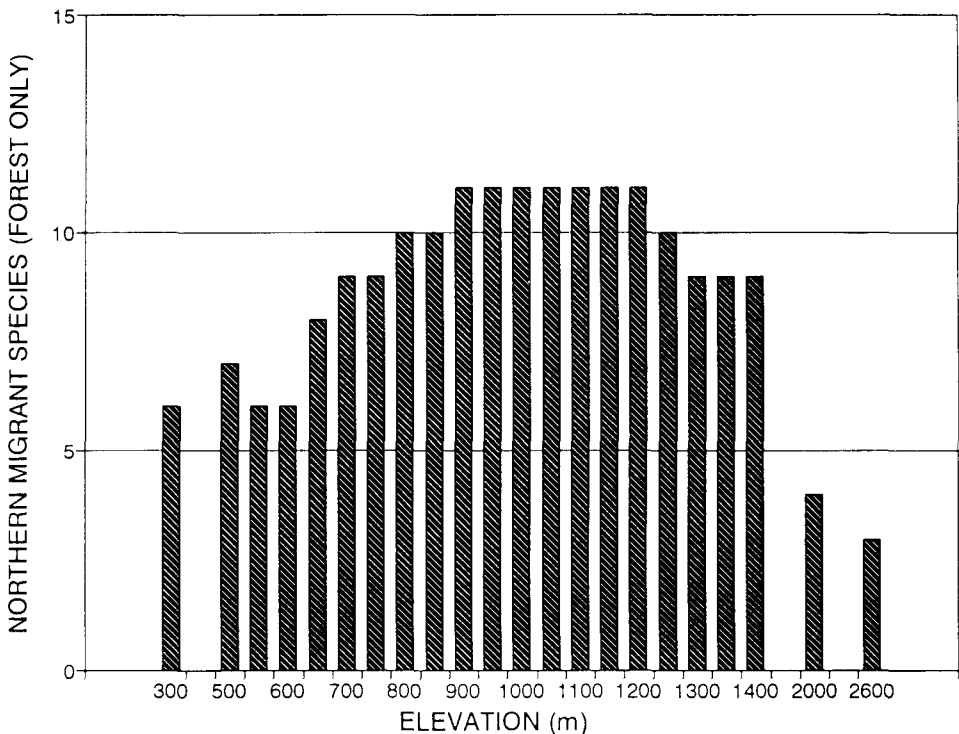
Figure 3. Numbers of migrant species observed in forest habitats along an elevational gradient in south-eastern Peru.

Migrants in the eastern Andean foothills

In the foothills and middle elevations of the forested eastern Andes, migrants made more extensive use of forest. Species richness of migrants in forest increased with elevation up to about 1,200 m (Figure 3), but decreased at higher elevations (see also Robinson *et al.* 1988, Robbins *et al.* 1992b). The proportion of *Catharus ustulatus* in mist-net samples in the Andes increased with elevation. Below 600 m, less than 5% of the captures were *C. ustulatus*, whereas samples between 700 and 1,500 m contained 10–22% *C. ustulatus* (J.W.F. unpubl. data). If *C. ustulatus* forages higher in the canopy in the taller lowland forests, however, these estimates of abundance could be biased in favour of the lower canopy of higher-elevation forests.

Use of flocks in south-eastern Peru

Observations of mixed-species flocks reported in Robbins *et al.* (1992b) showed that most foliage-gleaning migrants in South America join the flocks described by Munn and Terborgh (1979), Munn (1985) and Powell (1985). In south-eastern Peru, the number and species richness of northern migrants inhabiting flocks increases with elevation (Figure 4) and was inversely correlated with the species
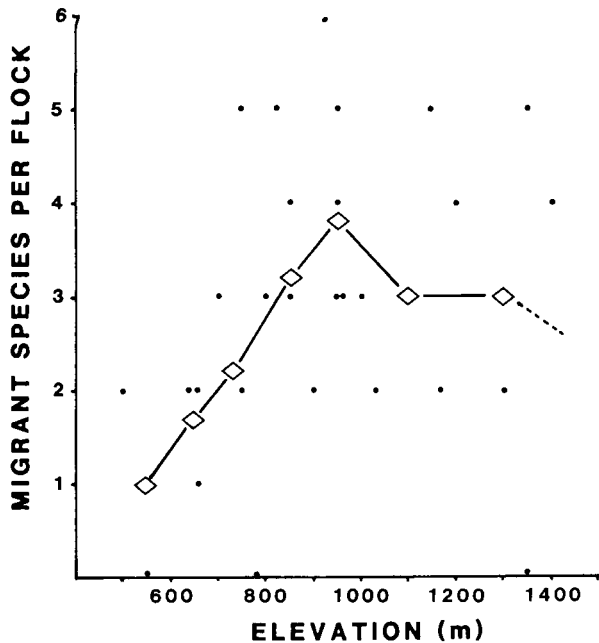
Figure 4. Species richness of northern migrants in 28 canopy flocks plotted against eleva-
tion. Mean values are shown (with open diamonds) for elevational intervals centred at
550, 650, 750, 850, 950, 1,100, and 1,300 m. Flocks above 1,400 m were not censused
quantitatively, but are known to contain fewer migrants.

richness of the total forest bird community (Figure 5). At 2,600 m, only two
migrant species were observed in flocks, one of which (*Pheucticus ludovicianus*)
was not recorded at lower elevations. The number of migrants in flocks reached
its peak between 800 and 1,000 m. The most abundant warbler in flocks was
Wilsonia canadensis, which occurred in virtually every subcanopy and canopy
flock from 600 to 1,400 m, occasionally in pairs (Robbins *et al.* 1992b). *Wilsonia*
forages lower in the canopy than *Dendroica cerulea* or *D. fusca*. These three
warblers have never been recorded in the lowlands around Cocha Cashu.
Interestingly, we never observed *D. fusca* and *D. cerulea* in the same flocks
(Robbins *et al.* 1992b). The geographical, ecological and elevational segregation
among the five species of migrant warblers in south-eastern Peru is shown
schematically in Figure 6. The Blackpoll Warbler *D. striata* occurs mainly north
of the Amazon.

In addition to the warblers, four other northern migrants were observed in
flocks along the elevational gradient. *Vireo olivaceus* was found in 25 of 28 flocks
between 500 and 1,400 m (total of 61 individuals), with no discernible decrease
in abundance at higher elevations. Of the two tanagers, *Piranga olivacea* was
more abundant (present in 16 of 28 flocks, 35 individuals) than *P. rubra* (6 of 28
flocks; seven individuals). Both species were absent at 2,600 m. *Coccyzus
americanus* was recorded in two flocks at 500 m and 920 m, but was observed at
all 10 sites between 300 and 900 m; *C. erythropthalmus* was only observed below
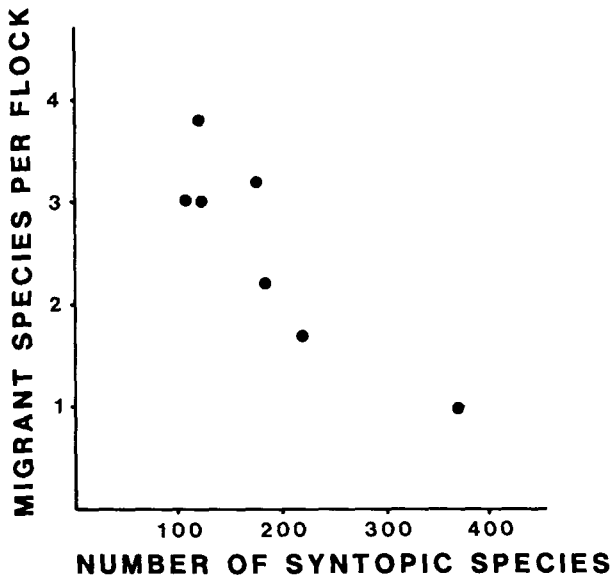500 m.

Figure 5. Mean species richness for migrants in mixed-species flocks plotted against richness of resident species at the same sites and elevations. Values for migrants are directly from Figure 4; those for residents are from our extensive, unpublished data on forest bird communities at these sites.

Ecuadorean Andes

Data from the eastern and western slopes of the Ecuadorean Andes (Table 2) showed general similarities to results from the Andes of south-eastern Peru. Migrants were rarely noted in primary forest in the lowlands of both slopes (sites 2 and 7), but were frequently observed in secondary habitats in the Amazonian lowlands (site 1) where *Dendroica striata* was the most abundant species. *Dendroica striata* was only observed in more disturbed forest, but Pearson (1980) has also observed it in primary forest in his far more extensive samples. Above 600 m on both slopes, migrants were found in both primary and secondary habitats. As in Peru, *Dendroica fusca* and *Wilsonia canadensis* were the most abundant species in flocks above 600 m on the eastern slope, but only *D. fusca* was observed on the western slope. *Dendroica fusca* tolerated highly disturbed habitats, whereas *W. canadensis* was most abundant in primary forest. *Contopus borealis* was also observed only in primary forest samples. *Dendroica cerulea* was observed only in primary forest at 1,330 m on the eastern slope, a similar elevation to its distribution in south-eastern Peru (Robbins *et al.* 1992b). *Empidonax virescens*, *Setophaga ruticilla* and *Contopus sordidulus* were found only on the western slopes of the Andes; these species were also absent from *south-eastern Peru*. Surprisingly, *Catharus ustulatus*, which was abundant in the eastern Andes of Peru, was far more commonly observed on the western slope in Ecuador. Two warblers that primarily winter farther north, *Vermivora chrysoptera* and *Oporornis philadelphia*, were both observed at middle elevations on the eastern slope of the Andes. Both *Piranga* tanagers occurred in disturbed
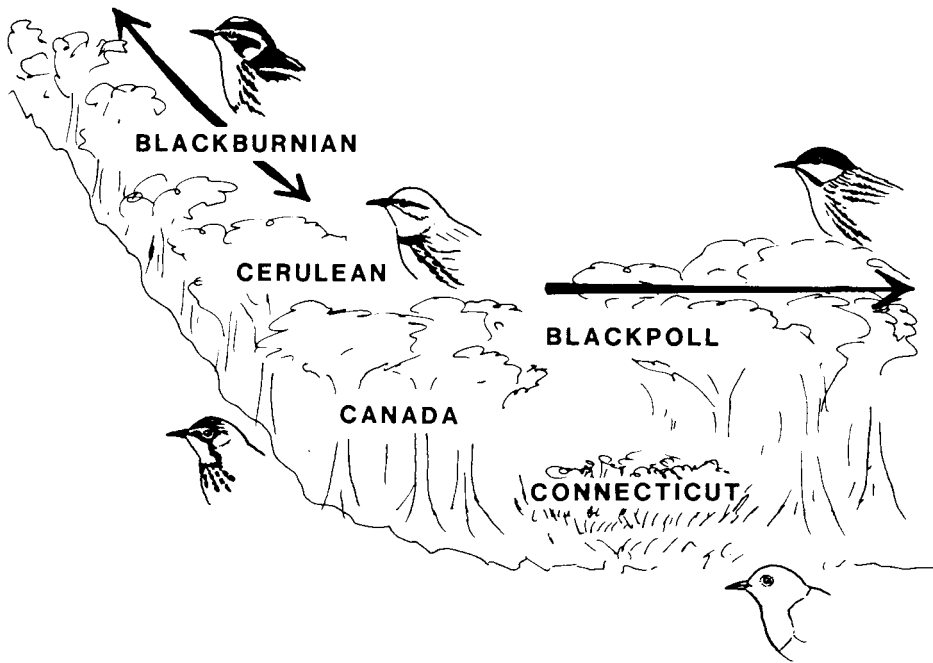
Figure 6. Schematic depiction of ecological and geographic segregation among five species of migrant wood warblers (Parulidae) in the Amazonian and eastern Andean forests (see text).

habitats on the eastern slope, and most migrants on the western slope were found in primary and secondary habitats.

Discussion

Our results generally show a relatively low abundance and richness of migrants in the vast tropical and subtropical forests of Amazonia and the Andes, which harbour the richest diversity of resident bird species in the world (Terborgh *et al.* 1990). The inverse pattern holds for the Central American tropics, where northern migrants abound for over half the year (Rappole *et al.* 1983) and resident tropical bird communities are depauperate by South American standards (Tramer 1974). In this paper, we have shown that this inverse relationship also holds at the local level among habitats within Amazonian lowlands and along an elevational gradient (Figure 2). These results support a general hypothesis that migrant and resident bird communities in the Neotropics do, to some extent, replace one another spatially (Slud 1976, Waide 1980, Leisler 1990). Evolution and radiation of a diverse resident fauna in South America may have inhibited a significant proportion of northern migrants from establishing their primary wintering grounds on that continent. Austral migrants also appear to be concentrated in early successional habitats in south-eastern Peru (Robinson *et al.* 1988). In turn, the vast numbers of northern breeders crowding into the smaller land area of Central America may in part

Table 2. Results of censuses of the eastern and western slopes of the Ecuadorean Andes, February 1986

	Eastern slope						Western slope				
Site number:	1	2	3	4	5	6	7	8	9	10	11
Elevation[1]:	380	600	600	1,330	1,400	1,600	225	760	760	1,500[b]	1,500
Forest type:	2°	1°	2°	1°	2°	1°	1°	1°	2°	1°	1°
Myiodynastes luteiventris	1										
Contopus virens	1			1							
C. sordidulus									1		
C borealis				3		2					
Empidonax virescens							1	1	2	1	
E. alnorum	1										
Catharus ustulatus				2				5	7	6	1
Vireo flavoviridis									1		
Vermivora chrysoptera						1					
Dendroica fusca				4	4	10			8		6
D. striata	8		2								
D. cerulea				4							
Wilsonia canadensis				14	1	4					
Oporornis philadelphia						1					
Setophaga ruticilla											4
Piranga olivacea				1	2			1			
P. rubra					1			1			
Total Migrants	12	0	2	28	9	18	1	6	21	8	11
Total Individuals	98	60	58	177	74	104	107	113	87	103	141
Percentage Migrants	12.2	0.0	3.4	15.8	12.2	17.3	0.9	5.3	24.1	7.3	7.3

[a] Locations: 1, Río Cocha (medium-tall second growth); 2, 3, between Puyo and Tena; 4, Salto de Coca; 5, Parque Nacional Sangay between Río Bamba and Puyo (second growth); 6, Volcán Reventador (primary cloud-forest), 7, Río Palenque; 8, Tinalandia; 9, Tinalandia (pasture with scattered trees); 10, 11, Hacienda San Vincente near Mindo (primary cloud-forest).
[b] Mist-net sample.

explain that subcontinent's failure to support as rich a resident community. Alternatively, Central America may contain more migrants for historical reasons – it is closer to the North American breeding grounds of most species. The unpredictable pulses of resources available in early successional habitats, especially those along rivers (Terborgh 1985, Robinson *et al.* 1988) might also provide migrants with food resources that are not being fully exploited by resident species (Waide 1980). Migrants in the tropical forests of Central Africa (Brosset 1990, Lack 1990, Leisler 1990) and south-east Asia (Wells 1990) are also most abundant in early successional vegetation.

Unfortunately, as with any such historical scenario, the tests that might confirm these competitive dynamics are indirect at best (e.g. Fitzpatrick 1980). Support for the notion that wintering ranges of different species have evolved in concert with one another (Chipley 1980) comes from the conspicuous patterns of geographical replacement among numerous groups of ecologically similar migrants, which includes separation between many species that are sympatric on their breeding grounds. It is therefore possible that the wintering ranges might be adjusted through time with respect to other, resident species as well, or that winter ranges are ancestral.

A second, confounding pattern of distribution and abundance characterizes those few species that do winter in the South American forests. Most of these species are concentrated toward the western regions of the Amazon basin and the forested slopes of the Andes that form the basin's western rim. This clustering of species appears to counter the above suggestion that species tend to space themselves evenly at a geographical scale. Evolutionary adjustments in distributions that minimize sympatry in winter would tend to produce a more uniform density of migrants than is actually observed (Figure 1). Moreover, the observed clustering of migrants in western Amazonia coincides with an *increase* in resident species diversity from east to west, exactly opposite to the predictions of the hypothesized inverse effects of residents upon migrants. Migrants may concentrate in the western part of South America because it is closest to the North American breeding grounds (Figure 1), but differences in productivity may also play a role.

The increase in resident species diversity toward western Amazonia characterizes virtually every group and guild of tropical birds (e.g. Haffer 1974 fig. 8.2, Haffer 1978). The same pattern apparently holds generally for mammals (Koopman 1982, Emmons 1984), possibly plants (Gentry 1977, Haffer 1978, Prance 1982), and even native human populations (Meggers 1975). The western Amazon basin supports a substantially more diverse biota than elsewhere. This pattern might reflect higher productivity along the base of the Andes than in the central and eastern Amazonian basin. Indeed, across the Amazon basin, rainfall is much the highest at the base of the Andes, where the foothills cool and condense the vanguard of moisture-laden breezes coming off the humid lowland forests (Simpson and Haffer 1978).

Productivity may also be higher in mid-elevation sites even though resident species richness declines with elevation (Figure 5). In Costa Rica and Venezuela, Janzen (1973, 1976) found insect diversity to reach a peak at middle elevations in the mountains, at about 1,200 to 1,500 m. He hypothesized that cooler night temperatures at these elevations promote higher plant productivity, in turn supporting more insect life, by reducing the energetic demands of transpiration. These lower cloud-forest elevations are close to where migrant bird diversity is highest in Peru (Figures 3, 4). Resident bird diversity at these elevations is lower than at tropical elevations (Terborgh 1977), for various reasons. A principal cause is that overall diversity of habitats in the montane forests is greatly reduced compared with the lowland Amazon, where river edges, canebrakes, marshes, palm forests, vine tangles, bamboo thickets and highly variable configurations of the forest canopy all contain bird species specializing in these habitats, thereby giving rise to an extremely high regional species richness (Terborgh 1980b, 1985, Remsen and Parker 1983, 1984).

Conservation implications

The distribution of migrants in Central America differs in several respects from our data from South America. In general, most species of migrant in Central America occupy disturbed, second-growth forests as well as primary forest (Karr 1976, Waide 1980, Martin 1985, Hutto 1989, Kricher and Davis 1992, Lynch 1992, Petit *et al.* 1992, Robbins *et al.* 1992a). Some species that winter in Central

America, however, are largely confined to forest habitats (Willis 1966, Powell 1980, Terborgh 1980a, 1989, Robbins *et al.* 1987, Lynch 1989, Rappole *et al.* 1992) and some species may be intolerant of habitat modifications (Rappole and Morton 1985, Winker *et al.* 1990, Rappole *et al.* 1992). Neotropical migrants are far more abundant in primary forest in Central than in South America (Terborgh 1989). Consequently, northern migrants that winter in Amazonia may be less negatively affected by deforestation than those that winter further north (Robinson *et al.* 1988). Population declines of species that winter primarily in the Amazon basin (e.g. *Vireo olivaceus*) are perhaps more likely to be attributable to factors associated with the breeding grounds such as forest fragmentation (Wilcove and Robinson 1990, Robinson and Wilcove 1994).

Habitat alteration in Amazonia, however, may still adversely affect some migrants. We know little about how species restricted to successional vegetation along rivers (e.g. *Empidonax alnorum*, *Oporornis agilis*) will adapt to human-altered landscapes. Alterations in the hydrology of rivers by damming the Amazon or its tributaries may halt or alter the riparian succession that creates most of the habitats currently used by migrants and many residents (Remsen and Parker 1983, Terborgh 1985, Bolster and Robinson 1990). Similarly, we know little about how deforestation will affect the tree species composition of successional forests. A decline in lauraceous fruits, for example, could adversely affect populations of *Tyrannus tyrannus* and *Myiodynastes luteiventris* (Morton 1971, Fitzpatrick 1980, S.K.R. unpubl. data). Some migrants would probably increase as a result of some kinds of human activity, but we know too little to predict which ones. Furthermore, Pearson (1980) has found that migrants make more extensive use of forests in northern Amazonia than we found in southern Amazonia. Stotz *et al.* (1992) also found that *Vireo olivaceus* winters in primary forest in Manaus, Brazil.

As argued by Robinson *et al.* (1988) and Robbins *et al.* (1992b), the area of greatest conservation concern for migrants in South America appears to be the lower- to middle-elevation forests of the Andes. Most wintering populations of *Contopus borealis*, *Dendroica cerulea* and *Wilsonia canadensis* appear to be restricted to primary forest within this region, which is under severe threat from logging and conversion to coffee, cacao, and coca plantations (Robbins *et al.* 1992b). *Dendroica fusca* is also confined to this area, but appears more tolerant of disturbance than the species listed above (Chipley 1976). The abundance of the geographically widespread *Catharus ustulatus* in the Andes suggests that their populations will also be adversely affected by deforestation of the lower slopes of the Andes.

In summary, our data strongly support the contention of Robbins *et al.* (1992b) that the lower slopes of the Central Andes should be of the highest conservation priority. Migrants of lowland areas may be more resistant to habitat alteration, but only if they use altered, secondary successional vegetation. Further studies of migrant use of human-altered habitats in Amazonia are necessary before we can evaluate the effects of tropical deforestation on Neotropical migrants.

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Appendix 1. North American landbird species with substantial winter populations in Amazonia and adjacent eastern Andes[a]

	Foraging guild[b]	Habitat[c]	Regional distribution[d]	Elevation (m)
Buteo platypterus	p	f	1–4	300–3,000
Coccyzus erythropthalmus	f	f	1–4	0–2,000
Coccyzus americanus	g	f	1–5, 7	0–2,000
Chordeiles minor	a	a	3–7	0–1,800
Chaetura pelagica[e]	a	a	3, 5?	0–?
Tyrannus tyrannus	a, fr	e	3, 4	0–500
Myiodynastes luteiventris	g, fr	f, e	2, 4	250–1,000
Contopus borealis	a	f, e	1, 2	350–2,000
Contopus virens	a	f, e	1–4	200–1,700
Contopus sordidulus	a	f, e	1, 2	900–2,800
Empidonax alnorum	g	e	3, 4	200–500
Progne subis	a	a	3–7?	0–300
Riparia riparia	a	a	3, 4, 6	0–500
Hirundo rustica	a	a	3–7	0–500
Catharus ustulatus	g, fr	f, e	1–4	200–2,150
Catharus minimus	g, fr	f, e	1, 3, 5	0–3,000
Catharus fuscescens	g, fr	f, e	5–7	0–300
Vireo olivaceus	g, fr	f, e	1–6	200–2,000
Vireo flavoviridis	g, fr	f, e	1–4	200–1,200
Vireo altiloquus	g, fr	f, e	3	0–?
Dendroica petechia	g	s, m	3, 5	0–300
Dendroica cerulea	g	f	1, 2	750–1,300
Dendroica fusca	g	f	1, 2	1,000–3,000
Dendroica striata	g	f	3–5	0–350
Oporornis agilis	g	e, s	3–6	0–350
Wilsonia canadensis	g	f	1, 2	600–2,500
Piranga rubra	g, fr	f	1–4	200–2,200
Piranga olivacea	g, fr	f	1–4	200–1,800
Pheucticus ludovicianus	g, fr	f	1, 2	1,000–2,800

[a] The following species, which winter in Amazonia in small numbers, are excluded from the list because their principal winter ranges lie elsewhere: *Tyrannus dominicensis, Empidonax traillii, Petrochelidon pyrrhonota, Vermivora chrysoptera, Seiurus noveboracensis, Oporornis philadelphia, Setophaga ruticilla.*
[b] p, vertebrate predator; g, foliage gleaner; fr, frugivore; a, aerial insectivore.
[c] f, primary forest; e, forest edge, openings; a, aerial; s, savanna; m, marshes.
[d] 1, eastern Andean slopes north of Río Marañon; 2, eastern Andean slopes south of Rio Marañon; 3, lowland forest north of Amazon, west of Rio Negro; 4, lowland forest south of Amazon, west of Rio Purus; 5, lowland forest north of Amazon, east of Rio Negro; 6, lowland forest south of Amazon, between Rios Purus and Tapajoz; 7, lowland forest south of Amazon, east of Rio Tapajoz.
[e] Winter range of *Chaetura pelagica* is still poorly known; Amazonian populations are assumed on basis of Gilliard (1944) and Lincoln (1944); large populations are known to occur in Peru west of Andes (Parker *et al.* 1982).