DIVERSITY AND CONSERVATION OF UNDERSTORY BIRDS IN THE TILARÁN MOUNTAINS, COSTA RICA

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ABSTRACT.—Using data from 10,726 captures of birds in mist nets, we document the high alpha and beta diversity of the understory avifauna in the Tilarán mountains of north-central Costa Rica. We grouped the capture data from 20 sampling sites into five Holdridge life zones that represent a gradient in elevation and seasonality of precipitation. Despite the limited size of the study area (200 km²) and the relatively small differences in elevation (700 to 1,700 m), major differences were found among each of the five life zones. We recorded a total of 235 species, with species richness increasing downslope on both the Pacific and Caribbean sides of the range. Rarefaction curves showed that the elevational zone of 650 to 750 m on the Caribbean side (Wet Premontane Transition Forest) was the most diverse per unit of mistnetting effort and that the Lower Montane Rain Forest on the continental divide (1,500 to 1,700 m) was the least diverse. Adjacent life zones had similarity indices ranging from 0.30 to 0.47; beta diversity for the region was 0.45. These measures are indicative of a high species turnover among our samples as delimited by Holdridge's life zone system, suggesting a concordance between the life zone system and the distribution of the region's diverse understory avifauna. Elevational migrants made up similar proportions of the avifauna in all five zones, whereas the diversity of long-distance migrants was inversely related to elevation. The distribution of species of conservation concern did not track the pattern of overall diversity. Our results provide several lessons for land managers and present a strong case for the need to preserve large areas with elevational diversity in mountainous regions of the tropics. Received 22 September 1997, accepted 2 April 1998.

ALTHOUGH ORNITHOLOGISTS have long been aware of the rapid turnover of bird species across elevational gradients in the Neotropics, quantitative studies of fine-scale distributional patterns are available for very few geographic regions (Terborgh and Weske 1975). Such studies allow us to examine the faunistic composition of communities in different elevational habitats, turnover in species composition among habitats (or beta diversity, sensu Whittaker 1972), and to evaluate the conservation status and determine area requirements for conserving montane biodiversity. The ongoing and projected crisis status of tropical forest conservation demands that we gather this information as rapidly as possible (Diamond 1985, Stotz et al. 1996).

We compiled data from a series of mist-netting projects to produce estimates of bird diversity in the Monteverde reserve complex, a composite of private reserves in the Tilarán mountains of north-central Costa Rica. The reserve complex has a rich history of ornithological investigation over the last 25 years, but few studies have addressed the distribution of species across an elevational gradient (Young and McDonald 1998). Previous distributional studies of birds have focused on individual species or restricted guilds (Feinsinger 1977; Tramer 1979; Tramer and Kemp 1980, 1982; Stiles and Smith 1980). Treatments of the entire Monteverde avifauna are currently restricted to observation check-lists (Stiles 1983, Fogden 1993).

Our goal was to use a compilation of capture data to describe and characterize the diversity and distribution of the understory avifauna between 700 and 1,700 m on both slopes and the crest of the Tilarán range. We analyzed the distributions of the entire understory avifauna and a subset that included only threatened spe-

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FIG. 1. Location of the Tilarán mountains, Costa Rica and distribution of Holdridge life zones along a west-east transect of the study area.

cies to learn how patterns of diversity in the two groups coincide. We use this information to provide general management guidelines and to identify where future habitat preservation efforts in the region should be directed.

STUDY AREA AND METHODS

The study area was a 200-km² area in the middle and higher elevations of the Tilarán mountains, which form the continental divide in north-central Costa Rica (10°18'N, 84°45'W). The Tilarán range is characterized by marked habitat heterogeneity due to the rugged topography and northeasterly tradewinds that buffet the area six months of the year (Fig. 1). The tradewinds strike the mountain range at right angles causing a steep moisture gradient under which the Caribbean slope receives heavy rainfall, the mountain crest is often covered in clouds, and the Pacific slope experiences an extended dry season. Vegetation reflects this moisture gradient. The Caribbean slopes are covered by tall evergreen forest, high elevations by dwarfed cloud forest, and the Pacific slopes by forests with a strong deciduous component (see Lawton and Dryer 1980, Hartshorn 1983, Lawton and Putz 1988). Much of the Tilarán mountains above 700 m on the Atlantic slope and 1,500 m on the Pacific slope are protected by a private reserve complex that has been developed over the last 25 years, including the Monteverde Cloud Forest Preserve, the Children's International Rainforest, the Santa Elena Reserve, and Arenal National Park (Powell and Bjork 1995; Fig. 2).

Although some authors use elevation to segregate bird communities in montane regions, we believe that life zones are a more specific characterization of habitat conditions than elevation alone because regional orographic features can have a strong influ-



FIG. 2. Holdridge life zones and protected areas in the Monteverde region of the Tilarán mountains. Protected areas include the Monteverde Cloud Forest Preserve (MCFP), the Children's International Rainforest (CIR), the Santa Elena Reserve (SER), and Arenal National Park (ANP). Numbered sites refer to mist-net locations described in Table 1.

ence on local climates. Life zones are climate associations based on mean annual biotemperature (excluding temperatures less than 0°C or more than 30°C), mean annual precipitation, and (derived from the first two) potential evapotranspiration ratio (Holdridge 1967). According to the Holdridge life zone system, the middle and upper elevations of the Tilarán mountains fall within five life zones: Premontane Wet; Lower Montane Wet; Lower Montane Rain; Premontane Rain; and Wet Premontane Transition (Figs. 1 and 2). In this region, the moisture shadow of the Pacific slope of the mountains causes life zones to occur in narrower belts on the Pacific slope than on the Caribbean slope (Fig. 1).

We compiled data from 11 independent studies collected over a 20-year period from 20 locations (Buskirk 1976, Powell 1979, Feinsinger 1977, Winnett-Murray 1986, Feinsinger et al. 1987, Murray 1988, McDonald 1993, Young et al. 1993, J. E. Arévalo unpubl. data, D. DeRosier and K. Nielsen unpubl. data, A. Suarez unpubl. data; Table 1). All studies involved the capture of birds in standard mist nets placed at ground level in secondary or undisturbed old-growth forest. All data sets: (1) included a complete listing of the birds captured in each mist-netting bout; (2) provided information about the location where the nets were set; (3) documented dates of net operation; and (4) were based on captures using nets with a mesh size of 30 or 36 mm. Because we received few records from the two lower life zones on the Caribbean slope, one of us (DD) made expeditions to these sites to collect several hundred more captures. We combined data sets on the basis of life zone and scored for the presence of each species in each zone. We eliminated captures of birds from four families, Cathartidae, Strigidae, Apodidae, and Hirundinidae, because they were considered accidental captures of nonforest or nocturnal species. Designation of elevational migrants is based on Stiles' (1985) list of species that undertake regular seasonal movements up and down the mountains of Costa Rica.

Our study has three potential biases. The first bias could be caused by using mist nets, which do not sample all bird species with equal efficiency. Mist nets sample only understory birds, underestimate abundances of large and very small birds that fail to become entangled in the net, and overestimate abundances of species that travel widely in search of food (e.g. a trap-lining hummingbird or fruit-searching manakin) relative to a more sedentary forager (Remsen and Parker 1983, Remsen and Good 1996). Because we analyze occurrences and not capture frequencies, our results are applicable to birds that can be captured in mist nets.

A second potential bias could result from combin-

					Mesh	
Site	Source	Year(s)	Habitat	No. of captures	size (mm)	Netting period
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	ri	remontane w	et rorest			
1–5	DeRosier and Nielsen unpubl. data	1993–1995	Second, old growth	926	36	AM
6	Winnett-Murray 1986	1983–1984	Second growth	90	36	AM, PM
7	Feinsinger 1977	1972–1973	Second growth	366	30	AM
8	McDonald 1993	1984–1993	Second, old growth	3,679	30	AM, PM
	Low	ver Montane	Wet Forest			
9-10	DeRosier and Nielsen unpubl. data	1993-1995	Second, old growth	397	36	AM
11	Young et al. 1993	1991	Second, old growth	61	30	AM
12	Buskirk 1976, Powell 1979	1970-1973	Second, old growth	1.098	36	AM, PM
13	K. Winnett-Murray unpubl. data	1987	Second growth	49	36	AM
	Low	er Montane	Rain Forest			
14	Feinsinger et al. 1987	1981-1982	Old growth	320	30	АМ
15	Winnett-Murray 1986, Murray 1988	1981–1994	Second, old growth	1,881	36	AM, PM
	Pr	emontane Ra	in Forest			
15	DeRosier (this study)	1994	Second, old growth	515	36	AM. PM
15	I. E. Arévalo unpubl. data	1994	Second growth	25	36	AM
15–16	B. E. Young unpubl. data	1987	Second, old growth	257	30	AM
	wet Pre	emontane Tra	Insition Forest			
17	B. E. Young unpubl. data	1993–1994	Second, old growth	673	36	AM
17	De Rosier (this study)	1994	Second, old growth	237	36	AM, PM
17	A. Suarez unpubl. data	1994	Second, old growth	152	36	AM, PM

TABLE 1. Sources of mist-netting data for understory birds in the Tilarán mountains, Costa Rica.

ing data collected from different projects. The data analyzed here were collected at different times of year in different-aged forests over a 25-year period. Although these factors can influence capture frequencies, none has a major effect on the general patterns of species distribution that we describe. The data set for each life zone included sampling from both wet and dry seasons, which affect breeding and elevational migration at Monteverde, and the September-October and March-April passage periods of long-distance (Nearctic-Neotropical) migrants. Also, captures in old-growth forest (defined as closed-canopy forest with no known previous human disturbance) make up a relatively uniform fraction (40 to 60%) of the data from each life zone, reducing the variance caused by heterogeneity of forest age. Several species have changed in abundance at Monteverde over the past 25 years (e.g. Great Green Macaw [Ara ambigua], Brown Jay [Cyanocorax morio], Great-tailed Grackle [Quiscalus mexicanus]; Fogden 1993, Williams et al. 1994), but none are understory forest species typically caught in mist nets.

A third potential problem is that the effort was unequal in each life zone. The species list certainly is not complete for any life zone and is less complete for some zones than for others. With more than 700 captures in the least-sampled life zone, we have a good estimation of the most important species that occur there. We also use rarefaction curves (see below) to compare diversity in life zones with unequal sample sizes.

In sum, we acknowledge that our data set includes some unavoidable heterogeneities, but by being careful to interpret only the major distributional patterns we avoid these pitfalls. In particular, we avoid making density estimates from mist-net data, a technique especially fraught with theoretical problems (Remsen and Good 1996). We suggest that effort put into a planned study of this nature would be unjustified considering our urgent need for information and the availability of these existing data sets.

We calculated a rough estimate of beta diversity (β) of understory birds in the study area as:

$$3 = \gamma / \alpha n, \tag{1}$$

where γ is the gamma diversity (i.e. total number of species found in the entire study area), α is the average alpha diversity or species richness of each life zone, and *n* is the total number of life zones sampled (Schluter and Ricklefs 1993). As another measure of the distinctness of understory bird communities in different life zones, we also calculated a matrix of Jaccard similarity indices. The Jaccard similarity index is the proportion of the total species found in two life zones that are common to both. Whereas a beta diversity measure characterizes the fauna of the entire study area, similarity values provide an indication of how rapidly the fauna turns over from one

Wet Premontane Transition	Premontane Rain	Lower Montane Rain	Lower Montane Wet	Premontane Wet	Species	
Wet Premontane	Premontane	Lower Montane	Lower Montane	Premontane		
		Life zone				
lature follows AOU	sta Rica. Nomenc	larán mountains, Co	/e life zones in the Til	ght in mist nets at fiv	. Occurrences of birds (per 1,000 total captures) cau;).	TABLE 2. (1998)
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			Life zone		
Species	Premontane Wet	Lower Montane Wet	Lower Montane Rain	Premontane Rain	Wet Premontane Transition
Barred Forest-Falcon (Micrastur ruficollis)	0.40^{a}	1.87	1.36	1.25	0
Black-breasted Wood-Quail (Odontophorus leucolaemus) ^b	0.20	0	0	0	0
White-throated Crake (Laterallus albigularis)	0	0	0	0	1.88
Short-billed Pigeon (Columba nigrirostris) ^c	0	0.62	0	0	0.94
Inca Dove (Columbina inca)	0.20	0	0	0	0
White-tipped Dove (Leptotila verreauxi)	4.54	1.25	0	0	0
Chiriqui Quail-Dove (Geotrygon chiriquensis)	0.79	0	0	0	0
Purplish-backed Quail-Dove (Geotrygon lawrencii) ^b	0	0	0	1.25	0.94
Buff-fronted Quail-Dove (Geotrygon costaricensis) ^b	0	0.62	0.45	0	0
Ruddy Quail-Dove (Geotrygon montana)	0	0.62	0	0	0
White-fronted Parrot (Amazona albifrons)	0.20	0	0	0	0
Groove-billed Ani (Crotophaga sulcirostris)	0.20	0	0	0	0
Common Pauraque (Nyctidromus albicollis)	0	0	0	0	3.77
Band-tailed Barbthroat (Threnetes ruckeri)	0	0	0	2.51	7.53
Green Hermit (<i>Phaethornis guy</i>) ^c	2.96	11.21	79.05	56.46	55.56
Long-tailed Hermit (Phaethornis superciliosus)	0	0	0	1.25	0.94
Little Hermit (<i>Phaethornis longuemareus</i>)	1.38	0	0	13.80	9.42
White-tipped Sicklebill (Eutoxeres aquila) ^c	0	0	0.45	5.02	24.48
Green-fronted Lancebill (Doryfera ludoviciae) ^c	0.20	0	0.91	1.25	0.94
Violet Sabrewing (Campylopterus hemileucurus) ^{b,c}	22.13	25.55	24.08	10.04	0.94
Brown Violet-ear (Colibri delphinae) ^c	0.20	0	0	0	0
Green Violet-ear (Colibri thalassinus) ^c	9.88	0.62	0.91	1.25	0
Violet-headed Hummingbird (Klais guimeti)	0	0	0	0	14.12
Canivet's Emerald (Chlorostilbon canivetii)	5.72	0.62	0.45	0	0
Violet-crowned Woodnymph (Thalurania colombica) ^c	0	0	0	7.53	37.66
Fiery-throated Hummingbird (Panterpe insignis) ^c	0	0	5.91	0	0
Blue-throated Goldentail (Hylocharis eliciae) ^c	1.19	0.62	0	0	2.82
Blue-chested Hummingbird (Amazilia amabilis)	0	0	0	0	2.82
Steely-vented Hummingbird (Amazilia saucerrottei)	37.94	1.25	0.45	2.51	3.77
Rufous-tailed Hummingbird (Amazilia tzacatl)	7.90	1.87	0	0	44.26
Cinnamon Hummingbird (Amazilia rutila)	0.20	0	0	0	0
Stripe-tailed Hummingbird (Eupherusa eximia) ^c	162.81	36.14	58.61	13.80	0
Coppery-headed Emerald (Elvira cupreiceps) ^{b,c}	2.17	8.72	7.27	20.08	7.53
White-bellied Mountain-gem (Lampornis hemileucus)	0.20	0	0	15.06	0

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TABLE 2. Continued.

			Life zone		
Species	Premontane Wet	Lower Montane Wet	Lower Montane Rain	Premontane Rain	Wet Premontane Transition
Purple-throated Mountain-gem (Lampornis calolaema)	17.98	15.58	164.02	12.55	0
Green-crowned Brilliant (Heliodoxa jacula)	0	4.36	64.06	18.82	7.53
Purple-crowned Fairy (Heliothryx barroti)	0	0	0	0	2.82
Plain-capped Starthroat (Heliomaster constantii)	0.59	0	0	0	0
Magenta-throated Woodstar (Calliphlox bryantae) ^c	1.98	1.87	0	0	0
Ruby-throated Hummingbird (Archilochus colubris) ^d	1.38	0	0	0	0
Orange-bellied Trogon (Trogon aurantiiventris)	0.40	1.25	0	1.25	0
Resplendent Quetzal (Pharomachrus mocinno) ^{b,c}	0	1.25	0	0	0
Blue-crowned Motmot (Momotus momota)	13.24	2.49	0.45	0	0
Rufous Motmot (Baryphthengus martii)	0	0	0	2.51	0
Green Kingfisher (Chloroceryle americana)	0.20	0	0	0	0
Lanceolated Monklet (Micromonacha lanceolata)	0	0	0	0	2.82
White-fronted Nunbird (Monasa morphoeus)	0	0	0	0	0.94
Rufous-tailed Jacamar (Galbula ruficauda)	0	0	0	1.25	2.82
Prong-billed Barbet (Semnornis frantzii) ^c	0	5.61	3.63	0	0
Emerald Toucanet (Aulacorhynchus prasinus) ^c	6.52	0	0.45	1.25	0
Keel-billed Toucan (Ramphastos sulfuratus)	0.20	0	0	0	0
Hoffman's Woodpecker (Melanerpes hoffmannii)	0.59	1.25	0	0	0
Smoky-brown Woodpecker (Veniliornis fumigatus)	0	0	0.45	1.25	0.94
Rufous-winged Woodpecker (Piculus simplex) ^b	0	0.62	0	0	0
Golden-olive Woodpecker (Piculus rubiginosus)	0	1.25	0	0	2.82
Slaty Spinetail (Synallaxis brachyura)	0	0	0	12.55	31.07
Red-faced Spinetail (Cranioleuca erythrops) ^b	0	6.23	0	0	0
Spotted Barbtail (Premnoplex brunnescens)	0	41.12	35.44	13.80	2.82
Ruddy Treerunner (Margarornis rubiginosus)	0	1.25	0.45	0	0
Striped Woodhaunter (Hyloctistes subulatus)	0	0	0	1.25	0
Lineated Foliage-gleaner (Syndactyla subalaris)	0	9.97	3.63	2.51	0
Scaly-throated Foliage-gleaner (Anabacerthia variegaticeps) ^b	0	0	0	1.25	0
Buff-throated Foliage-gleaner (Automolus ochrolaemus)	0	0	0	2.51	11.30
Streak-breasted Treehunter (Thripadectes rufobrunneus) ^b	0	2.49	1.82	0	0
Plain Xenops (Xenops minutus)	0	0	0	1.25	4.71
Tawny-throated Leaftosser (Sclerurus mexicanus)	0	2.49	2.27	0	1.88
Gray-throated Leaftosser (Sclerurus albigularis)	0	11.21	1.36	0	0
Ruddy Woodcreeper (Dendrocincla homochroa)	22.53	0.62	1.82	0	0

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			Life zone		
Species	Premontane Wet	Lower Montane Wet	Lower Montane Rain	Premontane Rain	Wet Premontane Transition
Olivaceous Woodcreeper (Sittasomus griseicapillus)	10.27	13.71	0	0	0
Wedge-billed Woodcreeper (Glyphorynchus spirurus) ^c	0.40	1.25	0	15.06	16.95
Northern Barred-Woodcreeper (Dendrocolaptes sanctithomae)	1.38	0	0	0	0
Spotted Woodcreeper (Xiphorhynchus erythropygius)	0	6.23	1.36	3.76	0.94
Steak-headed Woodcreeper (Lepidocolaptes souleyetii)	1.78	1.25	0	0	2.82
Brown-billed Scythebill (<i>Campylorhamphus pusillus</i>) ^c	0	0.62	0	1.25	0.94
Fasciated Antshrike (Cymbilaimus lineatus)	0	0	0	0	0.94
Barred Antshrike (Thamnophilus doliatus)	0.20	0	0	0	0
Plain Antvireo (Dysithamnus mentalis)	0	6.23	4.09	7.53	0
Slaty Antwren (Myrmotherula schisticolor)	5.33	0	1.82	8.78	8.47
Dusky Antbird (Cercomacra tyrannina)	0	0	0	0	16.01
Chestnut-backed Antbird (Myrmeciza exsul)	0	0	0	0	1.88
Dull-mantled Antbird (Myrmeciza laemosticta) ^b	0	0	0	2.51	0
Immaculate Antbird (<i>Myrmeciza immaculata</i>) ^c	0	0	0	1.25	0.94
Bicolored Anthird (Gymnopithus leucaspis)	0	0	0	1.25	2.82
Ocellated Antbird (<i>Phaenostictus mcleannani</i>)	0	0	0	5.02	8.47
Black-headed Antthrush (Formicarius nigricapillus) ^b	0	0	0	1.25	0
Rufous-breasted Antthrush (Formicarius rufipectus)	0	0	0	1.25	0
Scaled Antpitta (Grallaria guatimalensis) ^b	0.59	1.87	0	0	0
Ochre-breasted Antpitta (Grallaricula flavirostris)	0	0	0	1.25	0.94
Silvery-fronted Tapaculo (Scytalopus argentifrons)	0	1.25	0.45	1.25	0
Northern Beardless-Tyrannulet (Camptostoma imberbe)	0.20	0	0	0	0
Yellow Tyrannulet (Capsiempis flaveola)	0	0	0	0	2.82
Yellow-bellied Elaenia (Elaenia flavogaster)	0.20	0.62	0	8.78	0.94
Mountain Elaenia (<i>Elaenia frantzii</i>) ^c	7.51	21.81	0.91	0	0
Olive-striped Flycatcher (<i>Mionectes olivaceus</i>) ^c	0.79	39.88	68.61	35.13	13.18
Ochre-bellied Flycatcher (Mionectes oleagineus)	2.17	0	0.45	1.25	3.77
Slaty-capped Flycatcher (Leptopogon superciliaris)	0	0.62	0	1.25	6.59
Paltry Tyrannulet (Zimmerius vilissimus) ^c	0.79	6.85	0	3.76	1.88
Scale-crested Pygmy-Tyrant (Lophotriccus pileatus)	0.40	0	0	5.02	2.82
Common Tody-Flycatcher (Todirostrum cinereum)	0	0	0	1.25	2.82
Eye-ringed Flatbill (Rhynchocyclus brevirostris)	8.69	8.72	7.27	5.02	0
Yellow-olive Flycatcher (Tolmomyias sulphurescens)	0	0	0	1.25	1.88
White-throated Spadebill (Platyrinchus mystaceus)	13.24	21.81	22.72	12.55	0.94
Ruddy-tailed Flycatcher (Terenotriccus erythrurus)	0	0	0	0	3.77

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			Life zone		
Species	Premontane Wet	Lower Montane Wet	Lower Montane Rain	Premontane Rain	Wet Premontane Transition
Sulphur-rumped Flycatcher (Myiobius sulphureipygius)	0	0	0	3.79	1.88
Tufted Flycatcher (Mitrephanes phaeocercus)	0	0.62	0	12.55	0
Western Wood-Pewee (Contopus sordidulus) ^d	0	1.87	0	0	0
Eastern Wood-Pewee (Contopus virens) ^d	0.40	0	0	0	0
Tropical Pewee (Contopus cinereus)	0	0	0	0	0.94
Yellow-bellied Flycatcher (Empidonax flawiventris) ^d	0.20	0	0.91	0	2.82
Acadian Flycatcher (Empidonax virescens) ^a	0.20	0	0	0	0
''Traill's'' Flycatcher (Empidonax ''traillii'' spp.) ^d	2.96	0	0	0	4.71
Yellowish Flycatcher (Empidonax flawescens)	3.16	16.82	7.27	18.82	0
Black Phoebe (Sayornis nigricans)	0	0.62	0	0	0
Long-tailed Tyrant (Colonia colonus)	0	0	0	0	0.94
Bright-rumped Attila (Attila spadiceus)	0.20	0.62	0.45	0	1.88
Rufous Mourner (Rhytipterna holerythra) ^c	0	0	0	0	0.94
Dusky-capped Flycatcher (Myiarchus tuberculifer)	1.58	1.87	0	0	4.71
Nutting's Flycatcher (Myiarchus nuttingi)	0.20	0	0	0	0
Great Kiskadee (Pitangus sulphuratus)	0	0	0	0	1.88
Boat-billed Flycatcher (Megarynchus pitangua)	0	0	0	0	0.94
Social Flycatcher (Myiozetetes similis)	0.20	0	0	2.51	0.94
Streaked Flycatcher (Myjodynastes maculatus) ^c	0.20	1.87	0	0	0
Sulphur-bellied Flycatcher (Myiodynastes luteiventris) ^d	0.59	3.74	0	0	0
Tropical Kingbird (Tyrannus melancholicus)	0	0	0	2.51	0
Cinnamon Becard (Pachyramphus cinnamomeus)	0	0	0	0	5.65
White-collared Manakin (Manacus candei) ^b	0	0	0	0	18.83
White-ruffed Manakin (Corapipo altera) ^c	0.20	0	0	2.51	68.74
Long-tailed Manakin (Chiroxiphia linearis)	115.59	6.85	0.45	0	0
Yellow-throated Vireo (Vireo flavifrons) ^d	0.79	0	0	0	0
Brown-capped Vireo (Vireo leucophrys)	0.20	0	0	0	0
Red-eyed Vireo (Vireo olivaceus) ^d	0	0	0	0	1.88
Yellow-green Vireo (Vireo flavoviridis) ^d	0.59	0	0	0	0
Tawny-crowned Greenlet (Hylophilus ochraceiceps)	6.13	0.62	0	11.29	2.82
Lesser Greenlet (Hylophilus decurtatus)	5.14	1.25	0.45	0	2.82
Rufous-browed Peppershrike (Cyclarhis gujanensis) ^c	0.20	0.62	0	0	0
Brown Jay (Cyanocorax morio)	0.20	0.62	0	0	0
Azure-hooded Jay (Cyanolyca cucullata)	0	0	1.36	0	0
Black-throated Wren (Thrythorus atrogularis)	0	0	0	0	10.36

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			Life zone		
Species	Premontane Wet	Lower Montane Wet	Lower Montane Rain	Premontane Rain	Wet Premontane Transition
Bay Wren (Thryothorus nigricapillus)	0	0	0	0	8.47
Stripe-breasted Wren (Thryothorus thoracicus)	0	0	0	2.51	11.30
Rufous-breasted Wren (Thryothorus rutilus)	0.40	0	0	0	0
Rufous-and-white Wren (Thryothorus rufalbus)	54.14	3.74	0	0	0
Plain Wren (Thryothorus modestus)	4.94	7.48	0	0	0
House Wren (Troglodytes aedon)	21.51	24.92	1.82	40.15	10.36
Ochraceous Wren (Troglodytes ochraceus) ^c	0	1.87	0.91	2.51	0
White-breasted Wood-Wren (Henicorhina leucosticta)	4.94	0	0	5.02	16.01
Gray-breasted Wood-Wren (Henicorhina leucophrys)	0	72.27	73.15	31.37	0
Nightingale Wren (Microcerculus philomela) ^b	0	0	0	1.25	0
Song Wren (Cyphorhinus phaeocephalus)	0	0	0	3.76	4.71
Tawny-faced Gnatwren (Microbates cinereiventris)	0	0	0	7.53	6.59
Long-billed Gnatwren (Ramphocaenus melanurus)	0	0	0	1.25	2.82
Black-faced Solitaire (Myadestes melanops) ^c	0.20	64.17	125.85	23.84	5.65
Orange-billed Nightingale-Thrush (Catharus aurantiirostris)	44.66	3.12	0	0	0
Slaty-backed Nightingale-Thrush (Catharus fuscater)	0.20	42.99	32.26	21.33	1.88
Ruddy-capped Nightingale-Thrush (Catharus frantzii)	0	18.69	20.90	0	0
Black-headed Nightingale-Thrush (Catharus mexicanus)	2.17	7.48	0.45	7.53	6.59
Gray-cheeked Thrush (Catharus minimus) ^d	0.59	0	0	0	0
Swainson's Thrush (Catharus ustulatus) ^a	76.66	6.23	0.91	0	9.42
Wood Thrush (<i>Hylocichla mustelina</i>) ^{b,d}	17.19	1.87	0	3.76	4.71
Mountain Robin (Turdus plebejus) ^c	1.19	4.36	0.91	0	0
Pale-vented Robin (Turdus obsoletus) ^c	0	0	0	5.02	8.47
Clay-colored Robin (Turdus grayi)	6.51	2.49	0	21.33	10.36
White-throated Robin (Turdus assimilis) ^c	6.92	3.74	3.63	6.27	14.12
Black-and-yellow Silky-flycatcher (Phainoptila melanoxantha)	0	0.62	3.63	0	0
Golden-winged Warbler (Vermivora chrysoptera) ^{6,d}	2.37	2.49	1.82	0	1.88
Tennessee Warbler (Vermivora peregrina) ^d	0.40	1.87	0	0	2.82
Tropical Parula (Parula pitiayumi)	0	0	0	0	1.88
Chestnut-sided Warbler (Dendroica pensylvanica) ^d	0	0	0	2.51	11.30
Black-throated Blue Warbler (Dendroica caerulescens) ^d	0.20	0	0	0	0
Black-throated Green Warbler (Dendroica virens) ^d	0	0.62	0	1.25	0.94
Blackburnian Warbler (Dendroica fusca) ^d	0.20	0.62	0	0	0
Black-and-white Warbler (Mniotilta varia) ^d	1.38	2.49	0	0	0
Worm-eating Warbler (Helmitheros vermivorus) ^{6,d}	2.77	0	0	0	0

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			Life zone		
Species	Premontane Wet	Lower Montane Wet	Lower Montane Rain	Premontane Rain	Wet Premontane Transition
Ovenbird (Seiurus aurocapillus) ^d	31.61	2.49	0	0	0
Louisiana Waterthrush (Seiurus motacilla) ^d	0.40	0	0.91	0	0
Kentucky Warbler (Oporornis formosus) ^d	9.47	0.62	0.45	0	1.88
Mourning Warbler (Oporornis philadelphia) ^d	1.19	0.62	0.45	1.25	1.88
Olive-crowned Yellowthroat (Geothlypis semiflava)	0	0	0	33.88	14.12
Gray-crowned Yellowthroat (Geothlypis poliocephala)	4.15	3.74	0	3.76	4.71
Hooded Warbler (Wilsonia citrina) ^d	0.20	0	0	0	0
Wilson's Warbler (Wilsonia pusilla) ^d	8.89	8.10	4.09	12.55	9.42
Canada Warbler (Wilsonia canadensis) ^d	1.38	7.48	0	0	1.88
Slate-throated Redstart (Myjoborus miniatus)	5.33	81.62	9.54	49.93	0
Collared Redstart (Myioborus torquatus)	0	0	14.54	0	0
Golden-crowned Warbler (Basileuterus culicivorus)	62.04	16.20	0.45	5.02	7.53
Rufous-capped Warbler (Basileuterus rufifrons)	7.71	0.62	0	0	0
Three-striped Warbler (Basileuterus tristriatus)	0	35.51	49.98	12.55	0
Wrenthrush (Zeledonia coronata)	0	0	3.63	0	0.94
Bananaquit (Coereba flaveola)	0	8.10	0	11.29	9.42
Common Bush-Tanager (Chlorospingus ophthalmicus)	0.59	71.65	18.63	45.17	0
Sooty-capped Bush-Tanager (Chlorospingus pileatus)	0	0	3.63	0	0
Black-and-yellow Tanager (Chrysothlypis chrysomelas) ^b	0	0	0	0	4.71
Olive Tanager (Chlorothraupis carmioli) ^c	0	0	0	20.08	57.44
White-throated Shrike-Tanager (Lanio leucothorax) ^b	0	0	0	1.25	0
Red-crowned Ant-Tanager (Habia rubica)	2.37	0	0	0	0
Hepatic Tanager (<i>Piranga flava</i>) ^c	0.40	0	0	1.25	0
Summer Tanager (Piranga rubra) ^d	0	0	0	1.25	0.94
Scarlet Tanager (Piranga olivacea) ^d	0	0	0	0	1.88
Crimson-collared Tanager (Ramphocelus sanguinolentus)	0	0	0	3.76	6.59
Passerini's Tanager (Ramphocelus passerinii)	0	0	0	26.35	55.56
Blue-gray Tanager (Thraupis episcopus)	0.20	0	0	1.25	3.77
Palm Tanager (<i>Thraupis palmarum</i>)	0	0	0	0	0.94
Yellow-throated Euphonia (Euphonia hirundinacea)	12.25	1.87	0	0	0
Tawny-capped Euphonia (<i>Euphonia anneae</i>) ^{b.c}	0	0	0	13.80	16.95
Golden-browed Chlorophonia (Chlorophonia callophrys) ^c	0.20	1.25	1.36	0	0
Silver-throated Tanager (Tangara icterocephala) ^c	0	3.74	0	16.31	8.47
Bay-headed Tanager (Tangara gyrola) ^c	0	0	0	1.25	0.94
Golden-hooded Tanager (Tangara larvata)	0	0	0	0	1.88

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			Life zone		
Species	Premontane Wet	Lower Montane Wet	Lower Montane Rain	Premontane Rain	Wet Premontane Transition
Spangle-cheeked Tanager (Tangara dowii) ^c	0	6.85	0.45	0	0
Scarlet-thighed Dacnis (Dacnis venusta) ^c	0	0	0	1.25	0.94
Green Honeycreeper (Chlorophanes spiza) ^c	0	0	0	0	2.82
Red-legged Honeycreeper (Cyanerpes cyaneus)	0.20	0	0	0	0
Blue-black Grassquit (Volatinia jacarina)	0.20	0	0	0	1.88
Variable Seedeater (Sporophila americana)	0	0	0	21.33	24.48
Thick-billed Seed-Finch (Oryzoborus funereus)	0	0	0	0	16.95
Blue Seedeater (Amaurospiza concolor) ^b	0	0	0.91	0	0
Yellow-faced Grassquit (Tiaris olivacea)	13.04	18.69	0.91	44.91	10.36
Slaty Finch (Haplospiza rustica) ^c	0.40	2.49	0	0	0
Slaty Flowerpiercer (Diglossa plumbea) ^c	0	1.25	7.72	2.51	0
Sooty-faced Finch (Lysurus crassirostris)	0	1.25	0.45	0	0
Yellow-thighed Finch (Pselliophorus tibialis)	0	0	3.63	0	0
White-naped Brush-Finch (Atlapetes albinucha)	7.90	10.59	0.45	15.06	0.94
Chestnut-capped Brush-Finch (Buarremon brunneinuchus)	8.89	46.73	33.17	6.27	0
Orange-billed Sparrow (Arremon aurantiirostris)	0	0	0	1.25	22.60
Black-striped Sparrow (Arremonops conirostris)	0	0	0	7.53	10.36
White-eared Ground-Sparrow (Melozone leucotis)	44.46	9.35	0	0	0
Rufous-collared Sparrow (Zonotrichia capensis)	6.52	11.21	0	18.82	0
Grayish Saltator (Saltator coerulescens)	0.20	0	0	0	0
Buff-throated Saltator (Saltator maximus)	0.20	0	0	25.09	13.18
Black-faced Grosbeak (Caryothraustes poliogaster)	0	0	0	0	9.42
Rose-breasted Grosbeak (Pheucticus ludovicianus) ^d	0.20	0	0	0	0
Blue-black Grosbeak (Cyanocompsa cyanoides)	0	0	0	0	1.88
Eastern Meadowlark (Sturnella magna)	0	0.62	0	0	0
Baltimore Oriole (Icterus galbula) ^d	0	0	0	0	0.94
Montezuma Oropendola (Psarocolius montezuma)	0	0	0	0	0.94
Total captures	5,061	1,605	2,201	262	1,062
Total species	117	106	72	106	126
Total threatened species	4	6	6	10	9
* Although we analyze only presence-absence data, we provide actual capture	frequencies to allow others	to reanalyze our data. A di	gital copy is available from	the first author.	

Automotic we many ze outly presence above the adverted that we price the species (according to Parker et al. [1996]). • Elevational migrant. • Long-distance migrant.

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FIG. 3. Rarefaction curves of the expected number of species detected under varying effort for five life zones in the Tilarán mountains, Costa Rica.

zone to the next within the study area. We also calculated an overall similarity index for the five life zones as the proportion of the total species recorded in the study area that occur in every life zone.

Because the number of captures for each life zone was unequal, we estimated rarefaction curves for the number of species in each life zone that would be expected to be detected under different sampling efforts (James and Rathbun 1981). Essentially, rarefaction curves are idealized species-accumulation curves that allow us to compare the expected species richness of the different life zones for a constant sampling effort in each. Rarefaction models assume that sampling was adequate to characterize species distributions, individuals were randomly distributed spatially, samples of taxonomically similar organisms were drawn from similar community types, and sampling techniques were standardized (Gotelli and Graves 1996). We calculated rarefaction curves following Magurran (1988: equation 2.1).

To assign conservation status for the species detected, we adopted the conservation priorities used by Parker et al. (1996). We defined threatened species to be those listed by Parker et al. (1996) with conservation priority medium, high, or urgent.

RESULTS

We obtained records of 10,726 captures of 235 species in the five life zones of the study

area (Table 2). These species represent 162 residents, 41 elevational migrants, and 32 longdistance migrants. Estimated species richness in each life zone ranged from 72 to 126. Overall, species richness was lowest in the highest-elevation life zone (Lower Montane Rain Forest) and increased downslope on either side. The rarefaction curves show that the Wet, Premontane Transition Forest is more diverse than the other life zones based on the expected number of species to be found in samples of equal sizes (Fig. 3). The curves also show that, although more total species were recorded in Premontane Wet Forest than in either Lower Montane Wet or Premontane Rain Forests, this result is due to the much smaller sample sizes in the latter two life zones, which are actually more diverse for a given sample of captures, at least for samples of up to 797 captures. The curves show increasing slopes for each life zone, suggesting that additional netting effort would add new species to the lists for each life zone.

Each life zone had a distinctive fauna, sharing relatively few species with adjacent life zones considering the small spatial scale of each zone. The beta diversity for the study area was 0.45. Jaccard similarity indices for adjacent life zones were low, ranging from 0.30 to 0.47, and they declined for more distant life zones (Table 3). Most adjacent life zones were about equally distinct, sharing about half of their species (similarity indices of 0.47). The one exception was that the fauna of Lower Montane Rain forest shared less than a third of its species with the next higher elevation zone, Premontane Rain forest (similarity index 0.30). The overall similarity index for all five life zones was 0.06, indicating that very few species occurred in all five life zones, even though the most distant zones were separated by only 12

TABLE 3. Jaccard similarity indices of bird assemblages in five life zones, Tilarán mountains, Costa Rica.

	Lower Montane Wetª	Lower Montane Rain ^ь	Premontane Rain ^c	Wet Premontane Transition ^d
Premontane Wet ^e	0.47	0.29	0.27	0.24
Lower Montane Wet	_	0.47	0.31	0.24
Lower Montane Rain		_	0.30	0.19
Premontane Rain				0.47

^a Pacific slope, 1,400 to 1,550 m.

^b Continental divide, 1,500 to 1,700 m.

° Caribbean slope, 750 to 1,450 m.

^d Caribbean slope, 650 to 750 m.

* Pacific slope, 1,000 to 1,400 m.

			Life zone		-		No. of life
Family	PMW ^a	LMW ^b	LMR ^c	PMR ^d	WPTe	 No. of species 	zones per species
Falconidae	1	1	1	1	0	1	4.0
Odontophoridae	1	0	0	0	0	1	1.0
Rallidae	0	0	0	0	1	1	1.0
Columbidae	3	4	1	1	2	7	1.6
Psittacidae	1	0	0	0	0	1	1.0
Cuculidae	1	0	0	0	0	1	1.0
Caprimulgidae	0	0	0	0	1	1	1.0
Trochilidae	18	12	12	15	16	27	2.7
Trogonidae	1	2	0	1	0	2	2.0
Momotidae	1	1	1	1	0	2	2.0
Alcedinidae	1	0	0	0	0	1	1.0
Bucconidae	0	0	0	0	2	2	1.0
Galbulidae	0	0	0	1	1	1	2.0
Ramphastidae	2	1	2	1	0	3	2.0
Picidae	1	3	1	1	2	4	2.0
Furnariidae	0	7	6	7	5	12	2.1
Dendrocolaptidae	5	6	2	3	4	7	2.9
Thamnophilidae	2	1	2	6	7	10	1.8
Formicariidae	1	1	0	3	1	4	1.5
Rhinocryptidae	0	1	1	1	0	1	3.0
Tvrannidae	20	15	8	15	22	35	2.3
incertae sedis ¹	0	0	0	0	1	1	1.0
Pipridae	2	1	1	1	2	3	2.3
Vireonidae	6	3	1	1	3	7	2.0
Corvidae	1	1	1	0	0	2	1.5
Troglodytidae	5	5	3	7	6	12	2.2
Sylviidae	0	0	0	2	2	2	2.0
Turdidae	10	10	7	7	8	12	3.5
Ptilogonatidae	0	1	1	0	0	1	2.0
Parulidae	17	15	10	9	13	24	2.7
Coerebidae	0	1	0	1	1	1	3.0
Thraupidae	7	5	4	12	14	23	1.8
Emberizidae	7	8	7	8	7	15	2.5
Cardinalidae	3	0	0	1	3	5	1.4
Icteridae	0	1	0	0	2	3	1.0
No. of families	24	24	20	24	24	_	_

TABLE 4. Distribution of avian families in the five life zones, Tilarán mountains, Costa Rica.

^a Premontane Wet, Pacific slope, 1,000 to 1,400 m.

^b Lower Montane Wet, Pacific slope, 1,400 to 1,550 m.

^c Lower Montane Rain, Continental divide, 1,500 to 1,700 m.

^d Premontane Rain, Caribbean slope, 750 to 1,450 m.

* Wet Premontane Transition, Caribbean slope, 650 to 750 m.

¹New, unnamed grouping of seven genera previously included in the Tyrannidae, Cotingidae, and Pipridae (AOU 1998).

km. The species that spanned all five life zones included four hummingbirds, two flycatchers, one wren, three thrushes, three warblers, and two finches. Ecologically, the list includes two long-distance migrant warblers, six elevational migrants, four resident forest species, a hummingbird with irruptive population movements (Coppery-headed Emerald [*Elvira cupreiceps*]; Feinsinger 1977), and two species of disturbed habitats (House Wren [*Troglodytes aedon*] and Yellow-faced Grassquit [*Tiaris olivacea*]).

Many of the 35 families detected showed pat-

terns of being most diverse either on one slope, both slopes, or on the highest portions of the mountain range (Table 4). Furnariids, thamnophilids, and formicariids were more diverse in the wet forests of the Caribbean slope and crest and were less diverse in the drier life zone of the lower Pacific slope. The lone members of the Rhinocryptidae and Ptilogonatidae were recorded only from the highest life zones. Trochilids, dendrocolaptids, tyrannids, vireonids, troglodytids, turdids, parulids, and thraupids were more diverse on both slopes of the cordillera than on top. Other families either oc-



FIG. 4. Proportion of understory bird assemblages made up of long-distance and elevational migrants at different life zones. Life zone abbreviations as in Table 4.

curred in all life zones or were represented by rare species. Considering only families with at least four species recorded, the families with the species occurring in the most life zones were the emberizids, trochilids, parulids, dendrocolaptids, and turdids (Table 4). The families with the narrowest life zone occurrences were the cardinalids, formicariids, columbids, thamnophilids, and thraupids (Table 4). Overall, species were captured on average in 2.2 of the 5 life zones.

Long-distance migrants made up a greater proportion of total captures and total species in the lowest life zones of each slope, with a peak in Premontane Wet Forest (Fig. 4). Long-distance migrants represented 14% of all species considered and 9% of all captures. In contrast, elevational migrants made up similar proportions of the avifauna in all five life zones (Fig. 4). Elevational migrants represented 17% of all species and 28% of all captures.

Nineteen resident and three long-distance migrant species recorded in the study are threatened (Table 2). All of the threatened species were considered by Parker et al. (1996) to be of "medium" conservation priority; no species was of greater concern. The number of threatened species per life zone was not correlated with the species richness of each zone. Threatened species were concentrated in the life zones on either slope immediately below the uppermost life zone of the Tilarán mountains, whereas the total number of species detected was highest in the lowest life zone of each slope (Table 2).

DISCUSSION

Our analysis shows a high alpha and beta diversity of understory birds in a small geographic area. The large sample of captures we compiled makes the Monteverde fauna one of the most intensively documented elevational transects of bird assemblages known from the Neotropics. Similar high-diversity faunas have been documented in the much larger Andes mountains in South America (Terborgh 1977) but not in such a restricted area in modestsized mountains of Central America. Compared with temperate faunas, species richness in Monteverde understory communities is an order of magnitude greater than it is in breeding bird communities in montane areas of similar elevation. For example, in the northeastern United States, just 38 to 44 species occur on forested mountainsides between 500 and 1,400 m elevation (Able and Noon 1976) compared with 72 to 126 understory species recorded in this study.

The beta diversity of the study area was high, although few studies of a similar geographic and habitat range are available for comparison. Much of the faunal work in the tropics has concentrated on listing the species occurring in an area rather than examining species turnover among habitats (e.g. Ridgely and Gaulin 1980, Robbins et al. 1985, Karr et al. 1990, Terborgh et al. 1990). Studies that examine elevational ranges of species often do not clearly sort these ranges into ecological units in a manner that would allow reanalysis of the beta diversity of

these communities (e.g. Terborgh and Weske 1975, Parker et al. 1985). The best comparative data generally span habitat ranges or geographic scales much greater than in our analysis. One study in Trinidad recorded a beta diversity of 0.43 for birds of the entire 5,000-km² island in habitats varying from mangrove to cloud forest (Cox and Ricklefs 1977). Beta diversity varied from 0.51 to 0.72 in African and Central American moist-forest regions across habitats ranging from grazed pasture to mature forest (calculated from Karr 1971, 1976). In Mediterranean climates with habitat diversity ranging from grassland to scrub forest, beta diversity in study sites in the United States, Chile, and Africa ranged from 0.28 to 0.38 (calculated from Cody 1975). The montane fauna we studied clearly exhibited high beta diversity considering the small geographic scale of the study and the similarity of old- and secondgrowth habitats sampled in each life zone.

The high beta diversity led to a high overall (i.e. gamma) diversity for the study area. Species tended to occupy narrow ranges in the study area as indicated by the findings that: (1) each species occurred, on average, in slightly more than two zones; (2) similarity indices declined for more distant zones; and (3) the overall similarity of the five zones was low. An alternative hypothesis, that species were widespread but randomly sampled in our study, would not have caused the pattern of declining similarities of more distant zones.

The rarefaction curves showed that, despite the amount of netting effort in each life zone, the faunal lists for understory birds are not complete (Fig. 3). In Wet Forest-Premontane Transition, the most diverse site, one new species was added for approximately every 25 captures, even after 1,062 captures. In Premontane Wet Forest, the most intensively studied site (more than 5,000 captures), a new species is still detected on average every 100 captures. These species are rare but presumably regular residents of these habitats. This pattern of rarity conforms with findings of other studies of tropical bird communities, which have shown that many species occur at very low densities (Terborgh et al. 1990, Thiollay 1991).

Holdridge life zones proved to be a fruitful basis for our community comparisons. Although boundaries between life zones are not sharp (e.g. at an ecotone between two forests with different land use histories), they nonetheless provided logical if not absolute divisions among communities of understory birds. The similarity values showed that life zones with narrow elevational ranges, such as Premontane Wet forest, had bird assemblages as distinct from adjacent zones as other, much broader life zones (Table 3). Within the Premontane Wet forest, two sampling sites separated by 200 m of elevation shared 71% of their species. However, two sampling sites at 1,500 m on the Pacific slope, but in different life zones, shared only 53% of their species. Furthermore, faunas at the same elevation but on opposite sides of the cordillera showed strong differences in species composition, with many species occurring only on one side of the mountain (Table 3). A zonation scheme based on arbitrary elevational boundaries might not detect these subtleties. Thus, although the distributions of species rarely reach their limits at a life zone boundary (e.g. Lieberman et al. 1996), the locations and widths of the zones are good indicators of species turnover rates. A possible ecological basis for this finding is that the width of a life zone accurately reflects the steepness of moisture gradients, which in turn influences plant distributions (Hartshorn 1983). With most birds dependent on either plant reproductive rewards or phytophagous arthropods for food, their distributions logically track plant distributions. Regardless of the underlying ecological factors, the concordance between Holdridge life zones and beta diversity of understory bird faunas suggests that the Holdridge system can be useful to conservationists for predicting patterns of diversity of understory birds when distributional data are unavailable.

One factor contributing to the high diversity in Monteverde is that the bird assemblages on different sides of the mountain range originate from different zoogeographic regions. The Pacific slope species represent the extreme edge of a coastal dry forest fauna that stretches from the west coast of Mexico down to central Costa Rica (Stiles 1983). The Caribbean slope species are part of a South American fauna that extends north to southeastern Mexico (Stiles 1983). Because the study area is located on both sides of the continental divide, both of these faunas are represented. In addition, the Tilarán mountains lie at the northern end of the ranges of a number of endemic species restricted to the humid, montane forests of western Panama and Costa Rica (Stotz et al. 1996). These species include Black-breasted Wood-Quail (Odontophorus leucolaemus), Buff-fronted Quail-Dove (Geotrygon costaricensis), Prong-billed Barbet (Semnornis frantzii), Streak-breasted Treehunter (Thripadectes rufobrunneus), Silvery-fronted Tapaculo (Scytalopus argentifrons), Ochraceous Wren (Troglodytes ochraceus), Spangle-cheeked Tanager (Tangara dowii), and Blue Seedeater (Amaurospiza concolor).

Another factor contributing to the high species diversity of the Monteverde region is that many genera with more than one species of resident, territorial bird exhibited a pattern of elevational replacement. For example, the distributions of congeneric Geotrygon, Sclerurus, Formicarius, Myiarchus, Thryothorus, Henicorhina, Catharus (resident species only), Hylophilus, Geothlypis, Myioborus, Basileuterus, and Chlorospingus all showed patterns of nonoverlapping or incompletely overlapping elevational ranges. This finding is consistent with other studies showing such replacements on both tropical and temperate mountain ranges (Terborgh 1971, Noon 1981). In these studies, upward range extensions of middle-elevation species on isolated mountain ranges where high-elevation congeners are lacking has been interpreted as evidence that interspecific competition caused the patterns of elevational replacement (Terborgh and Weske 1975, Noon 1981). Although the evidence is very suggestive and may explain the basis of elevational replacements at Monteverde, recent work has demonstrated the need for experimental tests to identify ecological processes that cause the patterns we observe (Brown 1987, Feinsinger and Tiebout 1991). A removal experiment examining the elevational replacement of congeneric species described for the Cordillera de Tilarán and these same species on the smaller, more isolated volcanic peaks of the Guanacaste mountain range to the north would be very illuminating.

Our analysis allowed the distinction between families of species with wide habitat occurrences and those with narrow occurrences. Long-distance migrants tend to have broader habitat distributions than resident species (Stotz et al. 1996), and elevational migrants by definition occur over wide areas during their annual cycle. Thus, the hummingbird, thrush, and warbler families, with many long-distance and elevational migrants, average more life zones per species than the other groups. The emberizids, with few migratory species but many life zones per species, include many disturbed-habitat species with wide ranges. The woodcreepers, with few migrants and most species living in forested areas, appear to be truly more habitat generalists than the other groups of sedentary, forest dwellers. Among the families with narrow-ranging species in our study, the inclusion of the columbids, cardinalids, and, to some extent, the tanagers is an artifact caused by their being widespread at lower elevations and just reaching our study area in the lowest life zone on each slope. Tanagers in the genera Chrysothlypis, Lanio, Chlorothraupis, and Tangara, however, occur mostly in a narrow range in Premontane Rain and Wet Premontane Transition forests. The antbirds, antthrushes, and antpittas are mostly sedentary species with narrow ranges, perhaps due to narrow foraging requirements or interspecific interactions.

Most of the threatened species we detected also have very narrow ranges. Except for the two hummingbirds and the wood-quail, all threatened resident species occurred in two or fewer life zones. Also, the Black-breasted Wood-Quail, Buff-fronted Quail-Dove, Coppery-headed Emerald, Streak-breasted Treehunter, and Tawny-capped Euphonia (*Euphonia anneae*) occur in a restricted geographic range in mountainous Costa Rica and Panama. With such narrow habitat and/or geographic ranges, these species are especially vulnerable to deforestation.

Our findings provide several lessons for land managers. The first two lessons are especially valuable for poorly known areas for which life zones can be mapped but species ranges or even diversity is unknown. First, high beta diversity can lead to high gamma diversity. Thus, regions with many life zones probably will have higher total diversity than similar-sized regions with few life zones. Reserves in areas rich in life zones should include all representative zones to capture the biodiversity of the area. Second, tropical understory species tend to be distributed in few life zones. A reserve with several life zones will provide less total suitable habitat for most individual species that occur in the reserve than a similar-sized reserve in one life zone because the available land is subdivided into more heterogeneous habitats. Third, elevational migrants can be a regular feature of an avifauna. Consideration of the needs of local elevational migrants can be as important as the needs of long-distance migrants. Fourth, the diversity of threatened species does not necessarily track the diversity of all species. Therefore, managers should consider local distributions of at-risk species rather than focus entirely on general patterns of diversity. This idea recently has been promoted by conservation biologists (Stotz et al. 1996) and is now making its way onto the agenda of some conservation practitioners (e.g. The Nature Conservancy 1997).

The patterns of species diversity and distribution that we found in the Tilarán mountains provide three compelling reasons to extend existing reserves to lower sites on both slopes. First, avian diversity was highest at the lowest life zone studied on each slope, whereas most of the protected area was at the highest elevations. Second, long-distance migrants, including many species of conservation concern due to recently detected population declines (Askins et al. 1990, Askins 1993, James et al. 1996), were more diverse in lower life zones. Third, many known elevational migrants were found only in the lowest life zone protected by an existing reserve (e.g. Violet-crowned Woodnymph [Thalurania colombica], Blue-throated Goldentail [Hylocharis eliciae], Rufous Mourner [Rhytipterna holerythra], White-ruffed Manakin [Corapipo altera], Olive Tanager [Chlorothraupis carmioli], and Green Honeycreeper [Chlorophanes spiza]). The low-elevation migratory destinations of these species are currently unprotected. Without further protection, we predict that these species will be among the first to experience local population declines as lower-elevation forests disappear. The high diversity across an elevational transect shown in this study strongly supports the contention that reserves in mountainous tropical areas will be most successful at preserving avifaunas by protecting large areas across elevational gradients.

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