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Endemism and local rarity in birds of neotropical montane rainforest

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ABSTRACT

Species' rarity is expressed and measured at a variety of spatial scales, and rarity at different scales could be correlated. Considerable empirical evidence has supported a positive correlation between spatial distribution and local numerical abundance of species, which could create a syndrome of rarity for species limited in geographic distribution and occurring at low densities even in their primary habitats. We used auditory-count data and range information for birds in the Tilarán mountains of Costa Rica to examine the abundance–distribution relationship in cloud forest species and to determine if endemic species (limited to Costa Rican–Panamanian highlands or Central America) are locally rare or restricted in ecological distribution. We found a positive correlation between abundance and distribution at the smallest spatial scale: species occupying few sites in the study area had low abundances where they occur. At larger scales, geographical distribution measured categorically was correlated with local ecological amplitude (zones occupied). Local abundance, however, was not correlated across all species with estimates of range size (km²), although most endemics exhibited below-median abundance. Within families with endemics and cosmopolitan species, 72% of narrow endemics were among the rarest species. For most narrow endemics, we rejected the possibility that they are sufficiently specialized within their habitats to reach relatively high densities. A conclusive test of the abundance–distribution relationship at large spatial scales and evaluation of global population size for endemics will require a comprehensive analysis using abundance data from throughout species' ranges. Such analyses for tropical species will be a long time coming, but it is meanwhile prudent to recognize that many endemics are threatened at several spatial scales, including the risks of small local populations.

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1. Introduction

The causes and consequences of rarity are fundamental issues in ecology and conservation biology, including attempts to understand the local determinants of abundance, the variety of ecological specializations among species, the evolutionary histories of geographical ranges, and the prospects of

extinction for limited-range species (Brown, 1995; Gaston and Blackburn, 2000). Rarity is expressed and measured at a variety of spatial scales, and expressions at different scales could be correlated. Species that are globally rare, in the sense of having small geographical ranges, could nonetheless be locally common. Alternatively, if species with small geographic ranges also had narrow ecological distributions and low local

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densities, then they could have very small global populations. Such a positive association of rarity on different scales would make some species extremely vulnerable to extinction because of the common threats to small populations, including demographic stochasticity and loss of genetic diversity (Kattan, 1992; Johnson, 1998a). Endemism (limitation in geographical distribution to a small region) is an often-used early-warning criterion for identifying threatened species and priority habitats or regions for conservation efforts (Bibby et al., 1992; Stotz et al., 1996; Lombard et al., 1999; Brooks et al., 2002; de Klerk et al., 2002; Pimm and Jenkins, 2005; Orme et al., 2005; Das et al., 2006; Ribon et al., 2006). If endemic species are rare at every scale, they may be especially vulnerable, and habitats with concentrations of endemics especially fragile.

There is considerable empirical evidence, from a variety of taxa, for a positive correlation between spatial distribution and local numerical abundance (Bock and Ricklefs, 1983; Brown, 1984; Lacy and Bock, 1986; Bock, 1987; Hanski et al., 1993; Brown, 1995; Gaston, 1996; Blackburn et al., 1997; Johnson, 1998a,b; Gaston and Blackburn, 2000). This relationship has been shown to apply across spatial scales and to be unattributable to sampling artifact. Among the biological mechanisms proposed to generate this correlation is resource specialization that results in narrow distributions at the landscape and geographical scales, as well as numerical scarcity even within optimal habitats (Brown, 1984, 1995). More simply, dependence upon narrowly distributed resources could produce narrow distribution in consumers (Hanski et al., 1993), and density-dependence of movement and demography could also produce abundance–distribution correlations (Hanski et al., 1993 on metapopulation dynamics; O'Connor, 1987 on density-dependent habitat selection; Holt et al., 1997 on variation in intrinsic growth rates). The descriptions, associated predictions, and empirical support for these mechanisms are reviewed in detail elsewhere (Gaston et al., 1997). It can be practically and logically difficult to distinguish among these hypotheses on a local scale, and the evolutionary history of rarity in a particular species is generally inaccessible. The possibility, however, of “syndromes” of rarity produced by whatever mechanism is of immediate concern to conservation biologists. There is ample evidence that narrow endemics (especially island species) account for most historical extinctions (Diamond, 1984) and evidence in some lineages that locally rare endemics are especially extinction-prone (Johnson, 1998a,b).

While the interspecific abundance–distribution relationship has been explored in over 40 published studies of temperate regions, it has seldom been examined for the tropics (Gaston, 1996), where most biodiversity resides and where restricted-range species are concentrated (but see Arita et al., 1990 and Johnson, 1998a,b for mammals; Kattan, 1992; Goerck, 1997; Poulsen and Krabbe, 1997; Thiollay, 2002; and Ribon et al., 2006 for birds; and Pitman et al., 1999 for plants). Tropical species tend to have smaller ranges than related temperate species (Stevens, 1989), to be less numerically abundant (Terborgh et al., 1990; Johnson, 1998b), and to be threatened by rapidly expanding human impact. The combination of high levels of both species richness and endemism in many tropical habitats offers substantial opportunity for

testing abundance–distribution hypotheses. In addition, conservation needs in “megadiversity” areas are often compelling, although there are obstacles to addressing these hypotheses in tropical communities. Investigators are limited to studying the best known taxa (e.g., trees, butterflies, birds and mammals), and even for these taxa, estimates of abundance and range size necessary at landscape, regional and geographic spatial scales may be inaccurate or simply unavailable. Low population densities of tropical species hamper accurate measurement of local abundance and limit the range of variation across species. Tropical studies have often used simple categorical measures of population size, habitat restriction and geographic distribution to identify the various “forms of rarity” (Kattan, 1992; Goerck, 1997; Pitman et al., 1999), though quantitative measures of relative abundance and distribution permit better tests of the hypotheses.

This study assesses the relationship between abundance and distribution for cloud forest birds in the Tilarán mountains of Costa Rica. The highlands of Costa Rica and Panamá harbor the greatest avian species richness in Central American montane forests (Hernández-Baños et al., 1995) and one of the highest levels of avian endemism in the world (Bibby et al., 1992). Costa Rican birds are also comparatively well known in the Neotropics (Stiles and Skutch, 1989; Young and McDonald, 2000). In the Tilarán mountains, nearly 10% (41 species) of the forest avifauna is narrowly endemic to Costa Rica and Panamá and many more are limited to Central America. Most of these narrow endemics are included in the current study. We use quantitative measures of abundance, compensating for detectability, on the Pacific slope of the Tilarán range, a qualitative measure of abundance for Pacific and Caribbean slopes, and measures of distribution on three spatial scales: within our study area (<100 km²); within Costa Rica and Panamá (100–10,000 km²); and over species' geographic ranges (>10,000 km²). We test hypotheses suggesting a positive relationship between local abundance and distribution across all species as well as within families and genera, including other studies, and address the practical issue of whether the extent of a species' geographical range is a reliable indicator of its global population size and vulnerability to extinction.

2. Methods

2.1. Study site

The humid montane forests of Central America (Mexico–Panamá) contain 147 avian species endemic to that habitat. Avian species diversity and narrow endemism peak in the highlands of Costa Rica and Panamá, and these highlands have been recognized as a global conservation priority (Bibby et al., 1992; Hernández-Baños et al., 1995; Stotz et al., 1996; Orme et al., 2005). The mountain ranges of Costa Rica, from smallest to largest and northwest to southeast, are the Cordilleras Guanacaste, Tilarán, Central and Talamanca; these ranges harbor 28, 41, 45, and 54 species respectively that are narrowly endemic to the highlands of Costa Rica and Panamá (Stiles and Skutch, 1989; Sánchez, 2002; G. Barrantes, personal communication).

The Tilarán mountain range (10°18'N, 84°45'W; maximum elevation 1850 m) extends for 100 km northwest-southeast with the continental divide traversing its peaks. The Caribbean slope receives an abundance of rainfall (up to 6000 mm) and moisture from cooling northeasterly trade-winds. On the Pacific slope, the highest elevations in the study area of Monteverde support a lush, epiphyte-laden cloudforest or montane rainforest with up to 4000 mm rainfall and considerable precipitation from wind-driven mist and cloudwater. On this leeward slope, dissipating moisture driven across the continental divide creates a steep moisture gradient. Rapid change in habitats with increasing distance from the divide results, leading to a much drier and epiphyte-poor “rainshadow forest” with roughly half the precipitation of the cloudforest near 1000 m elevation. This precipitous habitat gradient occurs within 3–4 km of the continental divide, and results in representation of four climatic life zones (determined by potential evapotranspiration; Holdridge, 1967) within our study area: premontane moist forest; premontane wet forest; lower montane wet forest; and lower montane rain forest (Haber, 2000; Clark et al., 2000). Variation in tree and avian species composition on the Pacific slope is great, with nearly complete turnover across the study area (600 m altitude; Young et al., 1998; Haber, 2000; J.E.J. and K.N.R., unpublished data). The Monteverde Reserve Complex, which includes the Monteverde Cloud Forest Reserve, the Children’s Eternal Rainforest, and the Santa Elena Cloud Forest Reserve, protects 27,000 ha of montane forest in the Tilarán range (Powell et al., 2002). Most of this coverage, however, occurs on the Caribbean slope above 700 m. The Pacific slope, despite its habitat diversity, is relatively unprotected below 1500 m.

2.2. Count procedures

In the breeding season (May–June) of 2001, we conducted both point-counts and mist-netting between 1600–1700 m altitude near the continental divide and on the Pacific slope in the Monteverde Cloud Forest Reserve. Mist-netting was conducted at 33 sites separated by 100 m along a transect, using standardized sets of two 7 × 12 m nets (three standard 36 mm mesh nets stacked), resulting in 854 captures. The claws of captured birds were marked with nail polish for identification of recaptures. Nets were deployed for three mornings of fair weather or until most birds netted were recaptures. Point counts were conducted at alternate netting sites along the same transect, using the same methodology as in 2003 (see below), but without measurement of detection distances. These two methods reveal different characteristics of the community (e.g., hummingbirds are better sampled by netting, and canopy species are better sampled by point counts). We combined these data for the points where counts were made, pooling the netting data for two points with each count point. This resulted in a nearly equal number of detections at each pair of points by the two methods (~60), and we then used the maximum number of individuals detected by either method as the best estimator for a count point, resulting in a composite estimate of species’ relative abundances for a subsection of the larger 2003 study area (see also Rappole et al., 1998). We used these data to establish the spatial and

temporal integrity of the high-elevation bird community, and we used it here only as a preliminary test of the abundance–distribution hypothesis.

All other analyses used 2003 auditory and visual counts of forest birds on the Pacific slope from 1100 to 1700 m. The 36 km² study area was divided into six 100 m altitudinal zones, and within each zone 15 permanently marked count points were established along narrow trails, spaced 200 m apart in unfragmented primary forest ($n = 89$ points). We conducted 10-min counts at all points, repeated five times at weekly intervals in the breeding season, from 05:00 to 10:00 h on all mornings without heavy wind or rain, for a total of 445 counts. The positions, elevations, and distances from the continental divide of all points were determined with a GPS (global positioning system) device using an antenna elevated 7 m, yielding an accuracy within 10 m. These points were entered into a GIS (Geographical Information System (ArcView)) database with a digital elevation model. Observers had prior experience with the avifauna: three for several years, and the three others participated in both 2001 and 2003. Before each field season all observers studied recordings of vocalizations (Ross et al., 1997; Cornell Laboratory of Ornithology, and D. MacDonald, personal communication) for several months and the team conducted on-site calibrations for another three weeks. Counts were conducted in two teams of three observers with rotating membership. All species seen or heard from each point were identified within a radius of 100 m and distances estimated for all detections (for species identification we used the *American Ornithologists’ Union Check-list of North American Birds* (7th edition, 47th supplement). The area sampled for each site was therefore 3.1 ha, for a total maximum of 280 ha coverage in the 36 km² study area. Counts were recorded using a digital recorder and an omnidirectional microphone, and all data were later reviewed using the recordings, pooling expertise. Order of visitation of sites was reversed on alternate visits, so that the hour of sampling was varied to equalize biases due to hourly variation in detectability.

To accurately record the number of breeding pairs at each point without double counting, male territorial songs were distinguished from non-sex-specific calls. Single songs or calls were counted as representing a pair, and detection radii of different points did not overlap. Songs or calls heard within 50 m of a previously recorded vocalization were assumed to represent the same pair. Vocalizations at distances greater than 50 m at the same point were recorded as an additional pair. These rules were also applied to duetting species and group-singing or communal-breeding species (wrens: *Thryothorus*, *Henicorhina*; barbets: *Semnornis*; wood-quail: *Odontophorus*). Mixed-species flocks were considered to be independent when separated by >50 m, and each species in a flock was recorded as a single breeding pair. Our auditory counts were not sufficient to determine abundance for raptors, hummingbirds, parrots, swifts or swallows; as a result, these families are not included in our analyses.

2.3. Abundance and distribution data

Analysis of sampling sufficiency indicated that more than five visits to the count points would provide little additional infor-

mation (5–10%) on the number of pairs of each species present at each point. Resampling of points minimized underestimation of abundance for species that vocalize infrequently. Our quantitative estimates of species abundance were summarized using the maximum number of individuals detected in a single count over the five visits to a point. Abundance estimates were then corrected by species' detectabilities to adjust for species that could only be heard at short distances by the equation:

$$\hat{N} = \frac{C}{\beta}$$

where \hat{N} is the estimate of true abundance, C is the maximum recorded abundance, and β is the estimate of detectability ($\beta \leq 1$; Williams et al., 2002). Detectability was estimated for most species ($n = 69$) using program DISTANCE (version 4.0; Thomas et al., 2003; Buckland et al., 2001). We clustered detection distances into bins assuming that errors of estimation increase with distance from the observer. We used several candidate detection functions and picked the one that resulted in the lowest AIC value (Buckland et al., 2001). To determine detectability for species with too few observations to use DISTANCE, detectability values for the 69 species were ranked and divided into ten groups. The remaining 30 species were assigned to the group with most similar song qualities and assigned the average detectability of that group. Eight species detected only once during the study period were excluded from analyses to guard against inclusion of accidents and poorly known detectabilities.

Previous investigations of the abundance–distribution relationship have calculated average abundance (or density) using only sites, locales or habitats with non-zero values to avoid devaluing a species' abundance estimate by including areas outside its ecological range. They have also included patchiness of occurrence in estimates of abundance within appropriate habitat so that estimates are not being made only where density is high. For these reasons, studies have calculated abundance over areas large enough to encompass appropriate habitat even if some points within the area are not occupied, ranging from tens of hectares to hundreds of km² (Lacy and Bock, 1986; Bock, 1987; Brown, 1995; Gaston et al., 1997). Fine-scale habitat maps (based on vegetation or climate) do not exist for the study area, but we have described the major gradient of change in bird species composition as a moisture gradient that is well-represented by distance from the continental divide (J.E.J. and K.N.R., unpublished data). We have also found that tree species composition correlates well with bird species composition along this gradient (W. Haber and E. Cruz, unpublished data). We therefore used ten 300 m wide bands of distance from the divide as objective habitat categories that are more ecologically realistic than a grid system. We used data from two seasons, 2003 and 2006, to describe species' distributions on the mountainside, based on a sampling effort of more than 10,000 detections. We included 300 m bands with the most detections for a particular species in the characterization of the local range until 90% of observations were contained (to exclude uncharacteristic single observations). We then calculated abundance over this 90% range estimate ("kernel").

In addition to abundance data calculated across our point counts on the Pacific slope, we used a qualitative checklist of bird species in the Tilarán range (Fogden, 1993) to measure abundance and distribution at a broader scale that includes the Pacific and Caribbean slopes. Fogden's checklist is based upon life zones that are empirically derived from the avian distributions themselves. It is widely used by local ornithologists and agrees well with our distribution data. The number of Fogden's zones in which species are common was used as a composite measure of the abundance of species within zones and their distribution across zones on a landscape scale.

We used four estimates of species' spatial distribution on three scales. At the smallest scale (<100 km²), we used the proportion of our 89 points occupied by each species (1100–1700 m on Pacific slope) since this 36 km² area includes a range of habitats (Haber, 2000). This can be used as a measure of breadth of ecological distribution. This measure is highly correlated with altitudinal range on the Pacific slope and the number of Fogden zones occupied (Fogden, 1993). We used the recently compiled NatureServe digital distribution maps for birds of the Western Hemisphere (Ridgely et al., 2003) to estimate range size within Costa Rica and Panamá (100–10,000 km²) and total geographic range size (>10,000 km²). We projected the GIS layers in ArcInfo to a Universal Transverse Mercator (UTM) projection and calculated area of ranges in ArcView ver 3.2 (ESRI, 1999). Because area measurements made from GIS data can be significantly affected by digitizing accuracy and data projection, we rounded estimates obtained from ArcView to three significant digits. We also used a categorical measure of total range based on major dispersal barriers for highland birds in Central and South America (Watson and Peterson, 1999). These categories correspond well with measures of range size in km², and they recognize range crossings of the isthmuses of Panamá, Nicaragua and Tehuantepec (southern Mexico) and the constriction of the Andes near the border of Colombia and Ecuador. After collapsing poorly represented categories, these categories of geographical distribution can be described as (1) endemic to the Costa Rican–Panamanian highlands, (2) endemic to Central America (Mexico–Panamá), (3) ranging from Costa Rica into South America, (4) ranging from Mexico into South America, and (5) ranging from northern Mexico to Ecuador (or beyond).

Correlation analyses between abundance and distribution measures were examined using three taxonomic levels: across taxonomic families (all species); within families; and within genera. Analyses over all species were conducted using Mann–Whitney U tests, Spearman rank correlation coefficients and Pearson product-moment correlation coefficients (Pearson correlations used log₁₀ abundance and range size values). The correlation coefficients and significance values varied little between parametric and nonparametric tests, so only Spearman correlations are reported. Correlation analyses within families and genera used Wilcoxon Signed-Rank tests.

2.4. Comparison with other studies

We analyzed data presented in two published studies from altitudinal gradients in Costa Rica (Young et al., 1998; Blake and Loiselle, 2000). Young et al. presented data compiled from

11 independent studies of bird communities using mist nets to examine species composition across five Holdridge climatic zones on the Pacific and Caribbean slopes of the Tilarán range (10,726 total captures, 235 species). We averaged their measure of species' abundance (occurrences per 1000 captures) across occupied climatic zones and used the number of occupied climatic zones as a measure of distribution. Blake and Loiselle used mist-netting and point counts to sample birds along an altitudinal gradient on the Caribbean slope of the Central mountain range in Costa Rica from 50 to 2000 m altitude (7312 total captures, 17,071 detections, 261 species). We averaged their abundance data from point counts (percentage of total observations per altitudinal zone) across occupied sampling stations between 1000–2000 m altitude (6086 detections, 196 species), and we measured distribution as the number of sampling stations occupied.

3. Results

Species endemic to Costa Rica and Panamá were concentrated at high elevations where species richness was lowest: between 1600 and 1700 m, 40% of species were narrow endemics, compared to only 7% between 1100 and 1200 m. Species limited to Central America were not similarly concentrated at the higher elevations. The great majority of species occurred at fewer than half of the 89 sites distributed across 600 m of elevation (mean = 26%); 20 species occurred at fewer than 10% of the sites, and 17 species were limited to one or two 100 m altitudinal zones.

Abundance data combining netting and point counts in 2001 between 1600–1700 m indicated that 15 of 23 narrowly endemic species (65%) were below median abundance in that zone, and 8 of 23 (35%) were in the bottom quartile, but there was no significant difference in total detections between nar-

row endemics and all other species (Mann–Whitney U test, $P = 0.18$; Table S1). Central American endemics (not including those narrowly endemic to Costa Rica and Panamá), on the other hand, had significantly higher total detections compared to more cosmopolitan species ($P = 0.04$).

In our 2003 dataset of auditory counts on the Pacific slope, over 89 sampling sites, we recorded a total of 5513 detections of 103 species representing 23 families, 67 genera and 23 narrowly endemic species. Excluding species only recorded once and a few rarely-detected nonforest species leaves 82 species including 17 narrow endemics in the dataset for analysis of the abundance–distribution relationship. A significant positive correlation was found between abundance and proportion of points occupied on the Pacific slope (Spearman rank, $r = 0.60$, $P < 0.0001$; Fig. 1). There was, however, no trend for narrowly endemic species to show below-median abundance (7 of 17 endemics; Mann–Whitney U test, $P = 0.51$) or to occupy below-median proportions of points (10 of 17 endemics; $P = 0.66$). Species limited to Central America were not concentrated below median abundance (7 of 14 endemics; $P = 0.84$) or median proportion of sites occupied (8 of 14 endemics; $P = 0.92$). Local abundance measured across study points was not significantly correlated with distribution within Costa Rica – Panamá (Spearman rank, $r = -0.17$, $P = 0.14$) or with geographic range ($r = -0.17$, $P = 0.13$). However, a positive correlation was found between the composite measure of abundance and distribution from Fogden's (1993) qualitative checklist and the range-size categories (number of lowland barriers crossed; $r = 0.26$, $P = 0.02$; Fig. 2).

It is possible that a positive correlation between local abundance and distribution could result from the position of species' ranges with respect to our study area. Our sample along an altitudinal gradient inevitably intercepted the tail of some species' distributions and the center of other species'

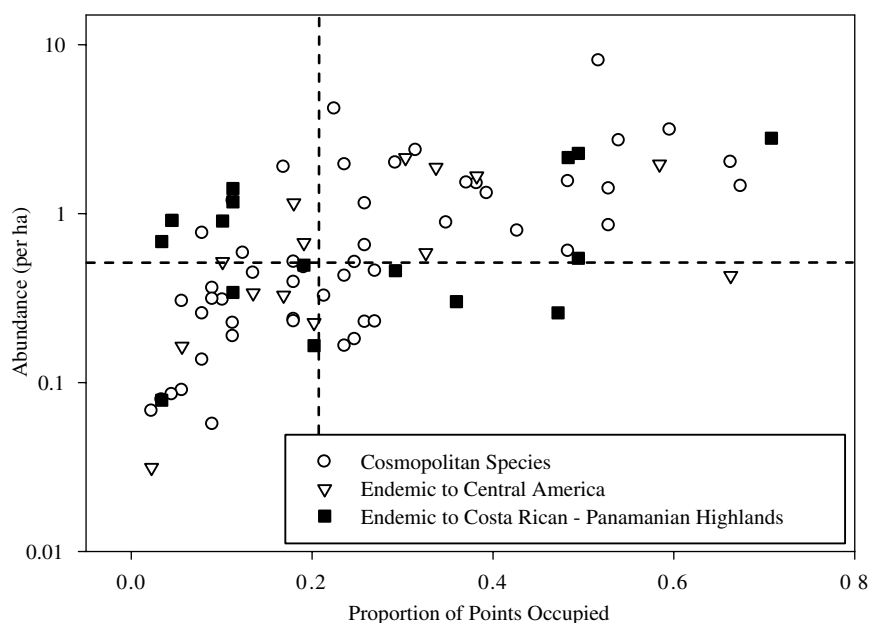


Fig. 1 – The relationship between local distribution (proportion of 89 points occupied, across a 600 m elevational gradient) and numerical abundance, measured by auditory/visual counts in 2003 and adjusted for detectability. Dashed lines indicated median abundance and distribution.

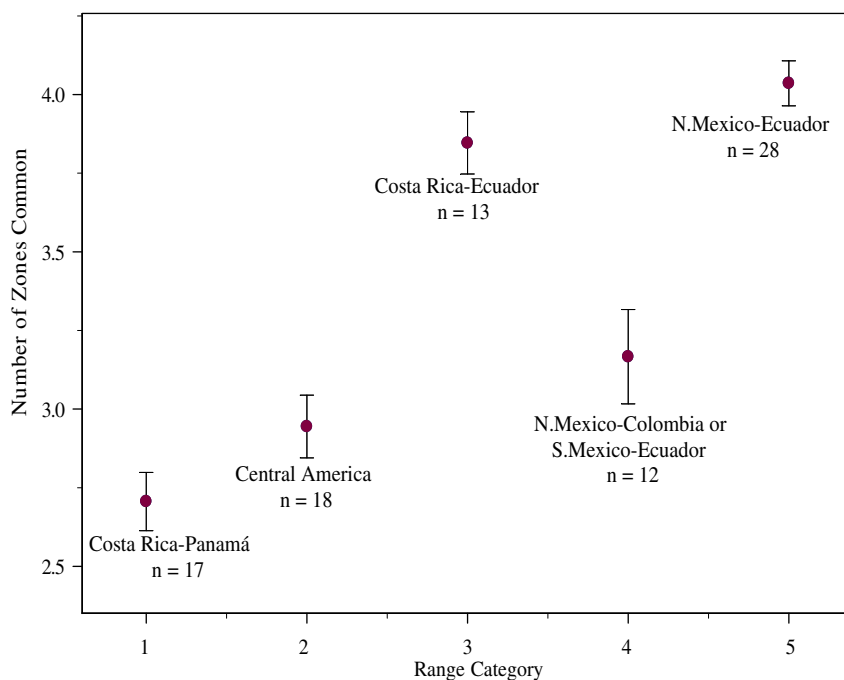


Fig. 2 – The relationship between geographical range size (“range category”; measured by the number of biogeographical barriers spanned) and local ecological amplitude (number of faunal zones in which the species was common; see text for description) for birds in the Tilarán mountains, Costa Rica, using the species list from this study, range data from [Ridgely et al. \(2003\)](#) and local ecological data from [Fogden \(1993\)](#). Range categories correspond to (1) crossing no lowland barrier, (2) crossing the Nicaraguan isthmus, (3) crossing the Panamanian isthmus and the Andean constriction, (4) crossing all but the northernmost (Tehuantepec) or southernmost barriers, and (5) ranging across all four lowland barriers.

distributions. Unimodal species distributions along the gradient could create a positive correlation if species occupying only a few sites also have low abundances because they are at their distributional limits altitudinally or latitudinally. We checked for this effect by removing those species that are at the edge of their altitudinal and latitudinal distributions within our study site. The relationship between local abundance and the proportion of sites occupied was strengthened ($r = 0.73$, $P < 0.0001$).

For paired comparisons of confamilial species, species with higher local abundances were more likely to occupy a higher proportion of sites within the study area compared to their confamilial species (comparing values above and below family median; Wilcoxon Signed-Rank test, $z = 3.28$, $P = 0.001$), but they were not more likely to have larger ranges in Costa Rica – Panamá ($z = 0.23$, $P = 0.82$) or larger geographic ranges ($z = 0.79$, $P = 0.43$). For paired comparisons of congeners, species with higher local abundances were more likely to occupy more sites within the Tilarán range compared to their congeners ($z = 3.04$, $P = 0.002$), but they were not more likely to have larger ranges within Costa Rica – Panamá ($z = 0.29$, $P = 0.77$) or larger global ranges ($z = 0.71$, $P = 0.48$). Most narrow endemics in this study were among the most numerically rare species in their families (8 of 13 in [Fig. 3](#)). If species detected only once were included (since confirmed as resident species), then 13 of 18 (72%) endemics that were not the sole representatives of their families were among the rarest (this adds Buff-fronted Quail-Dove (*Geotrygon costaricensis*), Buffy Tuftedcheek (*Pseudocolaptes lawrencii*), Black-

and-yellow Silky-Flycatcher (*Phainoptila melanoxantha*), Slaty Flowerpiercer (*Diglossa plumbea*), and Yellow-thighed Finch (*Pselliophorus tibialis*). Central American endemics were rarely the least or most abundant within their families.

Narrow endemics were consistently less abundant than their cosmopolitan congeners in the few cases where such comparisons were possible: Collared Redstart (*Myioborus torquatus* compared to *M. miniatus*); Sooty-capped Bush-Tanager (*Chlorospingus pileatus* compared to *C. ophthalmicus*), Spangled-cheeked Tanager (*Tangara dowii* compared to *T. ictercephalus*). Most Central American endemics were also less abundant than their more cosmopolitan congeners: Black-headed Nightingale-Thrush (*Catharus mexicanus*), Ruddy-capped Nightingale-Thrush (*Catharus frantzii*), and Plain Wren (*Thryothorus modestus*), but this pattern was not upheld in other genera (*Columba* (doves) and *Turdus* (robins)).

To determine whether the positive correlation between local abundance and distribution we found could be generalized to other tropical montane bird communities, we examined data from [Young et al. \(1998\)](#) and [Blake and Loiselle \(2000\)](#), from the Tilarán and Central ranges of Costa Rica, respectively. In both studies, we found significant positive correlations between average abundance and number of climatic or altitudinal zones occupied (Spearman rank correlations, respectively $r = 0.64$, $P < 0.0001$; and $r = 0.34$, $P = 0.001$). The study of Young et al. included many of the same species found in ours, but sampled over a narrower altitudinal range. In three of four comparisons, endemics showed lower abundances than cosmopolitan congeners. Using the data of Blake

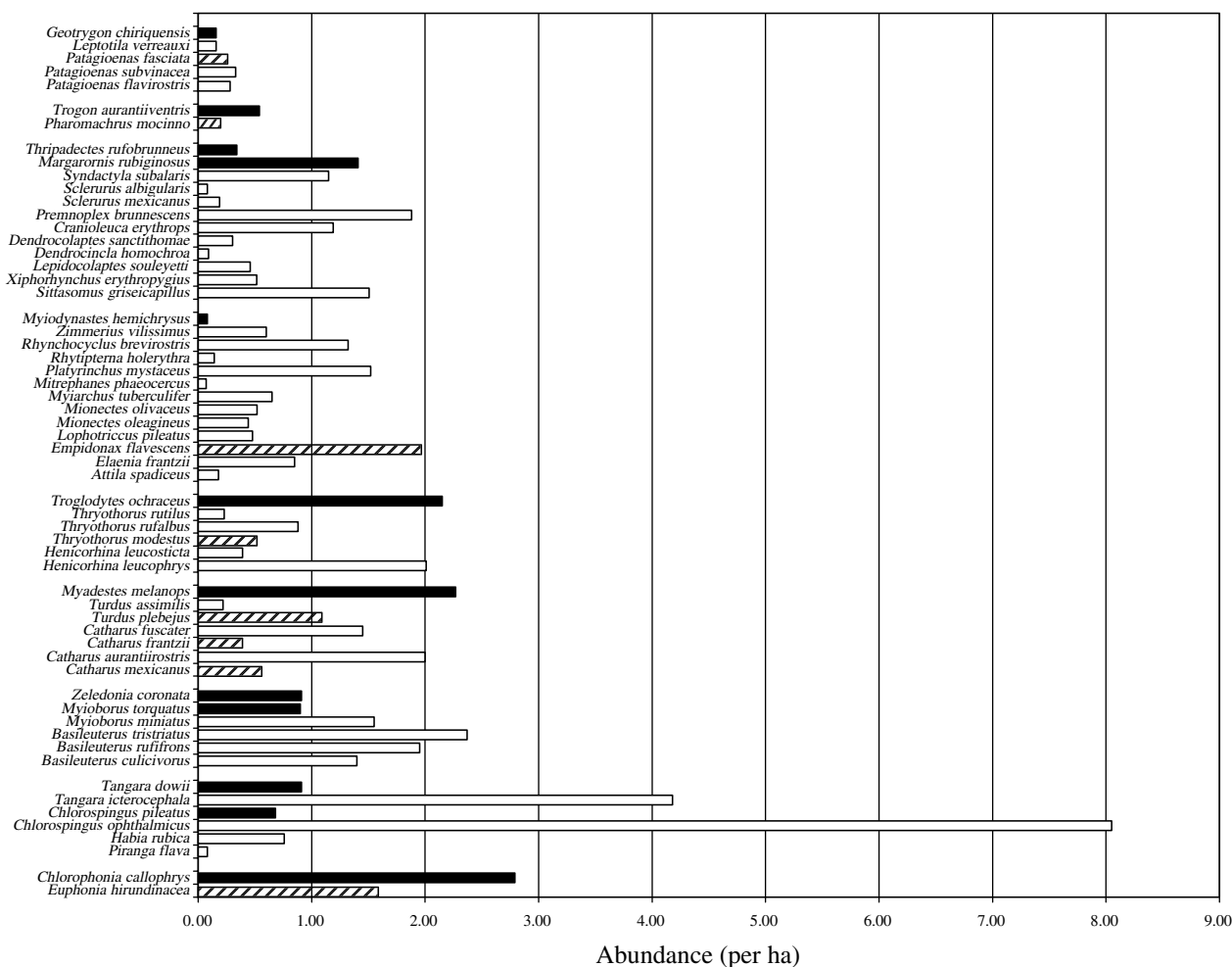


Fig. 3 – Abundances (breeding pairs per hectare) of species within families containing narrow endemics (Costa Rica – Panamá, shaded black). Species endemic to Central America are indicated by striped shading. Abundances are derived from visual/auditory counts, and are corrected for detectability (see text).

and Loiselle, we found abundance values for 30 narrow endemics and 22 Central American endemics for which confamilial comparisons were possible. We found no relationship between abundance and range size across confamilial comparisons for this dataset (Wilcoxon Signed-Rank test, $z = -0.24$, $P = 0.81$). Endemics had lower average abundances than cosmopolitan congeners in three of six comparisons.

4. Discussion

Tropical montane species generally have narrow local distributions, resulting in high variation in species composition within and between altitudinal zones (J.E.J. and K.N.R., unpublished data). As in many tropical landscapes, most species are “rare” in that they occupy only a small part of the ecological landscape (one quarter occur in one or two 100 m altitudinal zones; most occupy fewer than half of points over a 600 m altitudinal gradient), and most occur at relatively low densities (most below one pair per hectare; Fig. 1) compared to temperate forest birds (most well above one pair per hectare; e.g., Rabenold et al., 1998 and unpublished data from Great Smoky Mountains, USA). Species in this study also have small ranges

compared to temperate species, as might be expected (Stevens, 1989). Seventy-four percent have ranges smaller than one million km² (30 species have ranges of less than one fifth that size), while no species in a sample over a similar altitudinal range in the Great Smoky Mountains has a range that small (2–15 million km²; range data from Ridgely et al., 2003). Our analysis of the correlation between distribution and abundance for tropical birds is therefore constrained to the rare end of the spectrum for birds.

In the cloudforest avifauna of the Tilarán mountain range, we found a positive relationship between abundance and distribution at the local scale when considering all species together, in spite of substantial scatter in these relationships attributable to different abundance–distribution relationships among families with varying body size, habitat requirements, and trophic relationships. These results are supported by our analyses of data from other studies in Costa Rica. Species specialized to particular habitats or ecological zones tend to also be numerically rare within those habitats.

A number of biological mechanisms could be responsible for the local abundance–distribution relationship (predictions and evidence reviewed in Gaston et al., 1997). One such ap-

proach, “Brown’s Hypothesis” (Brown, 1984, 1995) suggests a syndrome of rarity in species with specialized niches. To separate this hypothesis from more demographically based hypotheses (e.g., Hanski et al., 1993), suggesting dispersal of individuals from centers of high productivity, would require spatially and temporally extensive data on demography, dispersal, and niche characteristics that are far beyond any study in the tropics so far. Studies of demography and dispersal in tropical birds do, however, suggest that dispersal can be very limited so that spatial patchiness can be associated with low productivity, consistent with metapopulation abundance–distribution hypotheses (e.g., Yáber and Rabenold, 2002; Williams and Rabenold, 2005).

The positive abundance–distribution relationship is not likely due to sampling or statistical artifact. First, we have probably not substantially underestimated the distribution of numerically rare species. Vocalizations that are detected only at short distances are not associated with rarity, and our use of the program DISTANCE adjusts for detectability. Resampling points also minimizes the possibility of missing species that are difficult to detect, and we demonstrated the sufficiency of this effort. A second potential statistical problem is the non-independence of phylogenetically related species (Harvey and Pagel, 1991); however, our analyses across all species, within avian families and within genera showed the same positive relationship between local abundance and distribution. Finally, it is possible that the position of our study site in the landscape sampled several species at the edges of their altitudinal or latitudinal distribution (range position hypothesis; Bock and Ricklefs, 1983). When species whose altitudinal (or latitudinal) limits are at the edge of our study area were removed, the relationship remained highly significant.

Although we documented a positive relationship between abundance and distribution at the local scale, evidence was equivocal considering geographical ranges, when abundance was not measured at the same scale as distribution. Considering all species together, neither narrow endemics nor species limited to Central America had consistently lower numerical abundances compared to geographically cosmopolitan species. If we used a spatially broader measure, in the form of the number of zones in which a species was common (Fogden, 1993), we found a significant correlation with range-size categories. This measure of local abundance, while qualitative, represents an estimate integrated over a broader scale (approximately 100 km² on both Pacific and Caribbean slopes) and longer time, compared to our more quantitative estimates over 36 km² on the Pacific slope.

Analyses of the relationship between abundance and distribution at the family and genus level sharpen the focus of the abundance–distribution hypotheses and control in large part for phylogenetic scatter. The expectation was generally supported that endemics would be less abundant locally than more cosmopolitan confamilial or congeneric species, although sample sizes were small for these matched comparisons, even in this speciose tropical landscape. The fact that most narrow endemics in this study were among the most numerically rare species in their families (13 of 18 when including species with single detections) should generate concern that endemics often are handicapped by rarity at multiple scales.

Few authors have addressed distribution at multiple spatial scales (e.g. local, regional and geographic; Bock, 1987; Hanski et al., 1993) although it has been recognized that the abundance–distribution relationship should grow weaker with increasing spatial scale as the heterogeneity of environments incorporated into analyses increases (Brown, 1995; Gaston et al., 1997) and as the error in measures of abundance and distribution increases. A more conclusive test of the abundance–distribution hypothesis at larger spatial scales (i.e., the abundance–range size relationship) would require what Gaston (1996) has described as a comprehensive analysis, where abundance is averaged over the entire ranges of species, or at least the range over which distribution is measured. We present a comprehensive analysis within the Tilarán mountain range, but only at the smallest spatial scale. While the measurement of species’ geographical ranges in the neotropics is improving with compilations like the NatureServe database (Ridgely et al., 2003), these measurements still have substantial error, especially for large regions of South America. It is meanwhile prudent to plan for the possibility that the threat to many endemic species might be greater than generally realized (see also Ribon et al., 2006). Given this strong possibility and the uncertainty in the relevant measurements, a conservative precautionary approach seems warranted (Thompson et al., 2000).

The first and most fundamental criterion for classifying species as threatened on “red lists” is based upon geographic distribution (e.g., IUCN), and prioritizations of threatened habitats or regions for conservation action often highlight the density of endemic species (Bibby et al., 1992; Stotz et al., 1996; Lombard et al., 1999; Brooks et al., 2002; de Klerk et al., 2002; Pimm and Jenkins, 2005). Some endemic species are sufficiently locally adapted that they are abundant where they occur despite their limited geographic distribution, but this does not seem to be the norm in montane rainforest birds. It seems likely that many limited-range species have much smaller global population sizes, and correspondingly greater risks of extinction, than their cosmopolitan relatives. Most of the narrowly endemic species within Costa Rica and Panamá are limited to cloud forest and higher elevations (Stiles and Skutch, 1989) and the same is true of species endemic to Central America (Hernández-Baños et al., 1995). Within the Tilarán range, we have detected 23 of these endemics, 17 of which were used for analyses of the abundance–distribution relationship, and at least two thirds of them appear to be numerically rare locally and to be habitat specialists. A syndrome of rarity at multiple spatial scales is also suggested by other studies of tropical birds. In Colombia, Kattan (1992) found that 24% of the forest species restricted to the northern Andes were scarce within their habitat (using a composite measure of their local abundance and distribution), and in Brazil, Goerck (1997) found that 56% of endemic species in Atlantic coastal forest had small population sizes. Ribon et al. (2006) found that endemics were extinction-prone and that levels of threat are underestimated for many tropical species because of patterns of local rarity.

In the Tilarán range of Costa Rica, 40% of avian species at the highest elevations are narrow endemics, as is also true for the other major mountain ranges in the country (Blake and Loiselle, 2000; J. Sánchez and G. Barrantes, personal commu-

nication). The bias in protected areas toward higher elevations therefore is effective in protecting these species, although richness often peaks lower and many endemics have peaks of abundance or significant seasonal peaks outside of protected areas. Overall, half of the distributions of species in the study ($n = 44$) were concentrated during the breeding season below the protected zones (75% of measured abundance below 1500 m on the Pacific slope). Extension of conservation areas just 2 km into the middle elevations of the Pacific slope, to include the rainshadow forest, would better protect endemics and a unique community that would approximately double the number of species under protection on the Pacific slope. Although this study does not consider latitudinal neotropical migrants, rainshadow forests are also important habitat for them. Forests such as these are poorly understood and poorly protected throughout Costa Rica and Latin America, and such landscapes offer high benefit/cost opportunities for conservation.

Tropical regions, with their high species diversity, also account for many of the areas of high endemism (Johnson, 1998b; Brooks et al., 2002). Within these regions, however, areas of high endemism often do not map closely onto areas of high species richness (Stotz et al., 1996; Peterson et al., 1998; Lombard et al., 1999; Poulsen and Lambert, 2000; Brooks et al., 2002; Harrison and Inouye, 2002; Orme et al., 2005) and endemics are often concentrated in areas of lower productivity, topographic or edaphic complexity, and insular or peninsular geography, like mountain ranges. As Brown (1984, 1995) has suggested, following Darwin's lead, this is consistent with an evolutionary history of endemics differentiating into ecological specializations that also bring a degree of demographic isolation and reduced gene flow. This perspective also suggests that endemic populations represent potential for future evolutionary innovation. The distribution and abundance of narrowly endemic birds in the mountains of Costa Rica fit this pattern in that they are often numerically rare, limited in their ecological tolerances, and concentrated at the highest elevations.

These mountaintop populations are not only handicapped by their limited global populations and patchy distributions, but are also threatened by the effects of climate change and human expansion (Pounds et al., 1999; Foster, 2001; see also Shoo et al., 2005). Understanding ecological specialization in tropical communities, particularly among endemics, will be central to conservation strategy.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2007.05.015.

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