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Elevational Patterns of Species Richness, Evenness, and Abundance of the Costa Rican Leaf-Litter Herpetofauna¹

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ABSTRACT

The abundance, species richness, and evenness of the Costa Rican leaf-litter herpetofauna was estimated during the late wet season of 1985 by quantitative sampling of replicate plots at ten sites encompassing an elevation range of 3 to 1670 m. Species richness was positively correlated with leaf-litter depth, and negatively correlated with elevation. Herpetofaunal density also tended to increase with litter depth and decline with elevation. A strong positive correlation existed between species richness and herpetofaunal density. Evenness was highly variable and independent of both leaf-litter depth and elevation. Analysis of a subset of the data, representing an elevational transect from Tortuguero to the Braulio Carrillo National Park Extension, yielded similar results.

Tropical leaf-litter reptiles and amphibians appear to be both more diverse and more abundant at lower elevations. Sites with deep leaf litter generally sustain dense and diverse reptile and amphibian populations. Local herpetofaunas typically consist of a few very common species along with a large number of comparatively rare species.

REPTILES AND AMPHIBIANS are a major constituent of the fauna inhabiting tropical forest litter. Studies of tropical leaf-litter herpetofaunas have emphasized patterns of abundance and distribution among geographic regions (Lloyd *et al.* 1968; Heyer & Berven 1973; Scott 1976, 1982; Inger 1980a, b; Heatwole 1982), vegetational zones (Brown & Alcalá 1961, Heatwole & Sexton 1966, Heyer 1967), and elevational gradients (Brown & Alcalá 1961, Scott 1976) as well as seasonal changes (Lieberman 1982, 1986). It has become generally accepted that leaf-litter reptiles and amphibians are more abundant in the New World Tropics than in Southeast Asia (Scott 1976, Inger 1980b, Duellman & Trueb 1986) although the exact reason remains a subject of debate (May 1980).

Similarly, the general consensus is that the abundance of tropical leaf-litter herpetofaunas increases with increasing elevation, while species richness and equitability both decline (Brown & Alcalá 1961, Scott 1976, Heatwole 1982, Duellman & Trueb 1986). Scott (1976) attributed this pattern to greater overall forest productivity at intermediate elevations, coupled with increased densities of the most common species at higher elevations.

Before attempting to determine the mechanisms responsible for observed patterns of tropical leaf-litter herpetofaunal abundance and diversity, we must document the phenomenon conclusively. Previous quantitative studies have sampled few sites, have been unable to provide replicated samples (Brown & Alcalá 1961), or may have

confounded site and year effects by sampling different sites in different years (Scott 1976). We surveyed the Costa Rican leaf-litter herpetofauna by quantitatively sampling replicate plots at ten sites, ranging from 3 to 1670 m in elevation, during the late wet season of July–September 1985. Our sampling strategy permitted statistical analyses to determine the relationship between litter depth and elevation, and leaf-litter herpetofaunal richness, evenness and abundance. The results of our study contradict several of the generally accepted patterns of tropical leaf-litter herpetofaunal abundance and diversity.

METHODS

SAMPLING METHODS.—We sampled 35 plots at 10 different Costa Rican sites (described below) between 5 July and 11 September 1985. The sites varied in elevation from sea level (Tortuguero, Palo Verde) to the continental divide (Monteverde). Site elevations were determined with an altimeter and cross-checked by interpolation from topographic maps.

To facilitate comparisons among sites, we selected plot locations according to three criteria: (1) presence of leaf litter, (2) absence of slopes, and (3) relatively low plant density, uncomplicated by major treefalls. Each plot was 5 × 5 m (with exceptions noted below). After we demarcated a plot we cleared a 1 m wide swath around the plot to reduce emigration during sampling. We removed leaf litter in a unidirectional search of the plot, examining vegetation within 0.5 m of the ground. Our methods are comparable to those of most previous studies (Heatwole & Sexton 1966; Scott 1976, 1982; Inger 1980b; Lie-

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berman 1982, 1986) except that we did not disturb the soil by digging (Brown & Alcalá 1961, Lloyd *et al.* 1968) since this method yields few additional animals (Scott 1976). Searches were conducted between 0700 and 1800 hours. Diel differences in leaf-litter herpetofaunal abundances are presented elsewhere (Slowinski *et al.* 1988).

We identified all animals captured using keys in Savage (1980). We made provisional identifications of escaped individuals in the manner of Lloyd *et al.* (1968). Captured individuals were identified, weighed to the nearest 0.1 g, measured (SVL) to the nearest millimeter, had their vertical position in the litter recorded, and were then released. We recorded litter depths 1 m from each plot corner and in the center of the plot (exceptions noted below), and also recorded air and substrate temperatures.

STUDY SITES.—Salient features of the ten Costa Rican sites are outlined briefly below. Most of these sites are regularly visited by Organization for Tropical Studies field courses. More complete descriptions of many of the locales are provided by Hartshorn (1983). Classification of life zones follows Holdridge *et al.* (1971).

Tortuguero (15 July): Tortuguero is in Heredia Province, on the Caribbean coast of Costa Rica. Two replicate plots were established at the base of Cerro del Tortuguero, across the Boca del Tortuguero from the Green Turtle Research Station (Carr 1982). Both plots were at 3 m elevation, and sampled 36 and 64 m² areas of forest floor. The plots were in selectively cut second-growth tropical wet forest. Leaf litter depth was estimated at several haphazardly selected points in each plot.

Palo Verde (29 July): Palo Verde lies along the Rio Tempisque, above the Golfo de Nicoya on Costa Rica's Pacific coast. Three 25 m² plots were established at 3 m elevation in tropical dry forest approximately 2 km east of the Palo Verde airstrip, Palo Verde Wildlife Refuge, Guanacaste Province.

Las Vegas (18 July, 9–11 September): On 18 July, three plots were sampled in an abandoned cacao grove (100 m elevation) in the Las Vegas tract of the Organization for Tropical Studies' La Selva Biological Reserve, Heredia Province. Seven additional plots were sampled there on 9–11 September. La Selva is classified as lowland moist rainforest, and the Las Vegas site has been described elsewhere (Slowinski *et al.*, 1988). Leaf litter depths sampled at 10 points in the cacao grove were used to estimate litter depth at this site.

Braulio Carrillo National Park Extension (17–18 August): Three replicate plots were established at each of three elevations (750, 1000, and 1120 m) in primary tropical wet forest in the Braulio Carrillo National Park Extension, Heredia Province. Plots were situated near a trail connecting the La Selva Biological Reserve with Braulio Carrillo National Park.

Las Cruces (27 August): Three plots were sampled

at 1050 m in tropical premontane wet forest at Finca Las Cruces, near San Vito de Java, Puntarenas Province. Two plots were in primary forest, while the third was in secondary forest.

Monteverde (7–8 August): Three sites were sampled in the vicinity of Monteverde, Alajuela Province. One site was near the village of Monteverde, in secondary tropical premontane wet forest adjacent to a relict pasture known as Campbell's Bullpen (1500 m). The other two sites were along the Sendero Chomogo in the Monteverde Cloud Forest Reserve. These two sites were in lower montane wet forest at elevations of 1640 and 1670 m. Three replicate plots were sampled at each site, except the 1670 m site, where a violent downpour halted study after only one 25 m² and one 12.5 m² plot were sampled.

STATISTICAL METHODS.—Four variables were calculated for each site: mean leaf litter depth, mean herpetofaunal density (mean number of individuals/m²), mean species richness (mean number of species per plot) and evenness. We chose J' of Pielou (1969) as our measure of evenness,

$$J' = H'/H'_{\max} = -\left(\sum p_i \log p_i\right) / \log s$$

where p_i is the proportion of individuals at the site belonging to the i^{th} species, and s is the total number of species collected at the site. To ensure conservative estimates of species richness and evenness, provisionally identified individuals were considered to be members of the most common species of that taxon at the site.

We also investigated the relationship between elevation and total herpetofaunal species richness, using species checklists compiled for Monteverde (Van Devender 1980), La Selva, Las Cruces, San José, Cañas/Taboga, Cerro de la Muerte, and the Osa Peninsula (Scott *et al.* 1983). We excluded turtles and crocodylians from these lists, since these species are primarily aquatic and might tend to bias the analyses.

We used linear regression to investigate patterns of herpetofaunal density, species richness, and evenness. We used multiple regression to investigate simultaneously the relationship between our predictor variables (leaf litter depth and elevation), and our dependent variables (herpetofauna density, richness, and evenness). Plot means constituted the independent units of statistical analysis. We used plot means, rather than individual plots as the unit of statistical analysis, since this procedure yields a more conservative statistical test, but still retains sufficient statistical power to identify trends in the data. Partial correlations were used to determine the relative importance of leaf litter depth and elevation, given that both measures were present in the regression model (Draper & Smith 1981). Semi-partial correlations partitioned the total variation due to regression (R^2) into additive components based on the order of entry of the regressor variables,

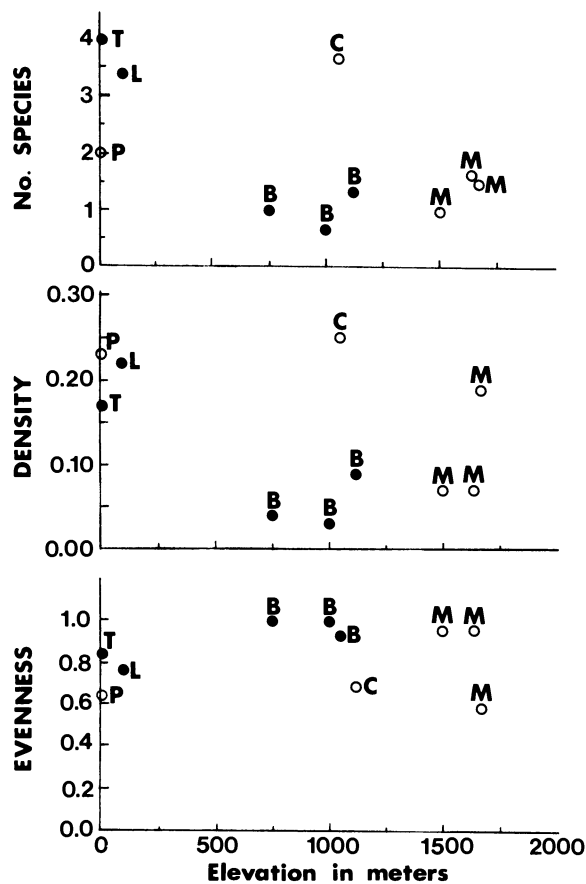
elevation and leaf litter depth, into the model (SAS Institute, Inc. 1982). Elevation was always entered into the regression models before leaf litter depth, since elevational patterns were of primary interest. We first analyzed the entire data set to uncover any broad patterns that might emerge. Then, since we might fail to detect patterns caused by elevational gradients in widescale comparisons across the entire expanse of Costa Rica, we analyzed only the data from 5 sites constituting a true elevational transect (*sensu* Heyer 1967): Tortuguero, Las Vegas, and three sites in the Braulio Carrillo National Park Extension (Fig. 1). All statistical analyses were performed using SAS (SAS Institute, Inc. 1982) maintained at the Triangle Universities Computation Center. The *a priori* level of significance was $\alpha < .05$ for all tests.

RESULTS

Three plots captured most of the litter-dwelling reptiles and amphibians encountered during casual collecting at each locality. At most sites, the rate of encounter of new species declined as the number of plots sampled increased, although this was not true for the two most diverse sites, Las Vegas and Las Cruces (Table 1). Data from the species-rich Las Vegas site demonstrated that three 25 m² plots captured 67 percent of all leaf-litter reptile and amphibian species encountered in ten total plots, and all of the common species (species captured more than once; Table 1). Three plots appeared sufficient to capture most of the commonly encountered litter-dwelling reptiles and amphibians in each local fauna.

Considerable variation existed among sites in the composition of the leaf-litter herpetofauna (Table 2), but frogs of the genus *Eleutherodactylus* were encountered at every site, and various species of *Norops* lizard were common at many sites. Three snakes (*Ninia maculata*, *Trimetopon simile*, and *Geophis* sp. and one salamander (*Bolitoglossa*

FIGURE 1. Species richness, density, and evenness as a function of elevation at ten Costa Rican sites. Site locality abbreviations are as follows: T = Tortuguero, P = Palo Verde, L = Las



Vegas, B = Braulio Carrillo National Park Extension, C = Las Cruces, M = Monteverde. Solid circles denote those sites along the Tortuguero-Braulio Carrillo transect. Regression statistics are as follows for overall patterns (solid and open circles; 1, 8 df): (TOP) $Y = 2.95 - 0.00104X$, $R^2 = .32$, $P < .09$; (MIDDLE) $Y = .186 - 5.66 \times 10^{-5}X$, $R^2 = .19$, $P < .20$; (BOTTOM) $Y = .795 + 4.77 \times 10^{-5}X$, $R^2 = .04$, $P < .58$. Regression statistics for the transect (solid circles only; 1, 3 df): (TOP) $Y = 3.72 - .00276X$, $R^2 = .88$, $P < .02$; (MIDDLE) $Y = .191 - 1.36 \times 10^{-4}X$, $R^2 = .71$, $P < .07$; (BOTTOM) $Y = .830 + 4.77 \times 10^{-5}X$, $R^2 = .03$, $P < .78$.

TABLE 1. Cumulative species-area relations for leaf-litter herpetofauna plots. All plots sampled an area of 25 m².

Locality	Elevation (m)	Plot number									
		1	2	3	4	5	6	7	8	9	10
Palo Verde	3	2	2	3							
Las Vegas	100	4	5	6	6	6	6	6	9	9	9
Braulio Carrillo	750	3	3	3							
Braulio Carrillo	1000	2	2	2							
Braulio Carrillo	1120	2	2	2							
Las Cruces	1050	1	3	9							
Monteverde	1500	0	2	3							
Monteverde	1640	1	4	4							

TABLE 2. Occurrence of leaf-litter reptiles and amphibians at 10 Costa Rican sites. Site locality abbreviations are as follows: T = Tortuguero, P = Palo Verde, L = Las Vegas, B = Braulio Carrillo National Park Extension. C = Las Cruces, M = Monteverde. Site elevations in meters are given in parentheses.

	T (3)	P (3)	L (100)	B (750)	B (1000)	B (1120)	C (1050)	M (1500)	M (1640)	M (1670)
Salamanders										
<i>Bolitoglossa colonnea</i>						1				
Frogs										
<i>Bufo coccifer</i>		3								
<i>Centrolenella</i> sp.							1			
<i>Dendrobates pumilio</i>			21							
<i>Smilisca</i> sp.		1								
<i>Eleutherodactylus altae</i>						1				
<i>E. biporcatus</i>				1						
<i>E. bransfordi</i>	3		16	1	1		2	1	1	
<i>E. longirostris</i>							1			
<i>E. podiciferus</i>							4	6	2	1
<i>E. punctariolus</i>							2			6
<i>E. sp. A</i>	1									
<i>E. sp. B</i>							4			
Unidentified <i>Eleutherodactylus</i>		1								1
<i>Leptodactylus fragilis</i>		12								
Lizards										
<i>Lepidoblepharis xanthostigma</i>	4		5							
<i>Norops humilis</i>	1		7							
<i>N. limifrons</i>			3							
<i>N. tropidolepis</i>								2	1	
<i>N. polylepis</i>							1			
<i>Norops</i> sp.										1
<i>Ameiva festiva</i>	1		1							
<i>Ptychoglossus plicatus</i>							1			
<i>Sphenomorphus cherriei</i>	7									
<i>Mabuya unimarginata</i>			1							
Unidentified scincid			1							
Unidentified gekkonid				1						
Snakes										
<i>Ninia maculata</i>			1							
<i>Trimetopbon simile</i>									1	
<i>Geophis</i> sp.							1			

TABLE 3. Total number of reptile and amphibian species (excluding turtles and crocodylians) at seven Costa Rican sites. Elevations are approximate, and represent the midpoint of elevations in the regions. Checklist data from Van Devender (1980) for Monteverde; all other localities from Scott et al., (1983).

Site	Elevation (m)	Number of species
Cañas/Taboga	80	73
La Selva	100	114
Osa Peninsula	250	112
Las Cruces	1200	71
San José	1200	33
Monteverde	1500	66
Cerro de la Muerte	3200	18

colonnea) were encountered in the total of 912.5 m² of tropical forest floor searched.

OVERALL PATTERNS.—Elevation alone accounted for little of the variation in species richness, evenness, or density at our sites (Fig. 1). Elevation was negatively correlated with species richness, but the relationship was only suggestive ($P = .09$). The rich herpetofauna of the 1050 m Las Cruces site heavily influenced this regression. Elevation was not significantly correlated with either herpetofaunal density or evenness, but the trend was for evenness to increase and density to decrease with increasing elevation.

Analysis of the more comprehensive checklist data revealed a highly significant negative correlation between elevation and the total number of reptile and amphibian

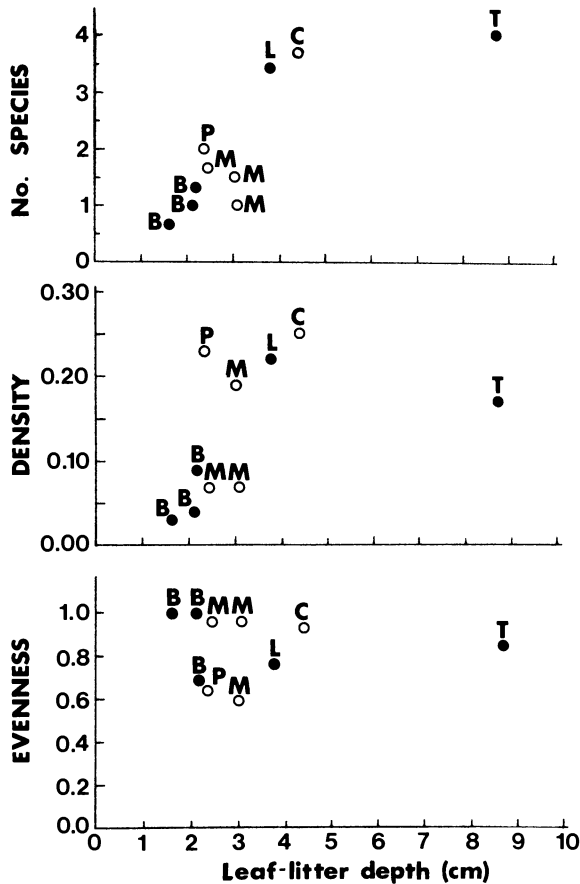


FIGURE 2. Species richness, density, and evenness as a function of leaf litter depth at ten Costa Rican sites. Site abbreviations are the same as in Figure 1. Solid circles denote those sites along the Tortuguero-Braulio Carrillo transect. Regression statistics are as follows for overall patterns (solid and open circles; 1, 8 df): (TOP) $Y = .407 + .477X$, $R^2 = .65$, $P < .005$; (MIDDLE) $Y = .0769 + .0174X$, $R^2 = .18$, $P < .22$; (BOTTOM) $Y = .846 - .00270X$, $R^2 = .001$, $P < .92$. Regression statistics for the transect (solid circles only; 1, 3 df): (TOP) $Y = .412 + .451X$, $R^2 = .77$, $P < .05$; (MIDDLE) $Y = .0436 + .0179X$, $R^2 = .41$, $P < .25$; (BOTTOM) $Y = .897 - .0105X$, $R^2 = .05$, $P < .72$.

species at a site (Table 3). The negative correlation became even more extreme if turtles and crocodilians were included in the data set, since these aquatic forms are primarily found at lower elevations.

Leaf litter depth was highly correlated with herpetofaunal species richness; species richness increased with increasing leaf litter depth (Fig. 2). Leaf litter depth was not significantly correlated with either evenness or herpetofaunal density, although density tended to be positively associated with litter depth. The deep leaf litter and

TABLE 4. Multiple regression of herpetofaunal species richness, density and evenness on elevation and leaf litter depth at ten Costa Rican sites. All correlations are Type I.

Dependent variable	Total R^2	Independent variables	Semi-partial correlation	Partial correlation
Species richness	.70	Elevation	.31	.51
		Litter depth	.39	.56
Density	.26	Elevation	.19	.21
		Litter depth	.07	.08
Evenness	.04	Elevation	.04	.04
		Litter depth	.004	.004

relatively moderate reptile and amphibian densities at Tortuguero considerably reduced the slope of this regression.

Herpetofaunal density and species richness were highly correlated (density = $.0289 + .0529$ species richness, $R^2 = .58$, $P < .01$). Sites with high densities typically had high species richness, while sites with low densities contained few species, as well.

Leaf litter depth was not significantly correlated with elevation ($R^2 = .020$, $P = .09$). A weak trend existed for leaf litter to be deeper at low elevations (litter depth = -1.42×10^{-3} elevation + 4.64), but this trend was heavily influenced by the extremely deep leaf litter found at one lowland site, Tortuguero.

Simultaneous inclusion of litter depth and elevation in a multiple regression model only slightly increased the total variance explained by regression (R^2 , Table 4). Only the regression of litter depth and elevation on species richness was significant. Litter depth explained as much of the total variation as elevation, even though elevation was entered into the model first (semi-partial correlation, Table 4). Analysis of the partial correlations, which indicate the relative contribution of each regressor to the model, given that the effects of the other regressor have already been removed, shows that litter depth contributes most to the observed correlation (Table 4).

ELEVATIONAL GRADIENTS.—Widescale comparisons across the range of habitats in an entire country may fail to detect patterns caused by elevational gradients if the magnitude of the gradient varies in different regions. For example, consider two regions where density increases with increasing elevation: in region one, the increase is moderate; in region two, the increase is much more substantial. If one sampled mainly high elevation sites in region one, and predominately low elevation sites in region two, then one might mistakenly infer that density is independent of elevation (or is negatively correlated with elevation) when in fact just the opposite is true. Thus, elevational effects may only be apparent in samples taken along a single

TABLE 5. Multiple regression of herpetofaunal species richness, density and evenness on leaf litter depth and elevation at five sites on the Tortuguero-Braulio Carrillo transect, Costa Rica. All correlations are Type I.

Dependent variable	Total R ²	Independent variables	Semi-partial correlation	Partial correlation
Species richness	.92	Elevation	.88	.92
		Litter depth	.04	.32
Density	.72	Elevation	.71	.72
		Litter depth	.01	.02
Evenness	.05	Elevation	.03	.03
		Litter depth	.02	.02

elevational transect (*sensu* Heyer 1967). Five sites, from Tortuguero (3 m) on the Atlantic Coast, westward through the Sarapiquí coastal plain to the Las Vegas site (100 m), and upward into the three Braulio Carrillo sites (750, 1000, and 1120 m) represent such an elevational transect.

Elevation accounted for substantial amounts of the variation in species richness and density, but not evenness ($R^2 = .88, .71, \text{ and } .03$, respectively; Fig. 1: closed circles) along the elevational gradient. Elevation was significantly negatively correlated with species richness ($P < .02$). While not significantly correlated with evenness, the negative correlation with herpetofaunal density ($P = .07$) suggests a strong tendency for densities of reptiles and amphibians to decline at higher elevations (Fig. 1: closed circles).

Leaf litter depth accounted for moderate amounts of variation in species richness and density, but not evenness ($R^2 = .77, .41, \text{ and } .05$, respectively; Fig. 2: closed circles). Only the regression of species richness on leaf litter depth was statistically significant. Leaf litter depth was negatively associated with evenness, and positively associated with herpetofaunal density (Fig. 2: closed circles).

Reptile and amphibian densities were highly correlated with species richness (density = $5.000 \times 10^{-3} + .051$ species richness, $R^2 = .86, P < .02$). Sites with the highest herpetofaunal densities were also the most species-rich sites along the elevational transect.

Leaf litter depth declined exponentially with increasing elevation across the elevational transect. In a log-linear model, elevation explained 98 percent of the variation in leaf-litter depth, and the regression was highly significant (litter depth = $9.75 - 2.65 \log \text{ elevation}; P < .001$). Simultaneous inclusion of litter depth and elevation in a linear multiple regression model only slightly increased the total variance explained by regression for each dependent variable (Table 5). None of the regressions were statistically significant, although the multiple regression of species richness on elevation and leaf-litter depth verged on significance ($P = .08$). Because of the high correlation between elevation and leaf-litter depth, elevation explained

the greatest amount of the variation, as measured by semi-partial correlations (Table 5). This is to be expected, since elevation was the first variable entered into each model. In contrast to the analysis of the full data set, partial correlations indicated that leaf-litter depth contributes little to the observed correlations across the elevational transect (Table 5).

DISCUSSION

Diversity is composed of two elements: species richness and equitability. Species richness is simply the number of species in a fauna, while equitability represents some measure of the evenness of their distribution. Several studies (Brown & Alcalá 1961, Scott 1976, Heatwole 1982, Duellman & Trueb 1986, as well as ours) have demonstrated that herpetofaunal species richness declines with increasing elevation in the tropics. In the Philippines, this decline is primarily caused by a decrease in the number of lizard species at higher elevations (Brown & Alcalá 1961). In Costa Rica, the decline in the number of frog species with increasing elevation is coupled with a concomitant decline in the number of lizard species. Non-anoline lizards in particular seem to be restricted to lower elevations (Table 2), perhaps because of an inability to withstand the thermal stresses encountered at higher elevations (Janzen 1967, Spellerberg 1972). Biogeographic factors may also be responsible for this trend: most upland Costa Rican reptiles and amphibians are representatives of an endemic montane herpetofauna, and invasion of the Costa Rican highlands by lowland faunal elements is restricted to only a few species (Savage 1982, Duellman 1970, Pringle *et al.* 1984).

Similarly, species richness increased rapidly with an increase in leaf litter depth, as did herpetofaunal density. Deeper leaf litter may provide a wider range of microhabitats, allowing more individuals and more species to coexist in the litter microhabitat. Lieberman (1986) speculated that the microhylid frog *Gastrophryne pictiventris* may be a habitat specialist at La Selva, remaining burrowed under the leaf litter by day, and emerging at night to prey upon ants. Deeper leaf litter may also provide a refuge from predation, especially for the non-toxic, diurnal frogs of the genus *Eleutherodactylus*, which dive beneath the litter when disturbed (Lieberman 1986). Deeper leaf litter may also support more numerous and diverse arthropod prey populations (Lieberman & Dock 1982), thus facilitating the coexistence of a both more abundant and more diverse herpetofauna. Leaf-litter herpetofaunas are generally more abundant when litter arthropods are also abundant (Lieberman 1986), and many tropical frog species are thought to coexist via feeding specializations (Toft 1980a, Lieberman 1986, but see also Toft 1980b).

Leaf litter depth and elevation were poor predictors of equitability, as measured by J' of Pielou (1969). In

contrast to previous studies of tropical (Scott 1976, Duellman 1978, Lieberman 1986) and temperate amphibians (Bennett *et al.* 1980) evenness varied greatly from site to site. This variability in evenness may be a real pattern, or a consequence of the relatively small fraction of the total herpetofauna that we sampled in our plots. At most but not all sites, however, one or two species were clearly dominant (Table 2). Unlike the example of tropical trees (Janzen 1970), the tropical herpetofauna seems to be composed of a few very common species, along with a large number of comparatively rare species (Lieberman 1986).

Our results concur with previous studies which found the density of leaf-litter reptiles and amphibians to be high in the Neotropics (Scott 1976, Inger 1980b, Lieberman 1986). The available evidence indicates herpetofaunal abundance is greater in the Neotropics than in Southeast Asia. This pattern appears to be general, since it is independent of season, year, locality, or microhabitat sampled (Heatwole & Sexton 1966; Scott 1976; Inger 1980a, b, Lieberman 1986; this study). The exact mechanism underlying this difference remains a subject of debate (May 1980). Scott (1976) dismissed differences in species richness, predatory snake abundance, and forest structure as causal mechanisms, and suggested that the greater abundance of Neotropical reptiles and amphibians may be a function of greater litter fall and faster decomposition rates in Neotropical forests. Inger (1980a) found no difference between forests in litter accumulation, and suggested the mast-fruiting habit of dipterocarp-dominated Asian forests may severely limit herpetofaunal abundances by decreasing the abundance of arthropod prey during non-mast years.

We failed to find evidence of an increase in herpetofaunal density with elevation, a widely-cited pattern of tropical herpetofaunal abundance (Brown & Alcalá 1961, Scott 1976, Heatwole 1982, Duellman & Trueb 1986). In fact, our data suggest the opposite: that the density of the Costa Rican leaf-litter herpetofauna declines with elevation, at least through the mid-elevation sites we sampled. For example, on the Caribbean coast of Costa Rica, a 1000 m increase in elevation results in a 71 percent decrease in herpetofaunal density (Fig. 1). Despite limited statistical power, the regression is nearly significant ($P < .07$).

We also failed to find evidence of an inverse correlation between herpetofaunal density and species richness, as suggested by Scott (1976). There was no evidence of an increase in abundance of the common species at depauperate sites (Brown & Alcalá 1961, Scott 1976). In fact, herpetofauna density was strongly positively correlated with species richness across our ten study sites. Lieberman (1986) also found a high positive within-site correlation between herpetofaunal density and species richness at her La Selva sites.

Our results clearly conflict with those of Scott (1976), who concluded that herpetofaunal abundance increased with elevation in Costa Rica, primarily because the density of common species increased greatly as species richness declined at higher elevations. Scott's (1976) analysis was based upon exhaustive sampling of replicate plots, but only three sites were sampled. The sites did not constitute an elevational transect (*sensu* Heyer 1967), and site and year effects were confounded, since different sites were sampled in different years. The differences in herpetofaunal abundance observed by Scott (1976) may be caused by site effects, or site by year interactions, rather than elevational differences. Las Cruces (=San Vito of Scott 1976), in particular, has an extremely dense and diverse leaf-litter herpetofauna for its elevation (Tables 2 & 3).

Several general patterns of abundance and diversity of the Costa Rican leaf-litter herpetofauna have been documented. Species richness and herpetofaunal density both increased with leaf-litter depth, and declined at higher elevations. Species-rich sites also had high densities, yielding a positive correlation between herpetofaunal richness and abundance. Greater faunal diversity at lower elevations may be a general pattern among inhabitants of tropical forest litter; Colwell (1969) found leaf-litter arthropods both more numerous and more diverse at lower elevations in Costa Rica. It should be possible to formulate testable hypotheses (*e.g.*, May 1980) to distinguish between alternative explanations for the observed patterns of tropical leaf-litter herpetofaunal diversity. Tests of many of these hypotheses will necessitate sampling many members of the leaf-litter community, including arthropods, onychophorans, birds, and mammals, as well as the herpetofauna itself (Scott 1976, May 1980).

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LITERATURE CITED

- BENNETT, S. H., J. W. GIBBONS, AND J. GLANVILLE. 1980. Terrestrial activity, abundance and diversity of amphibians in differently managed forest types. *Amer. Midl. Nat.* 103: 412-416.
- BROWN, W. C., AND A. C. ALCALA. 1961. Populations of amphibians and reptiles in the submontane and montane forests of Cuernos de Negros, Philippine Islands. *Ecology* 42: 628-636.
- CARR, A. III. 1982. Tropical forest conservation and estuarine ecology. *Biol. Conserv.* 23: 247-259.
- COLWELL, R. K. 1969. Ecological specialization and species diversity of tropical and temperate arthropods. Ph.D. Dissertation, The University of Michigan. 79 pp.
- DRAPER, N. R., AND H. SMITH. 1981. Applied regression analysis. John Wiley & Sons, New York, pp. 265-266.
- DUELLMAN, W. E. 1970. The hylid frogs of Middle America. *Monogr. Mus. Nat. Hist. Univ. Kansas* 1: 1-753.
- . 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. *Misc. Publ. Mus. Nat. Hist. Univ. Kansas* 65: 1-352.
- , AND L. TRUEB. 1986. Biology of amphibians. McGraw-Hill Book Company, New York.
- HARTSHORN, G. S. 1983. Plants. *In* D. H. Janzen (Ed.). Costa Rican natural history, pp. 125-144. The University of Chicago Press, Chicago.
- HEATWOLE, H. 1982. A review of structuring in herpetofaunal assemblages. *In* N. J. Scott, Jr. (Ed.). Herpetological communities: a symposium of the Society for the Study of Amphibians and Reptiles and The Herpetologists' League, August, 1977, pp. 1-19. U.S. Fish & Wildlife Res. Report No. 13.
- , AND O. J. SEXTON. 1966. Herpetofaunal comparisons between two climatic zones in Panama. *Am. Midl. Nat.* 75: 45-60.
- HEYER, W. R. 1967. A herpetofaunal study of an ecological transect through the Cordillera de Tilaran, Costa Rica. *Copeia* 1967: 259-271.
- , AND K. A. BERVEN. 1973. Species diversities of herpetofaunal samples from similar microhabitats at two tropical sites. *Ecology* 54: 642-645.
- HOLDRIDGE, L. R., W. C. GRENKE, W. H. HATHEWAY, T. LIANG, AND J. A. TOSI, JR. 1971. Forest environments in tropical life zones: a pilot study. Pergamon Press, New York.
- INGER, R. F. 1980a. Relative abundances of frogs and lizards in forests of Southeast Asia. *Biotropica* 12: 14-22.
- . 1980b. Densities of floor-dwelling frogs and lizards in lowland forests of Southeast Asia and Central America. *Am. Nat.* 115: 761-770.
- JANZEN, D. H. 1967. Why mountain passes are higher in the tropics. *Am. Nat.* 101: 233-249.
- . 1970. Herbivores and the number of tree species in the tropics. *Am. Nat.* 104: 501-528.
- LIEBERMAN, S. S. 1982. The ecology of the leaf litter herpetofauna of a Neotropical rain forest: La Selva, Costa Rica. Ph.D. Dissertation, University of Southern California.
- . 1986. Ecology of the leaf litter herpetofauna of a neotropical rain forest: La Selva, Costa Rica. *Acta Zool. Mex.* (ns) 15: 1-72.
- , AND C. F. DOCK. 1982. Analysis of the leaf litter arthropod fauna of a lowland evergreen forest site (La Selva, Costa Rica). *Rev. Biol. Trop.* 30: 27-34.
- LLOYD, M., R. F. INGER, AND F. W. KING. 1968. On the diversity of reptile and amphibian species in a Bornean rain forest. *Am. Nat.* 102: 497-515.
- MAY, R. M. 1980. Why are there fewer frogs and lizards in Southeast Asia than in Central America? *Nature* 287: 105.
- PIELOU, E. C. 1969. An introduction to mathematical ecology. Wiley-Interscience, New York.
- PRINGLE, C., I. CHACON, M. GRAYUM, H. GREENE, G. HARTSHORN, G. SCHATZ, G. STILES, C. GOMEZ, AND M. RODRIGUEZ. 1984. Natural history observations and ecological evaluation of the La Selva Protection Zone, Costa Rica. *Brenesia* 22: 189-206.
- SAS INSTITUTE INC. 1982. SAS user's guide: statistics. Cary, North Carolina.
- SAVAGE, J. M. 1980. A handlist with preliminary keys to the herpetofauna of Costa Rica. Allan Hancock Foundation, University of Southern California, Los Angeles, California. 111 pp.
- . 1982. The enigma of the Central American herpetofauna: dispersals or vicariance? *Ann. Missouri Bot. Gard.* 69: 464-547.
- SCOTT, N. J. 1976. The abundance and diversity of the herpetofaunas of tropical forest litter. *Biotropica* 8: 41-58.
- . 1982. The herpetofauna of forest litter plots from Cameroon, Africa. *In* N. J. Scott, Jr. (Ed.). Herpetological communities: a symposium of the Society for the Study of Amphibians and Reptiles and The Herpetologists' League, August, 1977, pp. 145-150. U.S. Fish & Wildlife Res. Report No. 13.
- , J. M. SAVAGE, AND D. C. ROBINSON. 1983. Checklist of reptiles and amphibians. *In* D. H. Janzen (Ed.). Costa Rican natural history, pp. 367-374. The University of Chicago Press, Chicago.
- SLOWINSKI, J. B., B. I. CROTHER, AND J. E. FAUTH. 1988. Diel differences in leaf-litter abundances of several species of reptiles and amphibians in an abandoned cacao grove in Costa Rica. *Rev. Biol. Tropical* 35: 349-350.
- SPELLERBERG, I. F. 1972. Thermal ecology of allopatric lizards (*Sphenomorphus*) in southeast Australia. I. The environment and lizard critical temperatures. *Oecologia (Berl.)* 9: 371-383.
- TOFT, C. A. 1980a. Feeding ecology of thirteen syntopic species of anurans in a seasonal tropical environment. *Oecologia (Berl.)* 45: 131-141.
- . 1980b. Seasonal variation in populations of Panamanian litter frogs and their prey: a comparison of wetter and drier sites. *Oecologia (Berl.)* 47: 34-38.
- VAN DEVENDER, R. W. 1980. Preliminary checklist of the herpetofauna of Monteverde, Puntarenas Province, Costa Rica and vicinity. *Brenesia* 17: 319-326.
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