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# Herpetofaunal diversity trends across disturbance levels in a Neotropical montane forest, Costa Rica

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## Abstract

Site-based differences in diversity within a single area ( $\beta$ -diversity) reveal unique ecological trends that can inform logistics of protected area delineation, resource management, and conservation of sensitive species. Particularly understudied is the role of anthropogenic—especially pastoral and agricultural—disturbance in herpetofaunal  $\beta$ -diversity, especially in Neotropical cloud forest communities where even general knowledge on specific-, generic-, and familial-level physiology and ecological interactions is highly limited. The influence of disturbance level, measured by forest age, on three diversity measures (richness, evenness, and composition) of the herpetofaunal community were tested at Cloudbridge Nature Reserve, a contiguous protected region of humid Talamancan montane forest at 1600m (5000ft) elevation bordering Chirripó National Park in Pérez Zeledón district, San José Province, southern Costa Rica. The total surveyed herpetofauna consisted of 16 squamate (5 Lacertilia, 11 Serpentes) and 6 lissamphibian (5 Anura, 1 Urodela) species. While species richness did not differ between disturbance levels, old-growth forest exhibited higher species evenness relative to secondary growth ( $t=17.34$ ,  $p<.05$ ); moreover, site-based segregation of two *Geophis* sp. suggests compositional differences across disturbance levels ( $t=5.20$ ,  $p<.001$ ). The findings suggest niche partitioning may be more developed in old-growth communities, and that a decline in old-growth specialists with increasing disturbance causes a reduction in evenness.

## Introduction

In ecological science, species diversity is far too often operationalized without attention to its component parts, the nature of which may vary heterogeneously within a single area. Diversity is commonly treated as synonymous with *species richness*, the total number of species belong to a given taxonomic group in a focus area. However, a sole emphasis on richness discounts the influence of abundance. For instance, an area in the tropical Andes may boast 30 species of Anurans, yet 50% of those represented species may be common only in very specific sites, and 20% may be so rare that they face local extinction. Moreover, sites of high species richness may be those in which uncommon species are especially rare, or vice-versa. As such, the concept of *species evenness* (or simply “equitability”) grants a level of specificity to diversity-focused research that is invaluable for conservation initiatives, by explaining the percentage of a

given community’s individuals that are represented by each species. Perhaps nowhere is this form of analysis more relevant than in landscapes which are undergoing, or have previously undergone, significant anthropogenic disturbance. In the Neotropics, especially in areas of high endemism like the tropical Andes, conservation decisions and protected area management must increasingly be made in the context of partially degraded buffer zones, compromises with low-intensity resource extraction (i.e. mixed silviculture), and regenerating areas under recent protection. As such, understanding the spatial heterogeneity of diversity’s two principal components—richness and evenness—in the context of disturbance is the focus of this study. The study’s focus on herpetofauna is based on the reality that Neotropical reptile and amphibian taxa are both poorly studied and at high risk of population declines and regional extinctions, as the drastic effects of

chytridiomycosis on anuran (and subsequently squamate) populations has made all too clear.

## Theoretical Framework

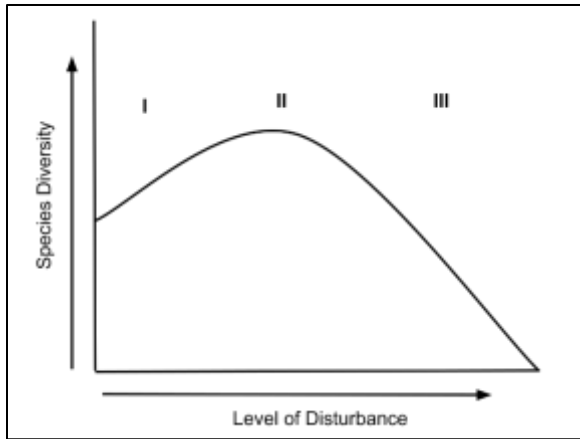
Research on diversity and disturbance has generally found that species richness increases at intermediate disturbance and decreases where disturbance is maximally low or high (Mackie & Currie 2001); this trend has been established for some vertebrate communities in tropical forests (Bongers et al. 2009) and is termed the “diversity-disturbance curve”. The relationship between evenness specifically and disturbance level is less clear. Biswas & Mallik (2011) found that in a Canadian boreal forest, riparian habitat was lower in vascular floral evenness relative to uplands, possibly a function of the greater disturbance level in the former ecotype; however, *within* riparian zones, the most-disturbed areas tended to exhibit higher floral evenness. The relationship between evenness and disturbance level is especially poorly understood for herpetofauna. Groen (2013) found that in a Caribbean lowland forest in Costa Rica, herpetofaunal evenness was higher in older-growth forest compared to secondary stands. Similarly, greater canopy cover (possibly a factor of disturbance level, as older-growth forests tend to have more developed canopies) predicted higher herpetofaunal evenness in a northeastern U.S. forest (Degraaf & Rudis 1990).

The relationship between richness and evenness has, on the other hand, been slightly better studied. The two diversity components have tended to either covary positively or be uncorrelated. A meta-analysis of 229 datasets of aquatic ecosystems by Soiminen, Passy & Hillebrand (2012) found only 31% of sets showing any correlation between species richness and evenness; of these, however, a slight majority (61%) revealed a positive trend. Another meta-analysis across five terrestrial taxonomic

groups found positive correlations between richness and evenness (Supp & Ernest 2014). For herpetofauna specifically, studies have likewise resulted in positive or nonexistent correlations. Fauth, Crother & Slowinski (1989) found that both richness and evenness increased along elevational and leaf-litter gradients across 10 Costa Rican sites, though at vastly different rates (evenness increase rate was less than that for richness). Similarly, Degraaf & Rudis (1990) found that herpetofaunal richness and evenness increased together with habitat type, with both being highest in uplands and lowest in riparian stands. Bock, Jones & Bock (2007) did not, however, find any richness-evenness correlations in the herpetofaunal community of a southwestern U.S. savanna.

Trivariate relationships between richness, evenness, and disturbance intensity have largely been explored only for vascular plant communities; however, these studies possibly reveal higher ecological trends that may well prove analogous in animal taxa. A Nepalese montane forest studied by Chapagain et al. (2021) exhibited a concomitant increase in both tree species richness and evenness with decreasing disturbance intensity. The same trend was found in an Indian lowland forest by Malik et al. (2014), where lower disturbance intensity predicted increases in both species richness and evenness. In a Chinese montane forest, Zhang et al. (2013) found a closer conformation to the aforementioned “diversity-disturbance curve” in that both vascular floral richness and evenness peaked at intermediate disturbance levels, decreasing at higher and lower intensities. All three studies suggest that initially, the ecological transition out of heavy disturbance is characterized by increases in both species richness and evenness, at least for vascular plants. Only two studies have clearly targeted richness-evenness trends along disturbance gradients for herpetofauna, and both yielded opposite trends. In a south Mexican montane

forest, Luja et al. (2017) found that richness and evenness both increased with increasing disturbance level. Vonesh's (2001) study of Ugandan mid-elevation and lowland forests, however, found an inverse relationship between herpetofaunal richness and evenness: species richness *increased* while evenness *decreased* with greater disturbance intensity. Both studies did, however, align in that herpetofaunal richness did increase as disturbance increased in intensity.



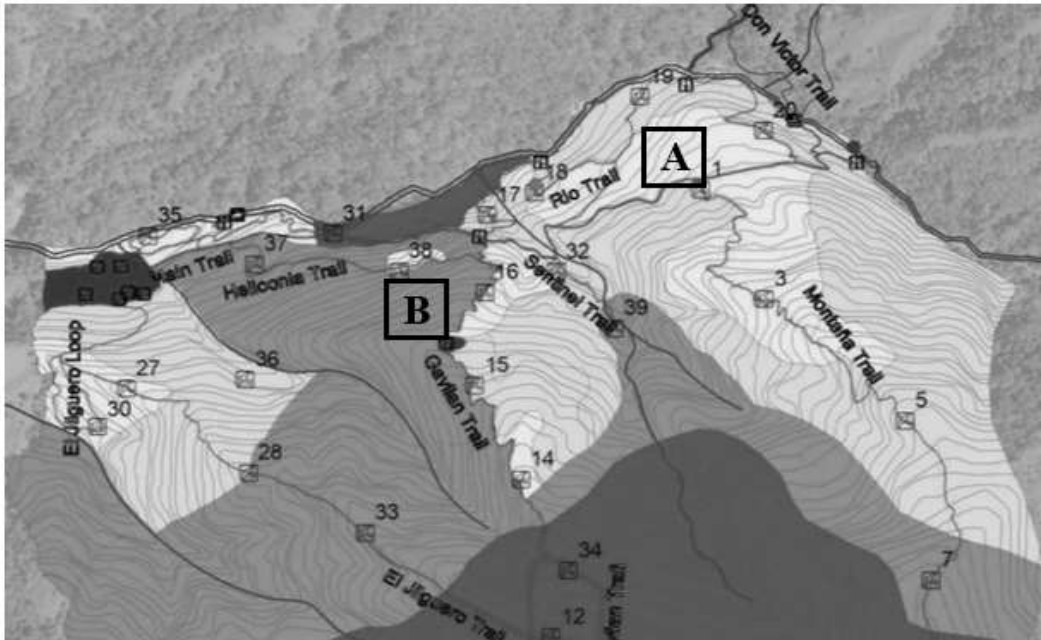
**Figure 1.** The Diversity-Disturbance Curve (DDC).

It is clear from results of bi- and trivariate studies of richness, evenness, and disturbance intensity that a better understanding of these ecological patterns is warranted, given their centrality to conserving herpetofaunal populations in the Neotropics, especially in cloud forest communities. The following 6-week study was undertaken in the southern Pacific highlands of Costa Rica where the relationship between herpetofaunal richness, herpetofaunal evenness, and disturbance level (measured as forest age since clearing) was closely monitored. The squamate and anuran community of the area was representative of the high-elevation Pacific-slope assemblage of the Talamanca Montane Forests ecoregion. While the herpetofauna of this ecoregion is not of particular conservation concern (due to almost 40% of its land area protected by Chirripó and La Amistad National Park,

respectively), it bears great similarity in climate and functional diversity with severely threatened ecoregions in the tropical Andes and the sky islands of northern Central America (Bullock et al. 2020; Redo et al. 2012; Hamilton 1995; Mutke et al. 2017). As such, it is the hope of the author that the results of this study may inform conservation decisions in analogous Neotropical regions, specifically those under much greater anthropogenic stress.

### Site Description

Two quadrants in Cloudbridge Nature Reserve were selected for comparison of the herpetofaunal community; these differed principally in forest age. While disturbance gradients exist within the reserve, the general layout corresponds to 20-year-old secondary forest below, and >80-year-old old-growth forest above, about 1700m (5577ft). The younger forest was before 2002 a contiguous area of *restinga* pasture which has since been left in a secondary successional state. The elevational transition line between younger and older forest on the reserve is, however, highly variable, allowing for altitudinal controls in disturbance-centric comparisons. The two selected 0.4km<sup>2</sup> quadrants (Figure 2) differed only by 48m (160ft) in average elevation, though their respective forest ages differed by at least 60 years. Topographic relief was very similar between quadrants, as both contained a 35-50° grade with 0-10° upper and lower edges, such that each quadrant consisted of approximately 60% slope with 42.5° average grade and 40% relatively flat terrain. Each quadrant was bisected by a stream of approximately 0.5m average width; both of



**Figure 2.** Map of Cloudbridge Nature Reserve with secondary forest light-colored, old-growth forest medium grey, and primary forest dark grey. [A] and [B] denote boundaries of 0.4km<sup>2</sup> study quadrants.

these drain north into the Rio Chirripó Pacífico.

Temperature, rainfall, and humidity measurements were not taken; however, it is assumed that given the quadrants' strong elevational and topographic similarity and the mere 0.5km distance between quadrant midpoints, differences in these measures are either wholly negligible or a redundant proxy for forest age. Under Köppen-Geiger classification, Cloudbridge Nature Reserve conforms largely to a Monsoon-influenced temperate oceanic climate (Cwb: temperate, dry winter, warm summer); during the dry season (*verano*) from mid-December to early May, nocturnal temperatures typically range from 15-20°C (59-68°F) and diurnal temperatures from 22-28°C (72-82°F). As such, nights are cool to cold and days are generally warm, depending on extent of cloud cover. Rainfall during the dry season is minimal and was sparse during the study period.

## Hypotheses and Rationale

Attempting to predict how richness and evenness trend with disturbance level is difficult because previous studies have shown conflicting trends. However, the diversity-disturbance curve (DDC) has been upheld by many studies (Mackie & Currie 2001; Bongers et al. 2009), which reveal an increase in species richness at intermediate disturbance and concomitant decreases at extremes of low and high disturbance. As such, if any conclusions are to be taken from the literature, it is hypothesized that the study would find lower species richness in the 20-year-old secondary forest and higher richness in the >80 year old-growth forest; because the old-growth forest being studied is not representative of “maximal” or very high maturation, it likely represents a successional state at or just beyond the DDC “hump”.

It should be noted, however, that DDC trends are mostly based strictly on richness and often do not account for

whether evenness follows the same pattern. In order to hypothesize species evenness trends, a theoretical approach is more appropriate. Old-growth forests are ecologically more ancient environments, not merely in a restricted temporal sense but also in the broader sense that old-growth forests may have existed longer than, and in a more stable and widespread state, than secondary forests across evolutionary time.

The sporadic occurrence of large tracts of secondary growth (i.e. results of landslides or fires, which are uncommon in Neotropical moist forests) coupled with their relatively rapid maturation rate suggest that the opportunity for biotic specialization for this habitat type (or its microhabitats) has been relatively limited, at least compared to mature forest counterparts. While treefalls do continuously create small patches of early-successional-state forest within a surrounding environment of mature growth, the majority of biota that have specialized in these microhabitats (“gap specialists”) appear to be flora, which may have an advantage in this regard by having the ability to distribute their gametes widely through the seed bank in a forest, the seeds lying dormant for long and then emerging when gap conditions happen to be met. There is less evidence of strong gap-specific specialization in vertebrate animals such as herpetofauna, for which the selective bottleneck for specializing in small gaps is likely much higher simply because of the differential logistics of gamete dispersal relative to flora, and the difficulty of deriving sufficient, consistent energy from gap services.

As such, Neotropical secondary forests may have over evolutionary history been largely occupied by a larger number of generalist species than specialists. On the other hand, the more ancient old-growth forest biota would be expected to have undergone extensive niche differentiation, permitted by the stability and wider distribution of older forests; these habitats

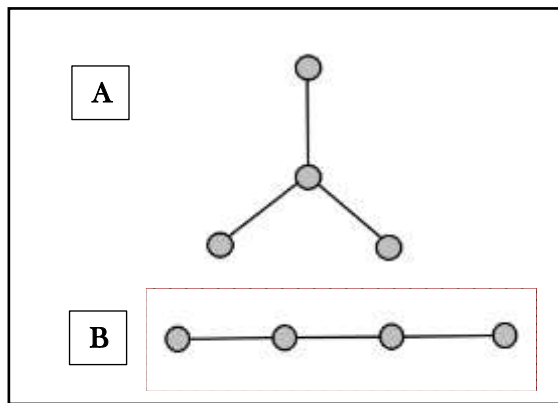
probably harbor a higher number of ecological specialists relative to generalists. The populations of those old-growth specialists that do utilize secondary forest would be expected to have a lower carrying capacity than old-growth specialists in old-growth and generalists in young-growth, respectively. As such, a secondary forest dominated by a few abundant generalists but with many low-abundance specialist species is likely *lower* in evenness than an old-growth forest dominated by a large quantity of specialist species of similar abundance, irrespective of generalists. (Decreases in generalist abundance likely have a lower impact on total evenness measure than decreases in specialist abundance, given how many more specialists there are than generalists in an ecosystem.) One would therefore expect evenness to decrease with disturbance level.

Like richness, evenness may well follow the DDC and thus begin to decrease at very high levels of maturation not tested in the study. However, this is not intuitive according to the logic previously laid out, since increasing maturation reduces the unpredictability of resource availability provided by disturbance events and disturbed states, thus further selecting *against* generalists and *for* specialists, which require predictability. We would then expect an extremely mature forest to be even lower in evenness since its generalists would be even less abundant. However, the possible extirpation of generalists in such a late stage of maturation would then *increase* the evenness rating of a given site, as it would then be composed only of specialists with relatively even abundances. Or, conversely, the processes of late-stage maturation in tropical forests may include the diminution of certain microhabitats to which some specialists are adapted, reducing abundance of some specialists and thus reducing overall evenness. These latter two scenarios represent evenness mirroring richness trends

across the entirety of the hump-shaped DDC curve.

## Methods

**Experiment setup.**—Two 0.4km<sup>2</sup> sections of forest at Cloudbridge Nature Reserve were selected for comparison. Selection was based on forest age, with one quadrant (Quadrant A) covering 20-year-old secondary forest and the other (Quadrant B) covering >80-year-old old-growth forest. Quadrants were selected such that other factors—primarily elevation, topography, and moisture—could be held constant as effectively as possible. For more information on site selection and features, see Site Description (p. 3).



**Figure 3.** Orientation of Y-trap [A] and line-trap [B]. Circles represent placement of buckets; lines represent tarp fence. Fence segments are 15m.

In each quadrant, two pitfall traps were constructed at randomly-selected locations (randomized GPS-marked selections were repeated until they landed on terrain suitable for trap construction). Following design recommendations for herpetological surveys from the U.S. Department of the Interior (Fisher et al. 2008) and influenced by the author’s previous experience in pitfall trap construction in Peru, each trap consisted of “fence” segments of 10 wooden stakes (harvested from banana plants outside the quadrant) upholding 15m of 1.5m-high

plastic rain tarp. Of the two traps in each quadrant, one was constructed as a Y-trap and the other as a line-trap. Both traps used the same number of materials but were arranged in a different configuration. Both were formed from three of the 15m-long fence segments: in the Y-trap, the three segments radiated outward from a midpoint, while in the line trap, the three segments were arranged in a single line. The result for each trap was 45m of tarp fencing upheld by 30 stakes. Each trap had four 5-gallon buckets (38cm tall x 32cm diameter) buried flush with the ground surface at the end of each fence segment. In this way, the Y-trap had one bucket in the center where all three fences converged, and one on each outer end of the three segments; the line-trap had one bucket on each end of the entire three-segment line, and two buckets between where the segments meet. The tarps were fastened to the stakes using zip ties, the bottom of the tarp was buried 5cm into the soil, and fences ended directly where buckets began. This ensured that any fauna that crossed the fences would be unable to dig underneath, climb over, or skirt around the ends of the traps.

**Sampling methods.**—Quadrants were sampled via transect surveys and routine checking of pitfall traps. From 3 Jan to 20 Feb 2022, traps were checked twice every 48 hours; any specimens caught were identified to species level and then released 6m from the bucket in which they were captured, in the opposite direction of the trap. The bases of buckets were lined with leaf litter and collected moisture, providing an acceptable temporary environment for specimens.

Walking transects occurred twice daily, alternating between quadrants by day. As such, one day would consist of a late morning survey (9:00am-12:00pm) and a night survey (7:00pm-10:00pm) both in Quadrant A, with the same schedule repeated the next day but for Quadrant B.

These time increments were selected to ensure that sampling would cover the range of activity patterns of the region's herpetofauna, targeting the pre-midday warming period favored by diurnal species and the early night period favored by nocturnal species. For each quadrant, two transects were selected by connecting three randomly-generated GPS coordinates and approximating them in the field to a walkable path. The order of walking the two paths in each quadrant was alternated by survey day; for instance, on day X1 transect T1 would be walked for the morning survey and T2 would be walked for the night survey, while on day X3 transect T2 would be walked for the morning and T1 for the night. This ensured there would be no pairing between factors of survey time and transect number.

Transects typically consisted of the author and two to three volunteers; each volunteer was tasked with observing a certain part of the visual field (i.e. leaf litter and understory to the right of the path). Species detected were identified to species level; capture was only undertaken for colubrid snakes and for those species (i.e. *Craugastor* anurans) where close inspection was required for identification purposes.

**Statistical methods.**—Differences in richness and evenness between quadrants were analyzed using the equal-variance *t*-test, and by obtaining the Simpson's and Shannon Diversity Indices, respectively, of each quadrant. The *t*-test measured differences in average weekly richness and evenness and thus allowed for an understanding of whether trends held constant over time via the formula

$$t = \frac{x_1 - x_2}{\sqrt{\frac{(n_1 - 1)s_1^2 + (n_2 - 1)s_2^2}{(n_1 + n_2 - 2)} \left(\frac{1}{n_1} + \frac{1}{n_2}\right)}}$$

where  $n$  = the total number of individuals,  $s$  = the number of time increments, and  $x_1 - x_2$  = differences in means between quadrants. In testing richness,  $x_1 - x_2$  represents the *difference in average number of species detected per week* between Quadrants 1 and 2. In testing evenness,  $x_1 - x_2$  represents the difference in the *weekly average number of individuals not belonging to the two most common species in their respective quadrants*.

Evenness was also tested using Simpson and Shannon-Wiener diversity indices, respectively. Simpson's index accounts for evenness using

$$D = 1 - \sum_{i=1}^n \left(\frac{n_i}{N}\right)^2$$

where  $n$  represents the number of individuals represented by a species  $i$ , and  $N$  represents the total number of all individuals in the sampled community.  $D$  ranges in value from 0 (zero species) to 1 (maximal equitability). The Shannon-Wiener index uses a different approach to calculate evenness in the context of richness with the formula

$$H = - \sum_{i=1}^s p_i (\ln p_i)$$

where  $p$  is the proportion of individuals represented by species  $i$ , and  $s$  is the total number of all species in the community. The value of  $H$  scales from zero to infinite; as such, there is no "maximal diversity" value in the Shannon-Wiener index.

The use of diversity indices serves as a reinforcement or counterpoint to the temporally incremented initial analysis. Though they do not measure the possibility of changes in community diversity trends over time, they operationalize evenness differently. Overreliance on a single measure of evenness as "proportion of species not

pertaining to the two most common species in the community” could obscure the detection of scenarios in which more than two species are extremely abundant and other species are rare—a case of actual low evenness which would be interpreted as high evenness under the metric used in the *t*-test. Convergence in significance along all three methods of analysis would suggest that across different operational approaches, evenness broadly differs between the quadrants.

## Results

21 species of reptile and amphibian were detected during the six weeks of survey; 15 (71.4%) of these were squamates, 4 (19%) were anurans, and 1 (4.8%) was an urodelan (Table 1). Of the squamates, 5 (33.3%) were lizards and 10 (66.6%) were snakes. Quadrant B had 3 more species (17 sp.) than Quadrant A (14 sp.). Quadrant B had 17% more species than Quadrant A and 33% more site-unique species than Quadrant A: Quadrant A had 4 unique species (28.5% of quadrant total) and Quadrant B had 6 (35.3% of quadrant total). 10 species (47.6% of total) were found to inhabit both quadrants.

The most numerically abundant species was the anuran *Craugastor crassidigitus*, which made up 46.8% of the herpetofaunal population in Quadrant A and 12.7% in Quadrant B. However, in Quadrant B, the congener *C. podiciferus* was equally abundant. Though all 5 detected species of anurans occurred at both sites, total anuran abundance was about 2.4 times higher in Quadrant A. *Anolis* lizard diversity was higher in Quadrant B, however, and total *Anolis* abundance was about 2.5 times higher in Quadrant B. Snake abundance and diversity was similar between quadrants. However, the quadrants shared only three snake species, the generalist diurnal colubrids *Dendrophidion percarinatum* and

*Lampropeltis micropholus* and the nocturnal lizard-eating dipsadine *Imantodes cenchoa* (Table 1).

Quadrants did not differ significantly in weekly average species richness. However, quadrants did differ along three species evenness measures. Quadrant B was higher in weekly average species evenness ( $t=17.34$ ,  $df=10$ ,  $p<.01$ ) and on the Simpson and Shannon-Wiener indices, respectively (Figure 4).

Consistently each week, Quadrant B had a greater proportion of species not represented by *Craugastor crassidigitus* and *C. podiciferus*, the two most abundant (Figure 5b); Quadrant A had a proportion of 0.33 and Quadrant B of 0.76. Only during Week 1 did any quadrant significantly possess more species than another, in which Quadrant B had three times the richness of Quadrant A (Figure 5a).

Diversity measure	Quadrant B – Quadrant A
Weekly average richness	1.22
Weekly average evenness	0.43*
Simpson’s Diversity Index	0.21 <sup>+</sup>
Shannon-Wiener Diversity Index	0.26 <sup>+</sup>

**Figure 4.** Differences between quadrants along four diversity-related indices.

\*  $p<.01$ ; <sup>+</sup> not evaluable for significance

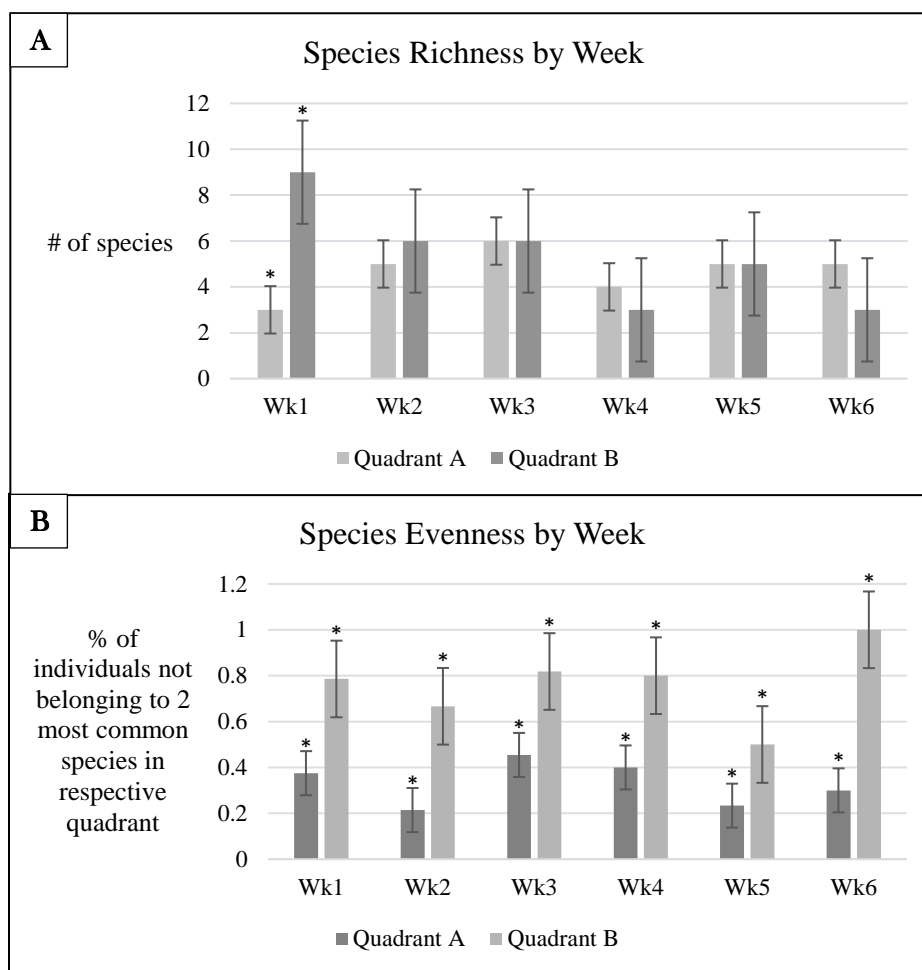


Quadrant A			Quadrant B		
1	Dactyloidae	<b><i>Anolis [Norops] polylepis</i></b>	1	Dactyloidae	<i>Anolis [Norops] humilis</i>
2	Dactyloidae	<i>A. [N.] humilis</i>	2	Dactyloidae	<b><i>A. [N.] limnifrons</i></b>
3	Dactyloidae	<i>A. [N.] woodi</i>	3	Dactyloidae	<i>A. [N.] woodi</i>
4	Colubridae: Colubrinae	<i>Dendrophidion percarinatum</i>	4	Dactyloidae	<b><i>A. [N.] pachypus</i></b>
5	Colubrinae	<i>Lampropeltis micropholus</i>	5	Colubridae: Colubrinae	<i>Dendrophidion percarinatum</i>
6	Colubridae: Dipsadinae	<i>Imantodes cenchoa</i>	6	Colubrinae	<b><i>D. paucicarinatum</i></b>
7	Dipsadinae	<b><i>Urotheca guentheri</i></b>	7	Colubrinae	<i>Lampropeltis micropholus</i>
8	Dipsadinae	<b><i>Geophis hoffmanni</i>*</b>	8	Colubridae: Dipsadinae	<i>Imantodes cenchoa</i>
9	Viperidae: Crotalinae	<b><i>Bothriechis nigroviridis</i></b>	9	Dipsadinae	<b><i>Trimetopon slevini</i></b>
10	Centrolenidae: Centroleninae	<i>Espadarana prosoblepon</i>	10	Dipsadinae	<b><i>Geophis brachycephalus</i>*</b>
11	Craugastoridae: Craugastorinae	<i>Craugastor underwoodi</i>	11	Viperidae: Crotalinae	<b><i>Bothriechis lateralis</i></b>
12	Craugastorinae	<i>C. crassidigitus</i>	12	Centrolenidae: Centroleninae	<i>Espadarana prosoblepon</i>
13	Craugastorinae	<i>C. podiciferus</i>	13	Craugastoridae: Craugastorinae	<i>Craugastor underwoodi</i>
14	Craugastoridae: Ceuthomantinae	<i>Pristimantis cruentus</i>	14	Craugastorinae	<i>C. crassidigitus</i>
			15	Craugastorinae	<i>C. podiciferus</i>
			16	Craugastoridae: Ceuthomantinae	<i>Pristimantis cruentus</i>
			17	Plethodontidae: Hemidactyliinae	<b><i>Oedipina uniformis</i></b>

**Table 1.** Species detected in Quadrants A (secondary forest site) and B (old-growth site). Binomials listed in boldface found only in a single quadrant. Alternative taxonomy by Guyer & Savage (1986) in brackets. Species with an asterisk (\*) were significantly segregated by quadrant ( $p < .001$ ).

The data also differed in a compositional way not detectable merely through the lens of richness and evenness trends. While 11 species were found only at a single quadrant, only two species were detected with enough frequency to establish evidence for site-based segregation. *Geophis hoffmanni* and *G. brachycephalus* are

fossorial dipsadine colubrids that were frequently caught in pitfall traps; *G. hoffmanni* was consistently found only in the secondary forest of Quadrant A and *G. brachycephalus* only in the old-growth of Quadrant B. There is extreme improbability that this relationship is caused by detection biases or random chance ( $t=5.20$ ,  $df=10$ ,



**Figure 5.** Weekly differences in species richness [A] and evenness [B] between quadrants. Brackets denote standard error of the mean.

$p < .001$ ) and suggest that these two closely related species may have undergone a recent speciation event along habitat-based lines.

## Discussion

The results support the theoretical logic, which predicted evenness decreasing with increasing disturbance. Given that Quadrant B does not represent extreme maturation, it is likely that its level of disturbance corresponds to an upper middle point on the DDC curve, and evenness could possibly be expected to decrease as forests age >200 years or more. The evenness trend

most closely matches findings by Vonesh (2001); however, though their study also found evenness decreasing along disturbance gradients, it also revealed an inverse relationship between evenness and richness. On the other hand, Luja et al. (2017) found that richness and evenness both increased with greater disturbance. This is opposite the findings of the study, as evenness is clearly higher in Quadrant B than A. Then there is the broader ecological data that clearly points towards richness *decreasing* with greater disturbance (Chapagain et al. 2017; Malik et al. 2014; Zhang et al. 2013). Regardless of richness trends or regional differences in

evenness trends, the higher evenness of the old-growth site may suggest that secondary growth harbors enough old-growth niche characteristics to support low-abundance populations of specialist species; these presumably share the habitat with a smaller number of abundant generalists.

Though the study did not find richness to significantly differ between quadrants, Quadrant B did have 3 more species than Quadrant A. If this represents a richness trend not accurately captured by the study, namely one where richness increases with *decreasing* disturbance and thus is positively related to evenness, it might suggest that increasing disturbance causes a greater loss of specialists than increasing maturation causes a loss of generalists. The result would be that older-growth forests tends to exhibit both higher evenness and higher richness.

Determination of which species correspond to “generalist” vs. “specialist” descriptions is difficult, not least because the life history of Neotropical montane herpetofauna is so understudied. Further complicating clear distinctions between ecological roles is the existence of species that occupy similar or identical niches but segregate by disturbance level. For instance, *Geophis hoffmanni* and *G. brachycephalus* presumably occupy very similar niches as fossorial invertebrate-eaters, yet the former occurred only in secondary growth and the latter only in old-growth. Perhaps differences in structure and composition of the fossorial habitat between forest ages (i.e. leaf litter origin, depth, and permeability) differ in such as way as to have promoted speciation in *Geophis*. Though leaf litter measurements were not taken, litter depth appeared greater in Quadrant A and was more heavily composed of palmate *Cecropia obtusifolia* leaves relative to Quadrant B, where pinnate leaves comprised more of the litter assemblage. Future studies are necessary to investigate whether these differences in leaf litter are significant and if they confer

different selection pressures on herpetofauna such as *Geophis* colubrids. Evidence that the leaf-litter assemblage is distinct enough to cause speciation may suggest that disturbed forests are specialist hubs of their own, instead of generalist domains where specialist species are low in abundance. It is possible that speciation events occurred in genera such as *Geophis* during the major ecological upheavals of the late Pleistocene, in which it is believed that forest gradually began replacing savanna across the Neotropics owing to climatic changes and the arrival of humans in the Americas (Häggi 2017; Salo 1987). Beginning around 15,000 years ago, megafaunal extinctions and anthropogenic forest alteration likely greatly expanded secondary forests, rendering a previously marginal habitat extensive. However, some studies suggest that the Holocene transition may well have been characterized by the expansion of Pleistocene rainforest “refugia” into savanna (Maslin et al. 2012).

Other elements of the data not explainable under cursory generalist-specialist distinctions concern specialists that occur across disturbance gradients. The arboreal colubrid *Imantodes cenchoa* feeds almost exclusively on lizards, especially *Anolis* spp. (de Sousa et al. 2014), and was found in both quadrants; no differences in *I. cenchoa* abundance between quadrants was determinable. This suggests that some niches indeed are conserved across disturbance levels. However, it remains to be known if conserved niches tend to be more fragmented and resource-poor in secondary growth compared to their strongholds in old-growth areas. If this is the case, then we would expect specialists to be lower in abundance in secondary growth, since its lower resource base would dictate a lower carrying capacity. The result would be that younger growth is lower in evenness, with a few generalists accompanied by many low-abundance specialist species that are much more common in older growth, and as such

would support the initial hypothesis and study findings (Figure 4). However, it is also possible that some specialists like *I. cenchoa* may be *more* abundant in secondary forest—increasing disturbance may amplify some niches that are constrained in old-growth assemblages. This is plausible since many *Anolis* species (i.e. *A. polylepis*) frequent disturbed areas, though *Anolis* abundance was about 2.5 times higher in Quadrant B than A. Another vexing question is *what degree of change can disturbance confer upon a given niche* (i.e. fossorial earthworm prey load, understory *Anolis* prey load) *before the niche begins to confer different selection pressures?* In other words, why does the fossorial invertebrate-feeding niche appear to have different predators in secondary (*Geophis hoffmanni*) and old-growth (*Geophis brachycephalus*) while the arboreal lizard-eating niche has a single main predator across disturbance levels? These are extremely difficult questions to test and require intensive future study to 1) determine *how* niches differ along disturbance gradients and 2) *how* utilizers of these niches differ along “niche gradients” (i.e. how leaf litter composition affects earthworm availability, or how understory structure affects ease of *Anolis* lizard capture).

In order to determine the extent to which the trend observed in this study conforms to the DDC and to other studies of herpetofaunal richness-disturbance trends (Luja et al. 2017), a number of additional experiments could be devised. Three distinct disturbance states could be compared, with one corresponding to a state of very high maturation (>200 years). This would allow for a determination of whether richness or evenness (or both) exhibit a hump-shaped curve. Ideally, to maximize statistical rigor, multiple quadrants in each of three disturbance states could be pooled and compared. However, construction of pitfall traps is labor-intensive; such an approach would best rely on visual and auditory transect surveys over physical trapping.

## Conclusion

The conservation implications of Quadrant B’s higher evenness level are significant. Species-rich areas with high evenness are of greatest conservation value: protecting them grants the highest likelihood of maintaining viable populations of each member species, as opposed to protecting an area where most species are too rare to guarantee the existence of viable local populations. Old-growth Neotropical montane forests are severely threatened in parts of the western Andes, the Chocó, and the ranges of northern Central America (Bullock et al. 2020; Redo et al. 2012; Hamilton 1995; Mutke et al. 2017).

The causal factors behind *how* old-growth forests come to exhibit a reduction in evenness are unclear and extremely difficult to test. However, it may be that the ancientness of old-growth forest has permitted the evolution of many specialist species that are tightly partitioned into specific niches and thus of similar abundance; these species decrease in abundance as their niche requirements are diminished through disturbance, though generalist species do not decline. The result is a secondary-growth assemblage of abundant generalists and rare specialists.

This study represents the first comparative analysis of herpetofaunal ecology at Cloudbridge Nature Reserve and has confirmed the formerly unclear presence of certain colubrid species at the reserve, such as the Talamancan endemic *Trimetopon slevini*, the patchily-distributed *Urotheca guentheri*, and an unusually high-elevation population of *Dendrophidion percarinatum*. Moreover, the study discovered that the reserve harbors both *Geophis hoffmanni* and *Geophis brachycephalus*. The study also represents the largest pitfall-trapping effort at the reserve, establishing the viability of pitfall-

trapping as a sampling method for cloud forest herpetofauna.

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