

Distance–decay differs among vertical strata in a tropical rainforest

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Abstract

1. Assemblage similarity decays with geographic distance—a pattern known as the distance–decay relationship. While this pattern has been investigated for a wide range of organisms, ecosystems and geographical gradients, whether these changes vary more cryptically across different forest strata (from ground to canopy) remains elusive.
2. Here, we investigated the influence of ground vs. arboreal assemblages to the general distance–decay relationship observed in forests. We seek to explain differences in distance–decay relationships between strata in the context of the vertical stratification of assemblage composition, richness and abundance.
3. We surveyed for a climate-sensitive model organism, amphibians, across vertical rainforest strata in Madagascar. For each tree, we defined assemblages of ground-dwelling, understory, or canopy species. We calculated horizontal distance–decay in similarity across all trees, and across assemblages of species found in different forest strata (ground, understory and canopy).
4. We demonstrate that within stratum comparisons exhibit a classic distance–decay relationship for canopy and understory communities but no distance–decay relationships for ground communities. We suggest that differences in horizontal turnover between strata may be due to local scale habitat and resource heterogeneity in the canopy, or the influence of arboreal traits on species dispersal and distribution.
5. *Synthesis.* Biodiversity patterns in horizontal space were not consistent across vertical space, suggesting that canopy fauna may not play by the same set of “rules” as their conspecifics living below them on the ground. Our study provides compelling evidence that the above-ground amphibian assemblage of tropical rainforests is the primary driver of the classical distance–decay relationship.

KEYWORDS

amphibian, arboreal, biodiversity, biogeography, distance–decay, ectotherm, habitat-niche partitioning, vertical stratification

1 | INTRODUCTION

The similarity in species composition between assemblages shows a decay relationship as a function of the distance between them (Barton et al., 2013; Morlon et al., 2008; Nekola & White, 1999). This turnover of species reflects organism dispersal limitation (Araújo et al., 2008; Pyron & Wiens, 2013) combined with changes in the physical (Levin, 1992; Stein, Gerstner, & Kreft, 2014; Tews et al., 2004) and climate environment (Janzen, 1967). Species turnover is tied to broad, landscape mosaic scales, but it is also evident at the fine (patch) scale (Barton et al., 2013; Wiens, 1989). For instance, small-scale vertical climate gradients created by habitat structure can be highly variable, resulting in vertically stratified assemblages (Scheffers, Phillips, et al., 2013). A large literature exists showing stratification of a range of animal taxa in both temperate and tropical ecosystems (Carvalho, Fabián, & Menegheti, 2013; Di Giovanni, Cerretti, Mason, Minari, & Marini, 2015; Moraes et al., 2015; Stork, Stone, & Sam, 2016; Ulyshen, 2011). It remains unclear, however, the extent to which vertical dimensions of climate and physical space (habitat) (Ashton et al., 2016) can influence horizontal distance-decay relationships at the landscape level (Morlon et al., 2008).

Exposure to stable temperature regimes selects for a narrow thermal tolerance (Janzen, 1967). For example, due to climatic stability tropical organisms are hypothesized to have overall narrower ranges of thermal tolerance, and consequently smaller range sizes than organisms from the more seasonal temperate regions (Hua & Wiens, 2010; Janzen, 1967; McCain, 2009; Olalla-Tárraga et al., 2011; Sunday, Bates, & Dulvy, 2011). Therefore, tropical species should be more prone to encounter physiological barriers to dispersal (Fine, 2015; Willig, Kaufman, & Stevens, 2003), resulting in higher turnover across space in the tropics (Baselga, Gomez-Rodriguez, & Jorge, 2012; Ghalambor, Huey, Martin, Tewksbury, & Wang, 2006; Janzen, 1967; Rodríguez & Arita, 2004). If we extend this paradigm to the vertical climate gradient created by trees, we would predict high turnover on the ground (stable: equivalent to tropical regions) and low turnover in the canopy (unstable: equivalent to temperate regions) (Scheffers & Williams, 2018). This is because canopy environments have higher thermal variability than ground environments (Didham & Ewers, 2014; Lowman & Rinker, 2004; Scheffers, Phillips, et al., 2013; Scheffers et al., 2017). Scheffers et al. (2017) tested this theory at a macroecological scale and found that arboreality (vertical movement) in vertebrate assemblages (mammal, bird, reptile and frog assemblages) is positively correlated with dispersal (horizontal movement), suggesting that arboreal species are more able to exploit climatically variable areas.

Another important force in structuring animal assemblages is physical habitat area available for colonization and usage (Lomolino, 2000; McCain, 2007; Rosenzweig, 1995; Tjørve, 2003). In the case of vertical rainforest strata, there are distinct differences in the distribution of suitable habitat-niche spaces available for species (e.g., area with substrate, moisture and microclimates necessary for populations to persist; Holt, 2009). Habitat-niche space lacks continuity along the horizontal plane within the above-ground vertical layers of

forests where physical habitat is fragmented by open space (Adams, Schnitzer, & Yanoviak, 2017; August, 1983; Holt, 2009; Hutchinson, 1957; Lowman & Rinker, 2004; Parker & Russ, 2004), while habitat-niche space is more continuous on the ground. Therefore, a “scattered” habitat (large distance between each habitable space; Morlon et al., 2008) in the canopy could lead to greater distance-decay compared to that on the ground.

Here, we document patterns of vertical stratification, and the decay in assemblage similarity across horizontal space in a humid rainforest. We ask whether patterns of richness, abundance and distance-decay relationships are similar between ground, understory and canopy assemblages—environments with different levels of climate variability and habitat continuity. To address this question, we used a climate-sensitive model organism, amphibians, which were sampled from the ground to canopy in Ranomafana National Park, Madagascar. Specifically, we explore whether patterns of assemblage turnover across horizontal space (distance-decay) vary *within* (i.e., canopy-canopy across horizontal space) and *between* (i.e., ground-canopy across horizontal space) vertical strata. *Within* describes how an assemblage inhabiting a particular stratum decays in similarity over horizontal distance, whereas *between* shows how distance-decay may occur when comparing assemblages of different strata over horizontal distance. High turnover may reflect local aggregation of species due to resource affinity and low habitat continuity.

2 | MATERIALS AND METHODS

2.1 | Study area

We surveyed an assemblage (all of the species that exist in a particular habitat) of amphibian species in an a seasonal montane broad-leaf rainforest with a high number of epiphyte microhabitats located within Ranomafana National Park, south-eastern Madagascar (21°17'S, 47°25'E; Figure 1). Identification was conducted in the field using the Glaw and Vences Field guide (Glaw & Vences, 2006). Our sampling areas (Vatoharana and Valohoaka) were confined to an altitude range of 969–1,171 m (Figure 1), with a yearly average rainfall of ~3,000 mm, though there is a considerable amount of inter-annual variation in the temporal distribution of rainfall (King et al., 2012). Temperatures range from lows in June–September (4°C–12°C) to highs in December–March (30°C–32°C; Deppe, Baden, & Wright, 2016).

2.2 | Vertical stratification of amphibians

Over a three-month period (November 2015–January 2016), we conducted vertical ground-to-canopy surveys for amphibians. Using survey methods in Scheffers, Phillips, et al. (2013), each survey was centred on a single canopy tree. Tree selection was randomized; however, each tree was inspected prior to sampling to ensure it met safety standards for arborist single-rope climbing (Jepson, 2000). As

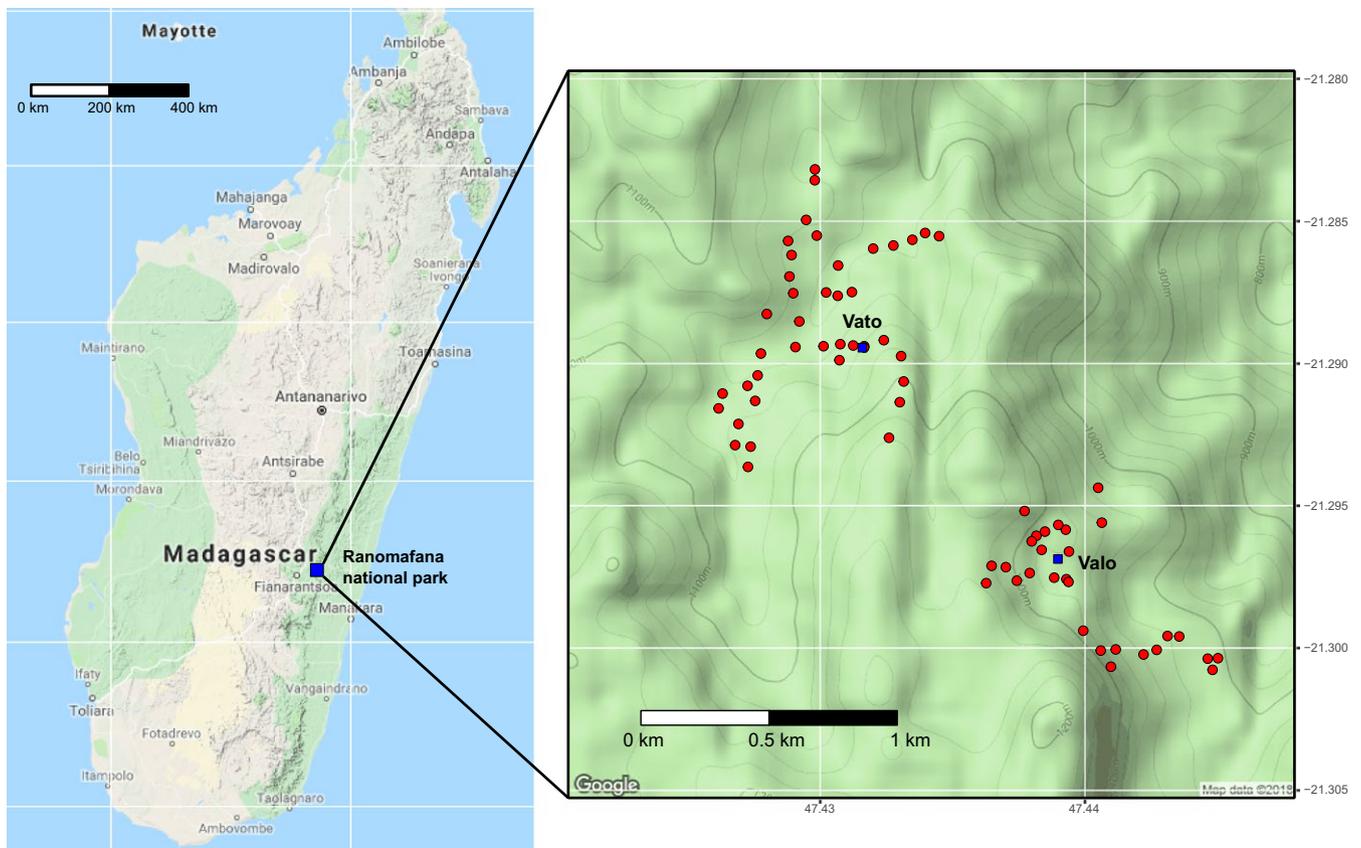


FIGURE 1 Maps showing the position of Ranomafana National Park in Madagascar and the extent of the study area. Each red circle represents a single sampling location (tree). The national park sites, Valo (Valohoaka) and Vato (Vatoharanana), are provided for reference

climbing towards the top crown of trees is dependent on suitable branches that allow for safe access, we could not always ascend to 100% of the total tree height, and we accounted for this in our analyses (see below).

We surveyed 70 trees with varied distance between each other (min = 28 m; max = 2.5 km; median = 910 m; $SD = 608$ m). In order to account for diurnal and nocturnal species, we performed one day (between 8 and 12 AM) and one night (8–12 PM) climb per tree (total of 140 surveys). We alternated the first survey, day or night, to avoid temporal biases in sampling. Maximum height climbed and tree height were recorded for each survey using a laser distance metre (Leica Geosystems, Leica Disto D2; <http://www.leica-geosystems.ca>). At each tree, we conducted 10-min surveys at the ground (base of tree), in the understory (1–4 m), sub-canopy (~ half of the max. height climbed) and canopy (max. height climbed). We allocated the remaining 20 min as a roaming survey from understory to canopy. Therefore, disturbance was standardized across vertical sampling, and sampling effort was 60 min/tree per survey, for 120 min/tree in total. Ground surveys were conducted first to avoid biases caused by amphibians jumping from the trees to the ground during arboreal survey. Ground surveys were confined to a single randomly selected 4×4 m plot at the base of the tree, and consisted of thoroughly searching leaf litter, logs and other microhabitats that could harbour animals (Heyer, Donnelly, Foster, & Mcdiarmid, 1994). During

arboreal surveys, we searched for amphibians in tree holes, moss, epiphytes and other microhabitat structures.

We defined three stratum classes for our analyses. We categorized strata as “Ground” (0–1 m), “Understory” (1–4 m) and “Canopy” (>4–30 m). The canopy was delineated by a dense understory that typically terminated at approximately 4 vertical metres. Furthermore, because of some unevenness in ground features, we allocated the ground layer to 0–1 m. We allocated individuals to these strata based on capture height. We sampled a mean of 67% ($SD = 10.3\%$) of the total tree height across our vertical surveys.

2.3 | Tree and habitat characteristics

For each surveyed tree, we used a laser distance metre to measure tree height (m), diameter at breast height (m) and canopy area (m^2). We walked two 10 m transects away from the tree and at 0 m, 5 m and 10 m at right angles to the transect recorded percentage canopy cover using a spherical convex densitometer (Forestry Suppliers; <http://www.forestry-suppliers.com>), leaf intersect (number of vegetation layers directly above the observer) and percentage herbaceous vegetation covering the ground surface in a $1 m^2$ quadrat. We also counted large stems (>8 cm) and small stems (<8 cm) 1 m on either side of the transect (a total of $40 m^2$) to calculate large and small stem densities (stems per m^2) (Supporting Information Table S2).

3 | DATA ANALYSIS

3.1 | Species richness and abundance

Amphibian species richness was compared between strata using abundance-based rarefaction curves with 95% confidence intervals, which allow for comparison of richness levels while controlling for different sample sizes (Colwell, Xuan Mao, & Chang, 2004). The completeness of the sampling method used was assessed by calculating the mean of four commonly employed abundance-based estimators of species richness (Abundance-based Coverage Estimator, CHAO1, JACK1 and Bootstrap) in ESTIMATES v.9.1. Differences in richness and abundance between strata were assessed with paired *t*-tests (Carvalho et al., 2013; Henry, Barrière, Gautier-Hion, & Colyn, 2016) and a generalized mixed-effect model (Didham & Ewers, 2014) which included sample site (tree) as random effect ["lme4" package in R, R Core Team (2013)].

3.2 | Kernel-density estimation

To estimate the distributions of amphibians across vertical forest strata, we used univariate kernel density (Silverman, 1986; Venables & Ripley, 2013). Kernel-density estimation generates a smoothed histogram of data, where the area under the histogram integrates to one. In our study, we estimate the probability density of the height at which amphibians were found. Therefore, the probability density we calculate can be thought of as the relative density of amphibians with height. We estimated a kernel bandwidth (see Silverman, 1986) for our complete dataset, and then used this bandwidth independently for each tree to perform kernel tree-specific density estimates. We combined our tree-specific kernels by a weighted mean, with each tree weighted according to the kernel describing the distribution of tree heights. We used this method to generate the relative density of amphibians with height for AM and PM surveys, and for a comparison of the vertical stratification of specific amphibian genera.

3.3 | Distance–decay of assemblage similarity

We calculated the pure turnover component of beta diversity (Baselga, 2010) using the "Jaccard" dissimilarity index (High dissimilarity = 1, High similarity = 0) which utilises a presence/absence approach,

TABLE 1 Amphibian abundance and richness across vertical layers in Ranomafana National Park, Madagascar. Values in parenthesis represent estimated richness (see rarefaction procedure in methods). Estimated sampled is estimated richness/observed richness

	Ground	Understory	Canopy	Total
Abundance	94	39	51	184
Richness	22 (29)	13 (15)	14 (19)	31 (37)
Estimated sampled	0.76	0.87	0.74	0.84

therefore removing the influence of abundance on assemblage similarity (Baselga, 2010). Therefore, we offer insights into changes in species composition over space that are due to gain/loss of species, independent of the effect of species richness and abundance differences between assemblages. Traditional distance–decay typically explores the turnover of assemblages sampled from a single point in space ignoring the vertical stratification of assemblages that are emblematic of the tropics. In our study, for each possible pairwise combination of trees each divided between ground, understory and canopy strata, we regressed similarity (1–Jaccard's Dissimilarity) against geographic distance using ordinary least squares models (maximum sample size = $(70 - 1) * (70/2) = 2,415$ comparisons). Regressions were performed *within* and *between* strata to assess different modes of horizontal distance–decay across the landscape. *Within* stratum comparisons describe the horizontal turnover in the independent stratum assemblages, whereas *between* strata comparisons describes vertical turnover (among strata comparisons) across horizontal space. To counter the effect of inflated power due to large sample sizes derived from pairwise comparisons, we also applied mantel tests with 999 randomizations ["vegan" package in R, R Core Team (2013)] to each set of strata comparisons, using the original dissimilarity measure. Significance here suggests a correlation between increasing distance and dissimilarity. We chose the mantel test as it performs well in determining the significance of correlative relationships between two arrays of dissimilarity ("Jaccard" and geographical distance) (Legendre, Fortin, & Borcard, 2015; Peixoto, Braga, Cianciaruso, Diniz-Filho, & Brito, 2014).

4 | RESULTS

4.1 | Richness and abundance

We sampled 184 individuals of 31 amphibian species (Table 1). Rarefaction analyses estimated a pool of 37 species through extrapolation, indicating that we observed 84% of the forest's amphibian species (Table 1). We caught ~71% of the 31 observed species (22/31) at ground level, 42% (13/31) in the understory and 45% (14/31) in the canopy. Richness and abundance were higher at the ground than in the canopy, though the canopy showed slightly higher values than the understory (Tables 1 and 2; Figure 2; Supporting Information Table S1; Figure S2).

4.2 | Species composition and turnover

We found a strong signal of vertical stratification, with 13 species exclusive to the ground and four species exclusive to the canopy (Figure 3). The understory served as a bridge between ground and canopy, with no species exclusive to this stratum. Stratification was roughly specific to genera, with *Mantidactylus*, *Gephyromantis* and *Plethodontohyla* living on the ground (68% of richness and 81% of abundance) and *Boophis*, *Spinomantis* and *Platypelis* living above-ground (83% of richness and 82% of abundance; Table 2, Figure 4). The vertical stratification of amphibians changed between diurnal

TABLE 2 Abundance of species across strata, with IUCN red-list status

Species	IUCN red-list status	Ground	Understory	Canopy	Total
<i>Anodonthyla boulengeri</i>	Near Threatened	7	1	7	15
<i>Anodonthyla moramora</i>	Endangered B1ab(iii)	1		1	2
<i>Boophis albilabris</i>	Least Concern		1	7	8
<i>Boophis brachychir</i>	Vulnerable B1ab(iii)		2	2	4
<i>Boophis madagascariensis</i>	Least Concern	2	3	1	6
<i>Boophis reticulatus</i>	Least Concern			4	4
<i>Boophis</i> sp. aff. <i>ankaratra</i>	Unknown			1	1
<i>Boophis</i> sp. aff. <i>boehmei</i>	Endangered B1ab(iii) ^a	1	6	1	8
<i>Boophis</i> spp. 1	Unknown		2	1	3
<i>Boophis</i> (unknown)	Unknown			1	1
<i>Gephyromantis asper</i>	Least Concern	3			3
<i>Gephyromantis boulengeri</i>	Least Concern	1			1
<i>Gephyromantis enki</i>	Vulnerable B1ab(iii)	2			2
<i>Gephyromantis plicifer</i>	Least Concern	3	4		7
<i>Gephyromantis sculpturatus</i>	Least Concern	5	4		9
<i>Gephyromantis</i> spp. <i>Luteus</i> group	Unknown	4			4
<i>Gephyromantis</i> (unknown)	Unknown	4			4
<i>Gephyromantis tschenki</i>	Least Concern	6	2		8
<i>Gephyromantis ventrimaculatus</i>	Least Concern	1			1
<i>Guibemantis liber</i>	Least Concern			6	6
<i>Mantidactylus betsileanus</i>	Least Concern	4			4
<i>Mantidactylus majori</i>	Least Concern	2			2
<i>Mantidactylus melanopleura</i>	Least Concern	30			30
<i>Mantidactylus opiparis</i>	Least Concern	1			1
<i>Mantidactylus</i> sp. aff. <i>moquardi</i>	Unknown	1			1
<i>Platypelis grandis</i>	Least Concern	1	6	11	18
<i>Platypelis pollicaris</i>	Least Concern		2	3	5
<i>Platypelis tuberifera</i>	Least Concern	2	5		7
<i>Plethodontohyla brevipes</i>	Vulnerable B1ab(iii)	1			1
<i>Plethodontohyla inguinalis</i>	Least Concern	2			2
<i>Plethodontohyla</i> sp. aff. <i>guentheri</i>	Endangered B1ab(iii) ^a	7			7
<i>Scaphiophryne spinosa</i>	Least Concern	1			1
<i>Spinomantis aglavei</i>	Least Concern		1	2	3
<i>Spinomantis fimbriatus</i>	Least Concern			1	1
<i>Spinomantis</i> (unknown)	Unknown	1			1
Unknown spp.	Unknown	1		2	3
Total		94	39	51	184

^aDenotes IUCN listing of the affiliated known species.

and nocturnal surveys (Supporting Information Figure S1), with the vertical distribution of individuals (density of individuals) shifting higher towards the canopy during the night.

Distance–decay was significant for tree–tree comparisons of the *total* assemblage, which combines all strata per tree and represents the scale traditionally used in distance–decay analysis (Morlon et al., 2008). For our *within* strata analysis, we found a pronounced distance–decay relationship for canopy–canopy and

understory–understory comparisons, but not for ground–ground comparisons (Figure 5, Table 3), demonstrating that above-ground (understory and canopy) species are driving turnover in the *total* assemblage. For our *between* strata analysis, we found no distance–decay relationship for ground–canopy and ground–understory comparisons, whereas understory–canopy does show a weak distance–decay in the linear model. Mantel tests concurred with *allwithin* and *between* strata comparisons except

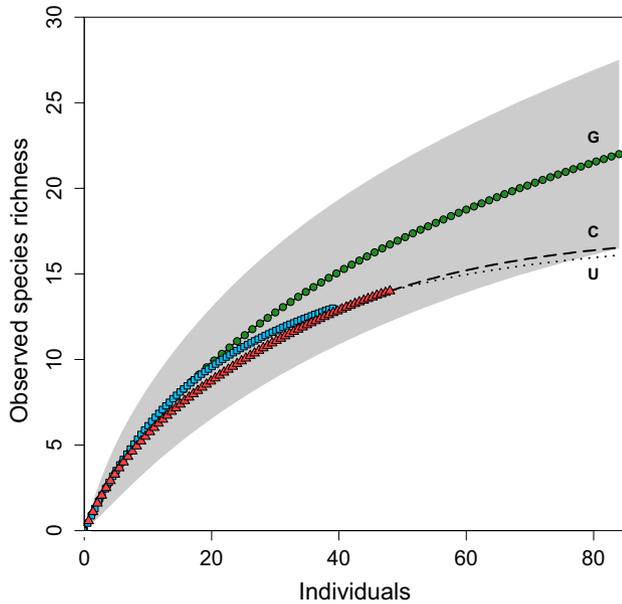


FIGURE 2 Observed species richness of ground (0–1 m, green circles), understory (1–4 m, blue squares) and canopy strata (<4 m, red triangles), calculated from sample-based rarefaction curves and scaled to show the number of individuals on the x-axis. Grey shading represents the 95% confidence interval (CI) for the ground. Dashed lines represent extrapolated results to the maximum number of individuals found in a habitat (84 individuals at ground)

understory–canopy, which was not significant according to the Mantel test (Table 3).

4.3 | Tree and habitat characteristics

Survey trees were tall canopy trees with large DBH and canopy area. Canopy area of each tree exhibited strong variation, but canopy cover was consistently high, with multiple vertical strata shading the forest floor (Supporting Information Table S2). The ground habitat followed the expected distribution of many more small stems than large stems, and exhibited an herbaceous cover (~40%) of understory plants which provided shade and calling positions for amphibians (Supporting Information Table S2).

5 | DISCUSSION

We observed a clear distance–decay relationship for the *total* amphibian assemblage at the scale of the tree. However, by partitioning the vertical components of the *total* assemblage, we show that distance–decay relationships differ by forest strata with the strongest distance–decay occurring in the canopy and no observed distance–decay on the ground. In summary, patterns observed at the ground strata do not align with the *total* analysis, whereas the decay in the canopy and understory does align with the *total* decay of the assemblage. This provides compelling evidence that the above-ground assemblage is the primary driver of the classical

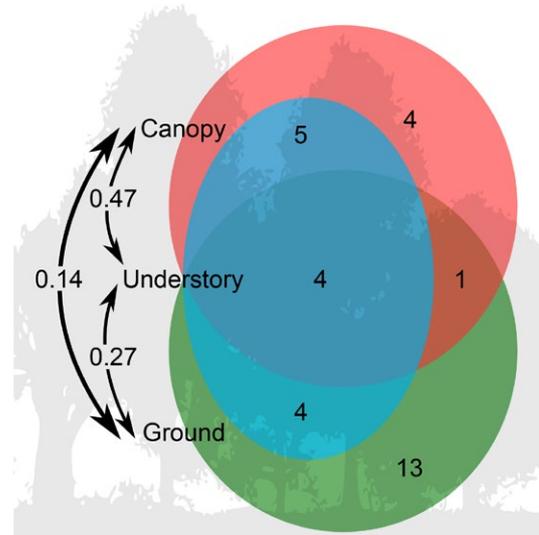


FIGURE 3 Venn diagram of shared species between ground, understory and canopy strata. Diagram is non-additive, meaning no species are represented in more than one category. Included is similarity (Jaccard's index: High similarity = 1, low similarity = 0) of each strata comparison (all trees combined into ground, understory and canopy strata)

distance–decay relationship in our study. Distance–decay relationships have commonly been used to better understand the forces driving assemblage turnover patterns such as dispersal limitation and environmental heterogeneity (Morlon et al., 2008; Qian, 2009; Soininen, McDonald, & Hillebrand, 2007). Considering that canopy species are often bypassed in standard herpetological surveys which do not access the canopy, our study provides a unique insight into how the vertical organization of assemblages may mask horizontal turnover in assemblages only sampled on the ground.

We found lower richness and abundance of amphibians in the canopy compared to the ground, consistent with patterns found in many taxa including nematodes (Powers et al., 2009), small mammals (Abreu & De Oliveira, 2014; Lambert, Malcolm, & Zimmerman, 2005), parasitoid wasps (Di Giovanni et al., 2015), termites (Roisin et al., 2006) and spiders (Aikens & Buddle, 2012). Our findings corroborate the prediction of lower richness and abundance in the hot and dry canopy (Parker, 1995). Desiccating conditions are relatively inhospitable to hydrophilic amphibians (Madigosky, 2004; Ulyshen, 2011), thus limiting available habitat (Lomolino, 2000; Tjørve, 2003). Furthermore, our findings support high assemblage turnover across vertical space (i.e., vertical stratification of assemblage composition; Figure 3), consistent with many other forest taxa such as nematodes (Powers et al., 2009), butterflies (Schulze, Linsenmair, & Fiedler, 2001) and bats (Bernard, 2001). This vertical turnover reflects the affinity of species' to resources, habitat, and climates distributed unevenly between the forest strata (Dáttilo & Dyer, 2014; Parker, 1995; Ribas, Schoereder, Pic, & Soares, 2003; Ulyshen, 2011; Wardhaugh, 2014).

Climatic variability selects for species with greater climatic tolerances, and therefore greater dispersal capacities (Stevens, 1989). High dispersal capacity can reduce turnover and beta diversity

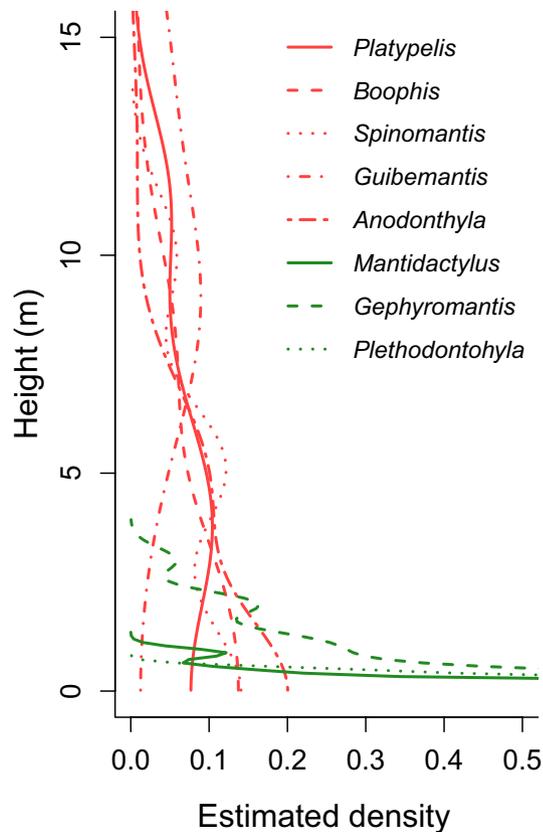


FIGURE 4 Vertical stratification of amphibian genera, split between primarily arboreal genera (red) and terrestrial genera (green). Curves are derived from kernel-density estimation methods and can be understood as the relative density of amphibians with height

as observed in vascular plants at regional scales (Qian & Ricklefs, 2007) and springtails at forest patch scales (Rodgers & Kitching, 1998). In canopies, exposure to higher climate variability resulting in broader physiological tolerances may lead to high dispersal capacity (Scheffers & Williams, 2018; Scheffers, Phillips, et al., 2013; Scheffers et al., 2017). For example, arboreal vertebrates living in unstable regions of Australia are highly mobile in both horizontal and vertical spaces (Scheffers et al., 2017). Therefore, we would expect higher turnover on the ground (stable; lower dispersal ability) than in the canopy (unstable; greater dispersal ability). Yet, in our study, based on our *within* stratum patterns (Figure 5), we show no distance-decay in ground-level assemblages and high distance-decay in canopy assemblages—opposite to what we might expect.

The configuration of available habitat in the landscape may influence turnover to a greater degree than the capacity of a species to disperse. It is well documented that canopies lack continuity in physical structure compared to high continuity at the ground level (Basset et al., 2015; Parker, 1995). Greater habitat heterogeneity in canopies may drive patchy species distributions, ultimately resulting in higher species turnover at local scales (Barton et al., 2013; Morlon et al., 2008). This was observed in the lowland tropical forests of Panama where lower connectivity between tree canopies decreased similarity in ant assemblages, such that trees functioned as islands

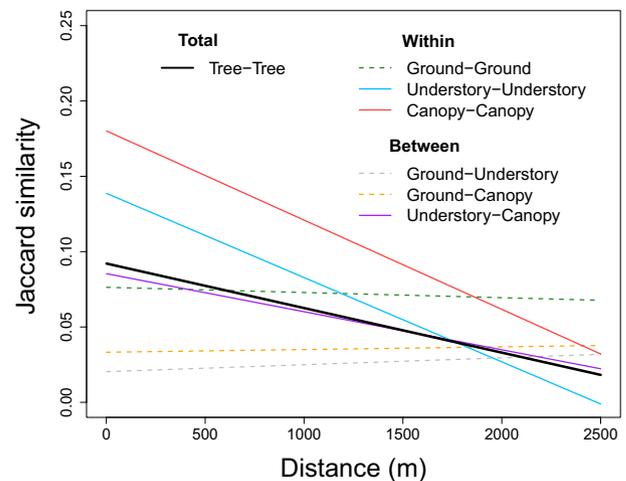


FIGURE 5 Similarity (1 - Jaccard's Dissimilarity index: high similarity = 1, low similarity = 0) of tree-tree and each strata comparison (each tree survey divided into Ground, Understory and Canopy) against distance between trees. Lines represent the fit of ordinary least squares regression model. Solid lines denote a significant distance-decay. Dashed lines represent a non-significant distance-decay. For model statistics, see Table 3

(Adams et al., 2017). When applying the theory of island biogeography (MacArthur & Wilson, 1967) to the distribution of canopy amphibians, above-ground space serves as the sea while the plant/organic structure in this space functions as the islands (habitat which can host populations). Thus, stratum-specific assemblages operate at different scales (Barton et al., 2013; Fordyce & DeVries, 2016; Wiens, 1989) due to the variation in available habitat between strata.

Our study shows overall similarity between understory and canopy assemblages and suggests that the canopy, in terms of assemblage composition, function, niche specialisation, and ecology, starts at 1 m above-ground (Figures 2, 3 and 5; Table 3). Similarly, Beaulieu, Walter, Proctor, and Kitching (2010) wittingly claim that the canopy starts at 0.5 m above-ground and formed this conclusion by comparing mite faunas living from ground to canopy. They found that the overlap in mite assemblages between 0.5 m and 20 m above-ground was far higher than that between the lowest height of 0.5 m and just below on the ground (Beaulieu et al., 2010). This is in agreement with our findings—which show a clear delineation between ground and above-ground (>1 m) fauna in their abundance, richness and distribution patterns.

To this point, we see that different genera dominate the ground and the canopy (Table 2, Figure 4). A similar pattern was observed in butterflies (Fordyce & DeVries, 2016), dung beetles (Stork et al., 2016) and spiders (Aikens & Buddle, 2012). This suggests that species tend to retain the ancestral niche, and that habitat-niche changes are rare (e.g., niche conservatism). For example, terrestriality is the ancestral state in amphibians and there have been very few clear reversions back to terrestriality from an arboreal state (Feng et al., 2017; Moen, Morlon, & Wiens, 2016). If morphological traits are phylogenetically conserved within terrestrial (ground) and arboreal ecomorphs (Duellman & Trueb, 1994; Moen et al., 2016), this may also include other traits which show clear associations with strategies of

Comparison	Y intercept	R ²	F	DF	p Value	Mantel p
Ground-ground	0.076	-0.0020	0.047	463	0.829	0.413
Understory-understory	0.138	0.0110	4.340	298	0.038	0.036
Canopy-canopy	0.180	0.0150	6.740	376	0.010	0.016
Ground-understory	0.020	-0.0008	0.364	773	0.546	0.110
Ground-canopy	0.033	-0.0011	0.043	866	0.834	0.831
Understory-canopy	0.085	0.0037	3.590	698	0.058	0.153
Tree-tree (total decay)	0.092	0.0186	17.29	1,483	0.00003	0.037

TABLE 3 Mantel test *p* values and linear model statistics presented in Figure 5 for within and between strata comparisons of Jaccard similarity between samples against geographic distance between samples. Italicized values denote significant *p* values (*p* < 0.05)

vertical habitat use, such as water retention/dehydration resistance (Pough, Taigen, Stewart, & Brussard, 1983; Tracy, Christian, & Tracy, 2010), thermal tolerances (Scheffers, Brunner, et al., 2013; Tracy et al., 2010), reproductive modes (Haddad & Prado, 2005) and microhabitat affinities (Mccracken & Forstner, 2014).

6 | CONCLUSIONS

Distance-decay relationships are a classical concept of biodiversity and biogeography. Our study reveals turnover in the canopy as the primary driver of general turnover patterns in this tropical rainforest. High local-scale habitat and resource heterogeneity in the canopy likely affect the ability of arboreal species to disperse across a discontinuous habitat. As a result, ecological patterns in horizontal space were not consistent across vertical space, suggesting that canopy fauna may not play by the same set of "rules" as their conspecifics living just below them on the ground. Therein, the spatial organization of assemblages does not function in single but rather multiple spatial dimensions with important impacts on the turnover of species.

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AUTHORS' CONTRIBUTIONS

B.R.S. conceived, designed and funded the study. E.W.B., B.R.S., C.M.S. and L.R.A. conducted fieldwork. E.W.B. and B.F.O. analysed the data and E.W.B., B.R.S. and B.F.O. wrote and edited drafts of the manuscript.

DATA ACCESSIBILITY

Data are available from Dryad Digital Repository: <https://doi.org/10.5061/dryad.3m1g61k> (Basham, Seidl, Andriamahohatra, Oliveira, & Scheffers, 2018).

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