Received: 18 September 2019 | Revised: 24 February 2020 | Accepted: 2 March 2020

DOI: 10.1111/jbi.13857

RESEARCH PAPER

Journal of Biogeography

WILEY

Vertical stratification collapses under seasonal shifts in climate

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Funding information
The American Museum of Natural History

Handling Editor: David Chapple

Abstract

Aim: Tropical forests are vertically complex, and offer unique niche opportunities in the form of climate, habitat and resource gradients from ground to canopy. Rainforest species organize within this vertical spatial gradient and recent macroecological research suggests that the highest levels of vertical stratification occur in structurally complex and climatically stable tropical rainforests. However, although the classical view of the tropics is that of aseasonality, particularly in temperature, there is strong seasonality in rainfall. Thus, we predict considerable variation in vertical stratification in time, characterized by a seasonal restructuring of communities across vertical space.

Location: Sierra Llorona, Colón Province, Panama.

Taxon: Amphibians.

Methods: We performed 121 ground-to-canopy surveys across the wet and dry seasons for amphibians. Using a bootstrap simulation method we calculated species-specific and community-wide vertical height and abundance shifts between seasons. Separately, we tested the importance of vertical height and season on the vertical distribution of species using a redundancy analysis, and employed linear models to explore turnover in species composition across vertical height between seasons.

Results: Our results show a clear downward shift of 5 m in height in amphibian communities from the wet season to dry season. We also observe significant changes in species composition across vertical strata in both seasons, driven primarily by nestedness in the dry season (loss of species over height) and genuine turnover in the wet season (loss and addition of species over height).

Main conclusions: The exploitation of canopy microhabitats and resources in the wet season resulted in complex patterns of stratification, whereas drying flattened the distribution and simplified the composition of arboreal communities. As such, pattern and process in the vertical dimension is not static in time but rather exists as a dichotomy with inverse patterns between wet and dry seasons. Complex, multidimensional distributions of diverse rainforest communities can be simplified by climatic constraints – an important consideration as anthropogenic climate change increases the magnitude of seasonal swings in temperature and precipitation.

KEYWORDS

amphibian, biodiversity, climate gradient, Panama, rainforest, seasonality, verticality

1 | INTRODUCTION

Patterns of biodiversity are known to track environmental gradients (Gaston, 2000; Gaston et al., 2007; Moura, Villalobos, Costa, & Garcia, 2016), especially those produced by latitude and elevation (Ashton et al., 2016; McCain & Beck, 2016; Qian, Badgley, & Fox, 2009; Sunday, Bates, & Dulvy, 2011; Wang et al., 2012). However, habitat vegetation forms a three-dimensional space which results in steep local-scale (vertical) gradients in resources and conditions. Species partition within this vertical space allowing for greater species coexistence (Basset et al., 2015; Beaulieu, Walter, Proctor, & Kitching, 2010; Bulleri, Benedetti-Cecchi, Acunto, Cinelli, & Hawkins, 2002; Enders, 1974; Gilbert, Srivastava, & Kirby, 2008; Vasconcelos & Vilhena, 2006). As such, these microgeographic processes in the vertical dimension are increasingly recognized as an influential contributor to macroecological patterns. For example, the exploitation of above-ground habitat is more common in tropical than temperate regions (Oliveira & Scheffers, 2019) where above-ground conditions are more physiologically challenging (Lowman & Rinker, 2004). Multidimensional species distributions that arise from the partitioning of niche space should therefore be susceptible to shifts in niche components both in space and time. Microgeographic processes in the vertical dimension can be an influential contributor to macroecological patterns – a concept that is increasingly recognized in the literature (Scheffers & Williams, 2018; Sheldon, Huey, Kaspari, & Sanders, 2018).

Arboreal species exploit above-ground niches in the form of microclimates, microhabitats and resources (Beaulieu et al., 2010; De Moraes Weber, De Arruda, Azambuja, Camilotti, & Cáceres, 2011; Karasawa & Hijii, 2008). Dense strata of vegetation buffer climate (temperature and humidity) from the canopy to the ground, which reduces climate variability at the forest floor (Lowman & Rinker, 2004; Ozanne et al., 2003; Parker, 1995) and produces a gradient that can be several magnitudes steeper than those driven by elevation and latitude (Scheffers et al., 2013). Indeed, diverse factors all stratify to some degree ranging from leaf area and vegetation connectivity (Arruda et al., 2016; Clark, Olivas, Oberbauer, Clark, & Ryan, 2008) to air turbulence and wind speed (Parker, 1995; Poggi, Porporato, Ridolfi, Albertson, & Katul, 2004). As a result, there are well-documented patterns showing biological communities, across diverse taxa, being structured by these climate and resource gradients in vertical space (Ashton et al., 2016; Basham, Seidl, Andriamahohatra, Oliveira, & Scheffers, 2018; Beaulieu et al., 2010; Chmel, Riegert, Paul, & Novotný, 2016; De Frenne et al., 2019; Schleuning et al., 2011; Stork, Stone, & Sam, 2016).

Furthermore, seasonality in climate, habitat and resources has major influences on ecological patterns and processes (Bishop, Robertson, van Rensburg, & Parr, 2014; Whitton, Purvis, Orme, & Olalla-Tárraga, 2012; Wiens, 1989). For example, phenological shifts are prominent across life cycle processes and as such, spatial patterns are often not static in time (Feeley & Silman, 2010; van Schaik, Terborgh, & Wright, 2003; Tang et al., 2016). This can be seen in classic megafaunal migrations where distributions shift across latitude (e.g. Wildebeest; Holdo, Holt, & Fryxell, 2009) and in migrations that occur across elevation (e.g. Southen monarch butterflies; Slager & Malcolm, 2015). In most cases, these phenological shifts in life cycle processes and distribution are triggered by seasonality in abiotic conditions such as light, temperature and precipitation (Holdo et al., 2009; Lampert, 2006; Semlitsch, 2007). Although the classical view of the tropics is that of aseasonality, a growing literature challenges this viewpoint by focusing on certain seasonal components of the tropics, specifically precipitation (Comita & Engelbrecht, 2009; Kumagai, Yoshifuji, Tanaka, Suzuki, & Kume, 2009; Nepstad et al., 2004). Oliveira and Scheffers (2019) show that verticality tracks precipitation in space at a macroscale. If we apply this spatial pattern to time, we would predict microscale adjustments in community verticality in response to seasonal changes in precipitation (see conceptual framework, Figure 1). Thus, although a single spatial pixel in Oliveira and Scheffers (2019) shows high arboreality in the tropics, there should also be considerable variation in vertical stratification across time, revealing the dynamism of distributions that span vertical and horizontal dimensions in the tropics.

Here, we explore the phenology of spatial distributions and community composition occurring along the vertical axis of a tropical rainforest. To do so, we analyse the seasonal vertical movement of amphibians in an Atlantic Isthmian forest of central Panama, and show that verticality in the tropics is not static in time. Correlating with seasonal swings in temperature and more importantly

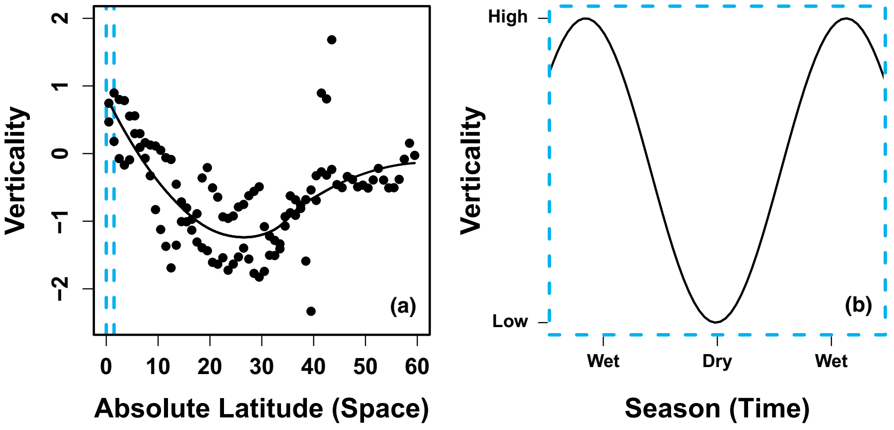

FIGURE 1 (a) Figure adapted from Oliveira and Scheffers (2019) showing the decline in verticality away from the tropics. (b) Conceptual figure predicting the temporal variability in verticality at a specific location in the tropics represented by the blue shading in (a) [Colour figure can be viewed at wileyonlinelibrary.com]

precipitation, we find reductions in amphibian height and richness during the dry season, with some species undertaking a full migration from canopy to ground. We discuss how compositional turnover across vertical height is primarily driven by species replacement with height in the wet season, but with species loss with height in the dry season. Our results highlight a seasonal waxing and waning of vertical stratification that results in a restructuring of richness, abundance and composition across vertical strata. Thus, ecological theory developed in context to vertical stratification such as niche dynamics and adaptive radiations requires careful consideration of both space and time.

2 | MATERIALS AND METHODS

2.1 | Study area

In central Panama, we surveyed an Isthmian-Atlantic Moist Forest located within the Esteban Alphonso Lee Natural Reserve (Lat 9.358555: Lon 79.7029; 499 m a.s.l), which borders the Chagres and Portobelo National Parks. Here, we focused our sampling in older growth areas, with primary canopy tree species including *Cedrela odorata*, *Vatairea erythrocarpa*, *Dipteryx oleifera*, *Manilkara zapota*, *Carapa guianensis*, *Ficus insipida* and *Anacardium excelsum*. Our sampling area was confined to an altitude range 333–473 m a.s.l (Figure S1). This area has seasonal shifts in temperature and rainfall, which were also measured at the site over the 2017–2018 study period (see Supplementary Material).

2.2 | Vertical stratification of amphibians

We surveyed for frogs during the wet season (April–December) and dry season (January–March; Figure S2). Using survey methods in Scheffers et al. (2013) and Basham et al. (2018), we conducted vertical, ground-to-canopy surveys for amphibians, with each survey centred on a single canopy tree. Tree selection was randomized; however, each tree had to meet safety standards for arborist single-rope climbing (Jepson, 2000). We did not limit our selection by tree species, and were only limited in selection by safety concerns. We surveyed 45 trees for amphibians in the wet season, and 43 trees in the dry season, totalling 46 trees (Figure S1) (Panama Ministerio de Ambiente Permit SE/A-26-2018). Of trees surveyed in the wet season, four were not resampled in the dry season and one tree surveyed in the dry season was not resurveyed in the wet season. Trees were surveyed on 1–3 occasions in each season resulting in 66 wet season surveys and 55 surveys in the dry season. For each tree we surveyed for 10 min at the ground, understory (2–4 m), sub-canopy (approx. half the maximum height climbed) and canopy (maximum height climbed), with a 20 min roaming survey between the strata totalling to 60 min. The 10-min ground survey consisted of searching through leaf litter and ground habitat in a 4 × 4 m area to standardize to the same search area available during climbing. In above-ground surveys, we searched for arboreal amphibians in tree holes, moss, epiphytes and other microhabitat structures (Heyer, Donnelly, Foster, & Mcdiarmid, 1994), and measured the height above ground of each individual using a laser distance metre (Leica Geosystems, Leica Disto D2; http://www.leica-geosystems.ca).

2.3 | Statistical analysis

We calculated the mean height and abundance for each species in wet and dry seasons using a randomization technique that accounts for differences in survey efforts (some trees were sampled multiple times in a season). We randomly resampled from our complete dataset using one survey per tree per season in each randomization (n = 1,000) to enable the use of all survey data without confounding the analysis with data from recaptured individuals. We calculated mean height and abundance of each species between seasons and then recorded shifts of abundance and vertical height in each resample (mean wet season minus mean dry season), and plot separately the histogram distribution of abundance and height shifts over the 1,000 resamples for all species. With these data, we calculated the proportion of shifts that fall on either size of 0. A significant negative or positive shift is obtained when 95% of the distribution falls in the negative or positive domain, respectively. For vertical height, this analysis was only possible for those species which occurred in both wet and dry seasons. Using the same resampled data, we constructed density curves (smoothed histograms) of relative density of individuals over vertical height, separated by season, for all species that showed a vertical shift and had sufficient abundance needed to build a density curve (Supplementary Material). All analyses were completed in R (R Core Team, 2019).

Community vertical stratification across seasons was assessed using a site (height intervals of 1 m) by species matrix. The first height category was for individuals captured at 0 m (i.e. site 1), then >0 & ≤1 m (site 2), >1 & ≤2 m (site 3) and so on. In each season, singletons were removed (to reduce the impact of rare species whose vertical range was not fully sampled), the data transformed to presence/absence (to isolate composition without abundance) and gaps between the lowest and highest recording for each species filled (the range where the species would be expected to occur).

To examine the drivers of decay in community similarity along vertical height, we took the pairwise similarity measures between sites (height intervals) within each season using the Jaccard similarity index. The Jaccard index is robust in handling presence/absence data (Beck, Holloway, & Schwanghart, 2013; Qian & Ricklefs, 2007) and provides values of similarity ranging from 0 to 1 (0 completely dissimilar – 1 most similar; Legendre & Legendre, 1998). We then partitioned the nestedness (differences in species composition caused by species losses) and pure turnover (differences in composition caused by species replacements) components (for comprehensive methods, see Baselga, 2010 and Baselga, Gomez-Rodriguez, & Jorge, 2012). For each pairwise comparison between height intervals we calculate the pairwise distance in meters and fit linear models of this distance against the corresponding pairwise values of nestedness and turnover.

To identify the heights at which the greatest changes in composition occurred (i.e. a break-point in composition change), we used the nestedness and turnover Jaccard measures between height intervals in a sequence where only communities immediately adjacent were compared (0–1 m, 1–2 m, 2–3 m, etc). Taking the height of the lowest community in each comparison, we fitted a linear model with each Jaccard measure as a response of height to demonstrate changes in the strength of turnover and nestedness by vertical height.

We used redundancy analysis (RDA) to examine the strength of vertical height and season on describing the Jaccard similarity (separately nestedness and turnover) between height intervals, using "season" as a binomial dummy variable (Draper & Smith, 1981; Legendre, 2008; Legendre & Legendre, 2012). RDA takes a site by species matrix as well as a site by environmental variable matrix to ordinate the samples. RDA constrains the axes to be a linear combination of the environmental variables, thus each axis isolates more variation in sample ordination compared with a principal component analysis (PCA) which ordinates before comparing with environmental variables (Lienesch & Matthews, 2000).

3 | RESULTS

3.1 | Climate

Rainfall increased from April to December, peaking at ~600 mm in November, and marking the wet season. Conversely, rainfall decreased to a low of ~1 mm in February 2018, marking the middle of the January–March dry season (Figure S2). During the dry season mean temperatures dropped by ~2°C across all strata. Minimum temperatures were lowest in the canopy and understory compared with the soil, the latter which was warmer by ~2°C. Maximum temperatures were ~2°C and 3°C warmer in the canopy than the understory and soil respectively. The range between maximum and minimum temperatures was highest in the canopy (4°C–6°C), moderate in the understory (3°C–4°C) and lowest in the soil (1°C) (Figure S2). Thus, wet season sampling occurred during periods of high temperatures and high rainfall, and the dry season during low temperatures and low rainfall.

3.2 | Richness and abundance

A total of 34 species were found during surveys. We found higher species richness in the wet season (29 species) compared with the dry season (23 species) (Table S1; Figure S3). There were 11 unique wet season species and 4 unique dry season species, with 19 species shared among seasons (Table S1). The most abundant species dominated specific seasons, e.g. the hyper-abundant *Diasporus vocator* during dry season (Table S1; Figure 2), and *Craugastor crassidigitus* during the wet season (Table S1; Figure 2). Although the wet season had a higher overall abundance than the dry season (Table S1; Figure 2), species-specific abundances were positively correlated between wet and dry seasons (Figure 3b). Furthermore, although wet and dry season abundances were positively correlated, the vertical distribution of these abundances transitioned from being highly stratified from ground to canopy in the wet season (Figure 3c) to almost entirely on or near the ground in the dry season (Figure 3d), with the exception of *Pristimantis ridens* which maintained its activity in the canopy.

3.3 | Vertical height shift

The mean vertical height of the wet season community was higher than the dry season community (downward shift from a mean of 6 m in the wet to 1 m in the dry season; Table S1; Figure 4). Species-specific mean heights were also lower during the dry season with the single exception of *Craugastor talamancae* (Table S1; Figure 4). We found that of the 13 species recorded in both wet and dry seasons with adequate abundance in each season to test for significances in height, 9 occurred above ground in at least one season. Of these 9 species, 5 utilized the full extent of the vertical strata (Figure S4b–f) and the remaining 4 occurred in vegetation close to the ground (Figure S4g–j). Of the 5 species which utilized vertical strata, 4 significantly reduced their mean vertical height, while the remaining 1 (*P. ridens*) had a lower mean but its height shift was not statistically significant (Table S1; Figure 4; Figure S4).

3.4 | Vertical turnover and stratification

From wet to dry seasons, a sharp drop in richness with vertical height coincided with a homogenization of the canopy community, dominated by three species of the *Pristimantis* genus (*P. ridens*, *P. cruentus* and *P. pardalis;* Figure 5a,c). Pure turnover – the loss and replacement of species – across vertical height was significant in the wet season but not in the dry season (Figure 5b,d). Conversely, nestedness – the loss of species with no replacement – across height was significant in both seasons (Figure 5b,d). Furthermore, in the wet season, turnover was inconsistent across vertical height with highest turnover occurring within the first 5 m of vertical height (Figure 5a).

Redundancy analysis confirmed significant effects of vertical height on pure turnover and season on nestedness, with significant interaction of height and season for both nestedness and turnover (Table 1).

4 | DISCUSSION

We observed a clear downward shift in the vertical niche space of amphibians from wet to dry season. This shift was clear across the whole community, but was particularly pronounced in specific

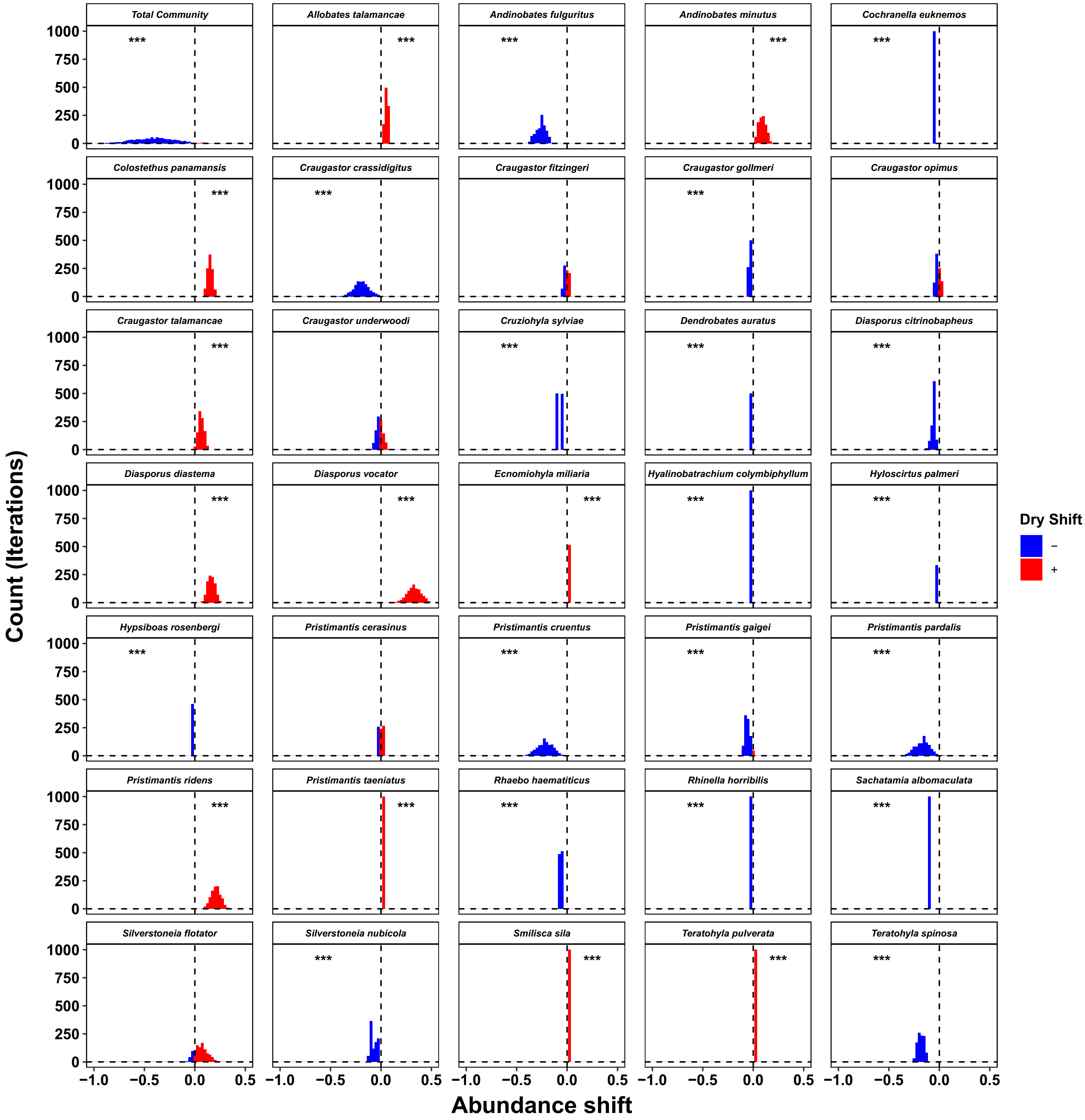

FIGURE 2 Abundance shifts of an amphibian community in central Panama from wet to dry season, presented as species-specific and total community histogram distributions of abundance shifts over 1,000 randomizations. Blue bars indicate a negative response in the dry season and red indicate a positive response. Where 95% of the distribution falls in the negative or positive domain, respectively, ***represents significance [Colour figure can be viewed at wileyonlinelibrary.com]

arboreal species that displayed likely migrations from the canopy to the ground. We also detected rapid changes in species composition across vertical strata in both seasons, driven primarily by the loss of species in the dry season compared with species replacement in the wet season. Thus, our study provides compelling evidence for an underappreciated element of phenology in humid tropical forest that the local-scale spatial distributions and composition of amphibian communities are highly sensitive to climate seasonality.

At a global scale this pattern of shifting verticality is expected. For example, the patterns of amphibian verticality uncovered by Oliveira and Scheffers (2019) revealed precipitation as the principal driver of verticality across latitude. High rainfall facilitates the packing and utilization of vertical niche space through the selection of arboreal species able to access the higher strata. However, our study reveals that this pattern of above-ground niche use in space (e.g. at a tropical latitude) is temporally constrained to periods during the

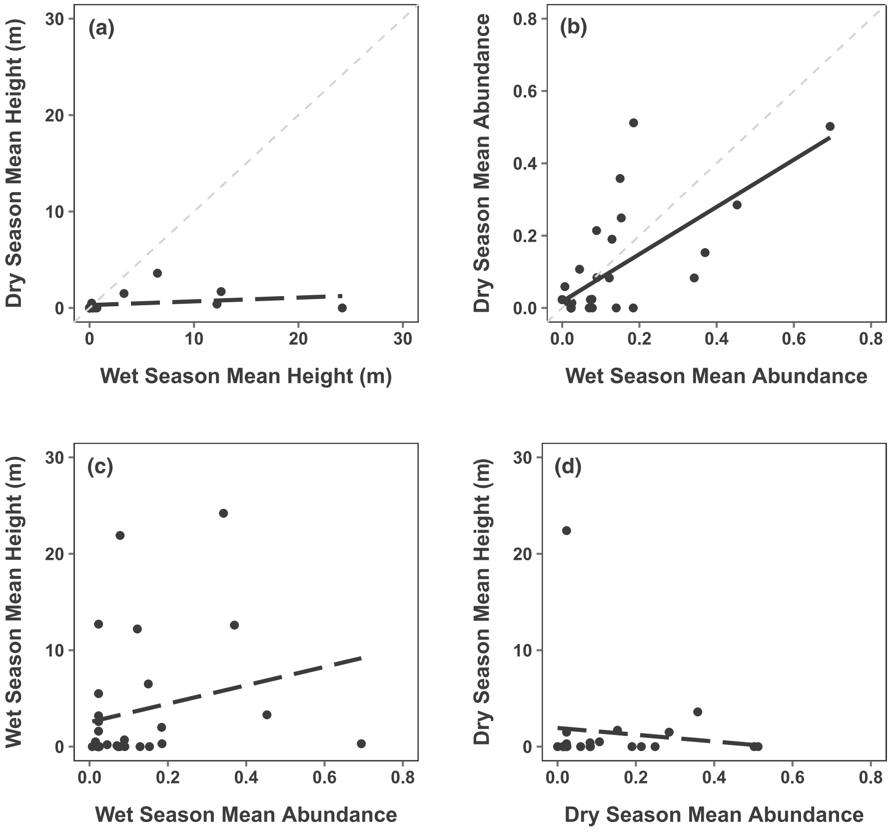

FIGURE 3 Comparisons of seasonal species means of height (m) and abundance (individuals per survey) of an amphibian community in central Panama. (a) Mean height by season (model $r^2 = .15$, $p = .278$), (b) mean abundance by season (model $r^2 = .47$, $p < .001$), (c) wet season mean height by wet season mean abundance (model $r^2 = .02$, $p = .227$) and (d) dry season mean height by dry season mean abundance (model $r^2 = .01$, $p = .38$). Dashed grey lines indicate $x = y$ slope, dashed black lines indicate non-significant linear models and solid black lines indicate significant linear models

year with adequate precipitation (see conceptual diagram, Figure 1). This demonstrates how resource availability constrained in time can lead to the development of migratory life cycles and behaviours in various taxa across different spatio-temporal scales. For example, zooplankton migrate vertically on diel time-scales over 10 s of meters (Lampert, 2006), whereas the arctic tern (*Sterna paradisaea*) migrates thousands of miles from the Arctic to South America and return within a year (Egevang et al., 2010). In the case of our study, frogs shift their vertical habitat niche by several meters over the course of months.

Arboreal fauna must withstand and/or avoid the relatively hot and dry climate of the canopy, and in cases of extreme climate events, arboreal organisms may seek refuge in climatically buffered microhabitats such as tree holes and epiphytes (Mccracken & Forstner, 2014; Scheffers, Phillips, & Shoo, 2014; Sunday et al., 2014; Teixeira, Schineider, & Almeida, 2002). Nevertheless,

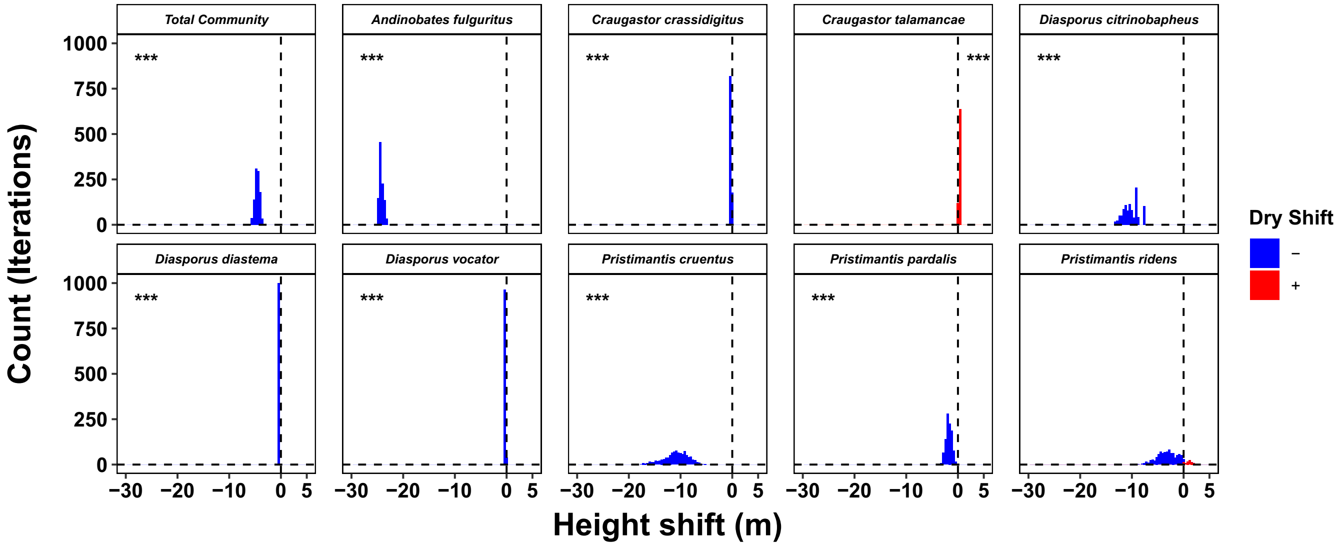

FIGURE 4 Height shifts of an amphibian community in central Panama from wet to dry season, presented as species-specific and total community histogram distributions of vertical height shifts over 1,000 randomizations. Blue bars indicate a negative response in the dry season and red indicate a positive response. Where 95% of the distribution falls in the negative or positive domain, respectively, ***represents significance [Colour figure can be viewed at wileyonlinelibrary.com]

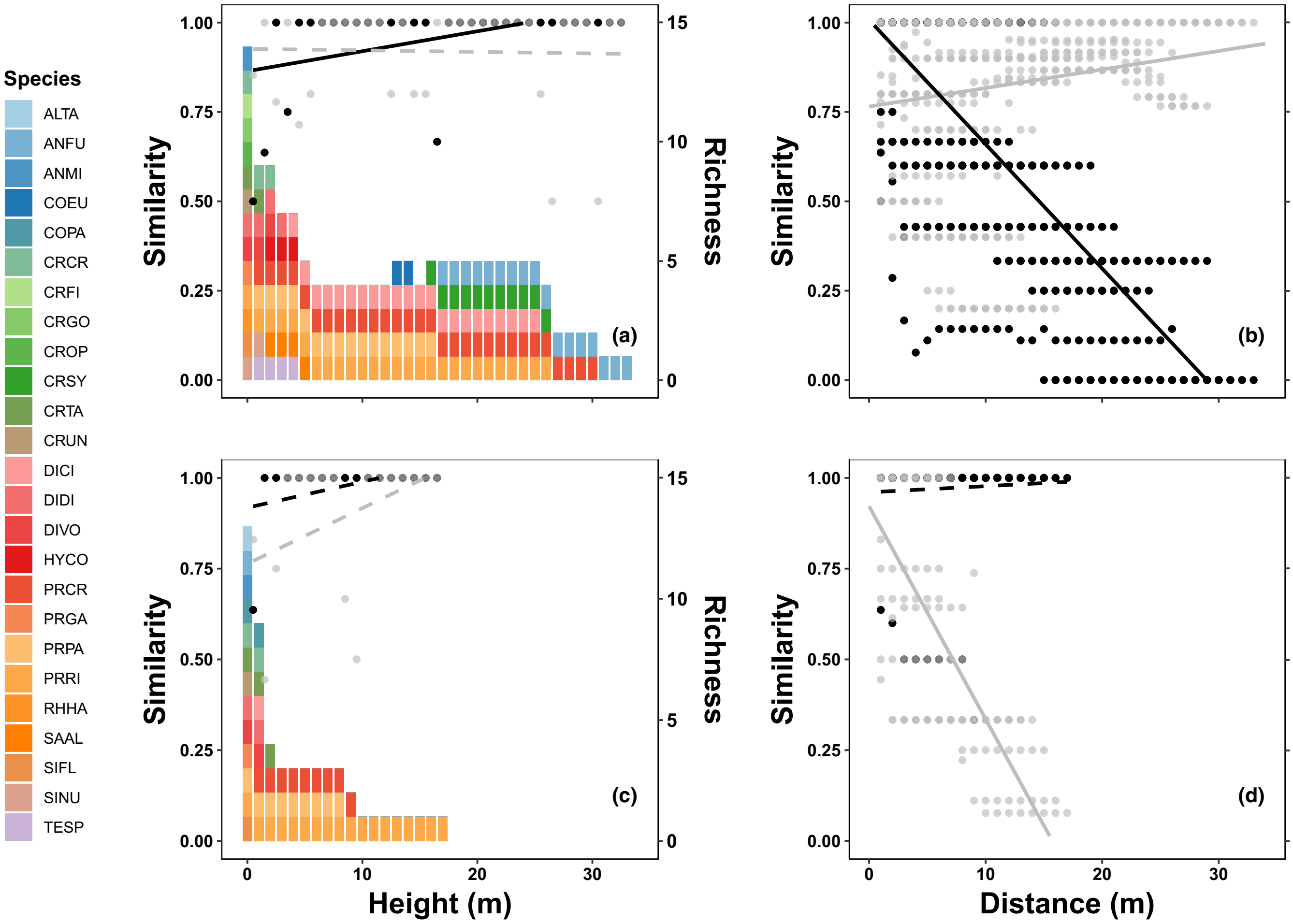

FIGURE 5 Vertical stratification and turnover of an amphibian community in central Panama. (a, c) Stacked plots of species found at each 1 m of vertical height (*z* axis), and pairwise similarity between 1 m binned communities in a sequence where only communities immediately adjacent were compared (0–1, 1–2, 2–3 ...), in the wet (a) and dry (c) seasons (*y* axis). Height represents the lowest community used in each comparison and points represent similarity − height. Species codes are listed in Table S1. (b, d) Pairwise similarity (1 most similar – 0 completely dissimilar) between 1 m binned communities against the distance in height between the communities in the wet (b) and dry seasons (d). Lines show linear models of similarity − distance. (a–d) Black points represent the species replacement component of beta diversity (turnover), and grey denotes the species loss component of beta diversity (nestedness). Solid lines indicate significant relationships and dashed indicate non-significant relationships [Colour figure can be viewed at wileyonlinelibrary.com]

although short-term, extreme climate events may be weathered by retreating to microhabitats, this may not be an effective strategy under prolonged dry seasons, especially for species that cannot estivate (to enter a state of torpor or dormancy; Storey, 2002; Wells, 2007). Thus, during dry periods, arboreal species may instead migrate from the canopy to the ground where climates are cooler and wetter.

The striking shift of composition across space and time (vertical height and season) can also be seen in ecological theory applied at much larger scales, e.g. lowland biotic attrition (hereafter LBA; Anderson et al., 2012; Colwell, Brehm, Cardelus, Gilman, & Longino, 2008; Huey et al., 2012). LBA describes the shift of species distributions in response to long-term changes in climate (Colwell et al., 2008; Feeley, Hurtado, Saatchi, Silman, & Clark, 2013; Feeley & Silman, 2010), leading to a loss of species without replacement by other species that are more climatically adapted. The lowland tropics are the most affected, where species have evolved narrow thermal niches due to niche specialization (Ghalambor, Huey, Martin, Tewksbury, & Wang, 2006; McCain, 2009) and there is no pool of species existing at lower, hotter altitudes for possible replacement following extirpations. Importantly, Colwell et al., (2008) show that biotic attrition in tropical lowlands is primarily due to high maximum temperature combined with low precipitation. Furthermore, the effects of warming can be mediated so long as precipitation is maintained or increased (McCain & Colwell, 2011). Based on this theory and applying it to a microgeographic scale, we would predict higher levels of attrition in the canopy than on or under the ground. This is because although temperature is relatively constant year-round (Figure S2), the canopy is on average several degrees hotter than the ground and soil. In addition, precipitation decreases dramatically from wet to dry seasons. Thus, a steep climate gradient at the microgeographic scale mirrors those altitudinal gradients proposed by Colwell et al., (2008). Our study suggests that biotic attrition is

TABLE 1 Redundancy analysis of the effect of vertical height and season on Jaccard index nestedness and turnover in an amphibian community of central Panama

Variables	DF	Variance	*p* value
Model: turnover ~ height × season			
Height	1	3.552	0.001
Season	1	0.988	1.000
Height:season	1	1.627	0.020
Model: nestedness ~ height × season			
Height	1	0.523	1.000
Season	1	3.036	0.001
Height:season	1	1.991	0.010

independent of space and time-scales so long as a sufficient climate gradient exists.

There is likely to be a wide variation in vertical shifts across taxa with differences in physiology, biology and ecology. In the case of small ectotherms with narrow climate niches, vertical shifts in temperature may play an equal, if not more important role than rainfall. For example, Cerambycid beetles track thermal conditions by shifting into the canopy during the wet season which exhibits a similar thermal niche to the ground during the dry season (Lee, Baxt, Castillo, & Berkov, 2014). Many taxa, and arthropods in particular, also shift vertically due to biotic interactions such as pollination, herbivory and frugivory (Lee et al., 2014; Wardhaugh, 2014). Furthermore, species that are highly dependent on plant resources may shift vertically to track these resources as they become available through seasonal phenology. For example, seasonal production of fruit and flowers in the canopy leads to a shift in the vertical niche of butterflies and moths (Molleman, Kop, Brakefield, De Vries, & Zwaan, 2006; Ribeiro, Williams, Specht, & Freitas, 2016). As such, although vertical distributions can be taxon or guild specific, future research on the phenology of vertical stratification, complementary to ours, may reveal cross-taxa generalities as to the long-term (decadal) changes in vertical distributions as a response to changes in climate.

Within the next century, climate change in the tropics is predicted to increase the magnitude of seasonal swings in temperature and precipitation (Chadwick, Boutle, & Martin, 2013; Chadwick, Good, Martin, & Rowell, 2016; Feng, Porporato, & Rodriguez-Iturbe, 2013; IPCC, 2014; Neelin, Munnich, Su, Meyerson, & Holloway, 2006), driving a reorganization of communities in terms of trait composition, richness and abundance (Corlett, 2011; Laurance et al., 2011; Oliveira & Scheffers, 2019). Oliveira and Scheffers (2019) predicted that climate change may even flatten the vertical distributions of communities in the tropics. Our study shows that tropical species are already shifting their vertical position in response to natural levels of climate variability. Thus, such plasticity in habitat use (a likely product of behavioural and physiological traits) by arboreal fauna may have equipped these species with intrinsic resistance to withstand some levels of anthropogenic climate change (Oliveira & Scheffers, 2019; Scheffers et al., 2017; Scheffers & Williams, 2018).

Despite the possibility of some intrinsic resistance to climatic change, any species subjected to a forced reduction in available habitat/niche space should suffer a reduction in fitness (Soberon & Peterson, 2005). Thus, future research that explores life cycle processes in species that shift their niche vertically within a habitat may more holistically characterize possible trade-offs of microhabitat shifts. Such work is akin to a growing literature that examines altitudinal range shifts in species. But questions remain; is arboreal living essential for these species? To what extent does their specialization to arboreal niche space limit their adaptability to the more competitive environment closer to the ground? Are they exploiting the canopy on an opportunistic basis, or is their fitness dependent on the resources that it provides? For example, some species require epiphytic bromeliads to reproduce (Silva, Carvalho, & Bittencourt-Silva, 2011), while others may require canopy-specific prey items to provide toxins for defence (Saporito et al., 2004; Vasconcelos & Vilhena, 2006). Thus, although vertical movement serves to protect species during seasonal shifts, under severe and prolonged climate change, such shifts may compromise critical life cycle processes. In summary, our study adds to a growing evidence base that climate change may threaten the ecological complexity of diverse tropical rainforests, especially in terms of verticality and composition.

ACKNOWLEDGEMENTS

We dedicate this publication to Heikki Rissanen, who made it possible. The American Museum of Natural History generously provided financial support through the Theodore Roosevelt Memorial Grant. We thank Noel Rowe for his logistical support and permission for use of his research station facilities. We also thank Macario Gonzalez, Eliecer de Yacia and Luis Alberto for their assistance during field work. University of Florida IACUC no. 201709756. Work completed under Panama Ministerio de Ambiente Permit SE/A-26-2018.

DATA AVAILABILITY STATEMENT

The tree survey, individual capture, rainfall and temperature data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.dr7sqv9vk (Basham & Scheffers, 2020).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Basham EW, Scheffers BR. Vertical stratification collapses under seasonal shifts in climate. *J Biogeogr*. 2020;47:1888–1898. https://doi.org/10.1111/jbi.13857