



# Large, old trees define the vertical, horizontal, and seasonal distributions of a poison frog

Edmund W. Basham<sup>1</sup> · Macario González-Pinzón<sup>2</sup> · Angel Romero-Marcucci<sup>2</sup> · Noah Carl<sup>3</sup> · J. Alex Baecher<sup>1</sup> · Brett R. Scheffers<sup>1,4</sup>

Received: 4 September 2020 / Accepted: 29 December 2021

© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2022

## Abstract

In tropical forests, large, old trees (LOTs) can be considered keystone structures for provisioning unique habitats such as decaying wood, roots, cavities, and epiphytes, including those that hold water (phytotelmata). These habitats may also be stratified in vertical space, for example, root structures occur at ground level and below, whereas epiphytes occur above-ground. Canopy habitat is utilized by a diversity of amphibians, but canopy habitat may only be viable in the wet season when epiphytes and surfaces are sufficiently saturated. Here, we examine how the provisioning of microhabitats and structures by LOTs influence the horizontal, vertical, and seasonal distribution patterns of phytotelmata-breeding poison frogs. We conducted ground-to-canopy surveys over 4 years, constituting 6 seasons, in Panama and used mark-recapture techniques on a population of the yellow-bellied poison frog, *Andinobates fulguritus*. We found that *A. fulguritus* migrated vertically, tracking seasonal rainfall, and displayed strong philopatry to individual trees. Furthermore, *A. fulguritus* almost exclusively inhabited the largest trees at the study location, which provided disproportionately high-quality microhabitats and epiphytes compared to other trees. LOTs, and specifically *Anacardium excelsum* at our site, appear to serve as keystone structures with high conservation value due to their provisioning of unique habitats. We conclude that the distribution of *A. fulguritus* is defined vertically by the stratification of arboreal microhabitat resources, horizontally by the presence of LOTs providing the resources, and temporally by the seasonal viability of the resources.

**Keywords** Amphibian · Biogeography · Migration · Philopatry · Pond-breeding · Dendrobatid

## Introduction

Tropical forests are heterogeneous environments (Kitching et al. 2013; Basset et al. 2015), which contain the greatest structural complexity, species richness (Janzen 1970; Ashton et al. 2015), and potential niche space of any terrestrial system (Tews et al. 2004; Chambers et al. 2013). Trees form distinct physical scaffolding for other organisms to distribute across, and large, old trees (LOTs) in particular serve as keystone structures in forests. Tews et al. (2004) define LOTs as “distinct spatial structures providing resources, shelter, or ‘goods and services’ crucial for other species”. Specifically, LOTs provide woody materials at various states of decay (Penone et al. 2019), water filled cavities (phytotelmata; Yanoviak 2001; Cockle et al. 2012), epiphyte masses (Woods et al. 2015; Spruch et al. 2019), and numerous additional microhabitats that may require many years to develop and accumulate (Franklin et al. 2002; Woods et al. 2015; Mahmoud et al. 2015; Lindenmayer 2016).

Communicated by Raoul Van Damme.

We find that the provisioning of unique resources by large, old trees reveals their high conservation importance, with the potential for even single tree logging to threaten commensal poison frogs.

✉ Edmund W. Basham  
ebasham1@ufl.edu

<sup>1</sup> School of Natural Resources and Environment, University of Florida, Gainesville, FL 32611, USA

<sup>2</sup> Escuela de Biología, Facultad de Ciencias Naturales y Exactas, Universidad Autónoma de Chiriquí, David, Panama

<sup>3</sup> Department of Herpetology, Zoo Atlanta, Atlanta, GA 30315, USA

<sup>4</sup> Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL 32611, USA

The ‘goods and services’ provided by LOTs are stratified in vertical space; for example, root structures provide unique habitat at ground level, whereas large water-holding epiphyte structures and cavities occur mostly in the mid to upper-canopy (Parker et al. 1995; Cascante-Marín et al. 2006; Mccracken and Forstner 2014; Basham et al. 2019; Seidl et al. 2019). Furthermore, such trees often exist in low densities due to natural mortality caused by disease (McDowell et al. 2018), storms (Manning et al. 2006), and lightning strikes (Magnusson et al. 1996; Yano-viak 2013), among other natural disturbances, as well as anthropogenic disturbances such as targeted harvesting (Sist et al. 2014), fragmentation (D’Angelo et al. 2004; Hillers et al. 2008), and anthropogenic forest fires (Lindenmayer 2016). Thus, the horizontal distribution of LOTs and the vertical stratification of their unique ‘goods and services’ produce a complex pattern of isolated resources, much like islands in an archipelago (MacArthur and Wilson 1967; Adams et al. 2017; Méndez-Castro et al. 2018).

Importantly, the high-quality arboreal habitats such as cavities and epiphytic masses supported by trees are strongly linked to tree age and size, due to the length of time required for microhabitat development (Cascante-Marín et al. 2006; Ranius et al. 2009; Cockle et al. 2012; Manning et al. 2013; Woods et al. 2015). Moreover, arboreal habitats may only be viable (i.e. saturated with water) during periods of sufficient rainfall. Thus, species which utilize arboreal habitat may be constrained vertically by the stratification of resources, horizontally by the presence of provisioning LOTs, and temporally by the seasonal availability of the resources. Yet, these relationships have not been well explored in the vertical dimension across temperate and tropical systems alike.

Where resources are limited or isolated, but their presence remains relatively predictable over space and time (e.g. LOTs) (Stacey and Ligon 1991; Part 1991), specific ecological behaviours may develop to track these patterns. Philopatry—a tendency to return to or remain near a particular site or area—is one such behaviour (Part 1991). In combination with periodic availability of habitat and resources, philopatric strategies may result in migratory behaviours to maximise fitness and population persistence over time (Semlitsch 2008; Cayuela et al. 2020). For example, seasonally inundated wetlands function as seasonal keystone structures (Tews et al. 2004), and many pond-breeding frog species show a high degree of philopatry by returning to the same pond year on year, often the natal pond (Elewa 2005; Rittenhouse and Semlitsch 2007; Pittman et al. 2014). Here, we consider amphibian migration as defined by Semlitsch (2008) in his review of a large literature pertaining to amphibian movement ecology, as the seasonal movements, primarily by resident adults, between terrestrial overwintering sites and aquatic breeding sites, with secondary

migrations also possible between foraging habitat, summer refugia, and overwintering sites.

Many tropical forest frogs show a high degree of philopatry and some species are loyal to alternative ‘ponds’, such as tree cavities and epiphytic phytotelmata (Schiesari et al. 2003; Ringler et al. 2009; Pašukonis et al. 2016; Beck et al. 2017; Nothacker et al. 2018). For example, the Amazonian canopy frog (Hylidae: *Phrynohyas resinifictrix*) returns to the same tree holes across years (Schiesari et al. 2003), and the strawberry poison frog (Dendrobatidae: *Oophaga pumilio*) clusters around remnant trees in pastures in Costa Rica (Robinson et al. 2013). Additionally, in French Guiana, Beck et al. (2017) found that tadpole transport by the brilliant-thighed poison frog (Aromobatidae: *Allobates femoralis*) was strongly directed towards known deposition sites. However, while forest frogs have regularly been observed to contest small territories (Werner et al. 2011; Beck et al. 2017), display impressive homing abilities (Pašukonis et al. 2014; Nothacker et al. 2018), and travel from ground to canopy daily to and from breeding locations (Pašukonis et al. 2016, 2019), to our knowledge, none have been observed and quantified seasonally migrating *en masse* between overwintering habitat on the ground and breeding habitat in the canopy. Although these movement behaviors are a well-known phenomenon, studies which combine individual tracking and vertical surveys are limited in the tropics and globally. Therefore, data regarding the distances, timing, and extent to which frogs migrate throughout the canopy are lacking in the literature.

Here, we study the seasonal movement and distribution of a phytotelmata-breeding frog over 4 years across vertical and horizontal space to determine if ecological constraints between the canopy and ground result in philopatric and migratory behaviours. Basham and Scheffers (2020) found in central Panama that 8 out of 9 arboreal frog species moved vertically in response to changes in seasonal climate, particularly precipitation. However, one species, *Andinobates fulguritus* (the yellow-bellied poison frog), moved 25 m on average from the canopy during the wet season down to the ground in the dry season. These vertical movements were larger and more predictable than those of other species in the community (Basham and Scheffers 2020) and sufficiently long in duration to drive changes in their alkaloid defence compounds (Basham et al. 2021), therefore, potentially representing evidence of migratory behaviour. Furthermore, *A. fulguritus* individuals were found almost exclusively on the largest trees, *Anacardium excelsum* in particular, which supported high densities of epiphytes and microhabitats.

We established the following three principal objectives for this study:

1. Determine which primary “goods and services” provided by trees predict the horizontal distribution of a

canopy specialist species, *A. fulguritus*. Understanding the effect of local landscape and tree habitat characteristics on species distributions will help pinpoint the occurrence and impact of LOT keystone structures in the landscape.

2. Assess patterns of philopatry, migration, and emigration in adult *A. fulguritus*.
3. Estimate tree-based population sizes of *A. fulguritus* across occupied trees.

We confirm that canopy breeding tropical frogs may exhibit seasonal migratory behaviour, dispersing from ground habitats in the dry season to canopy habitats in the wet season, similar to that of migratory pond-breeding frogs. Akin to the classical literature on the ecology of pond-breeding amphibians across temperate and tropical regions (Semlitsch 1998; Semlitsch and Bodie 1998; Linsenmair and Spieler 1998; Elewa 2005; Neckel-Oliveira and Gascon 2006), canopy epiphytes provided by LOTs represent the “ponds” and general breeding habitat, and leaf litter accumulations and tree roots at the base of the tree represent the terrestrial “overwintering” habitat—with seasonal rainfall patterns driving migrations back and forth between the forest floor and the forest canopy (conceptual Fig. 1a, b). We provide evidence that the vertical migrations and horizontal distribution of *A. fulguritus* are tied to LOTs and their provisioning of resources, highlighting their high conservation value.

## Methods

### Study area

In central Panama, we surveyed an Isthmian-Atlantic Moist Forest located within the Esteban Alphonso Lee Natural Reserve (latitude = 9.35855 N, longitude = 79.7029 W; 499 m.a.s.l), which borders the Chagres and Portobelo National Parks. Our sampling area was confined to an altitudinal range of 200–500 m.a.s.l (Fig. S1a, b). The landscape is topographically diverse, with many gullies and streams and mostly devoid of flat areas or standing water. The forest is largely comprised of primary growth with a standard canopy height of 30 m and emergent trees reaching 40–50 m. This area has a seasonal climate with a pronounced dry season from January to March and a wet season from April to December (Comita and Engelbrecht 2009; Basham and Scheffers 2020; Fig. S1c).

### Survey methods

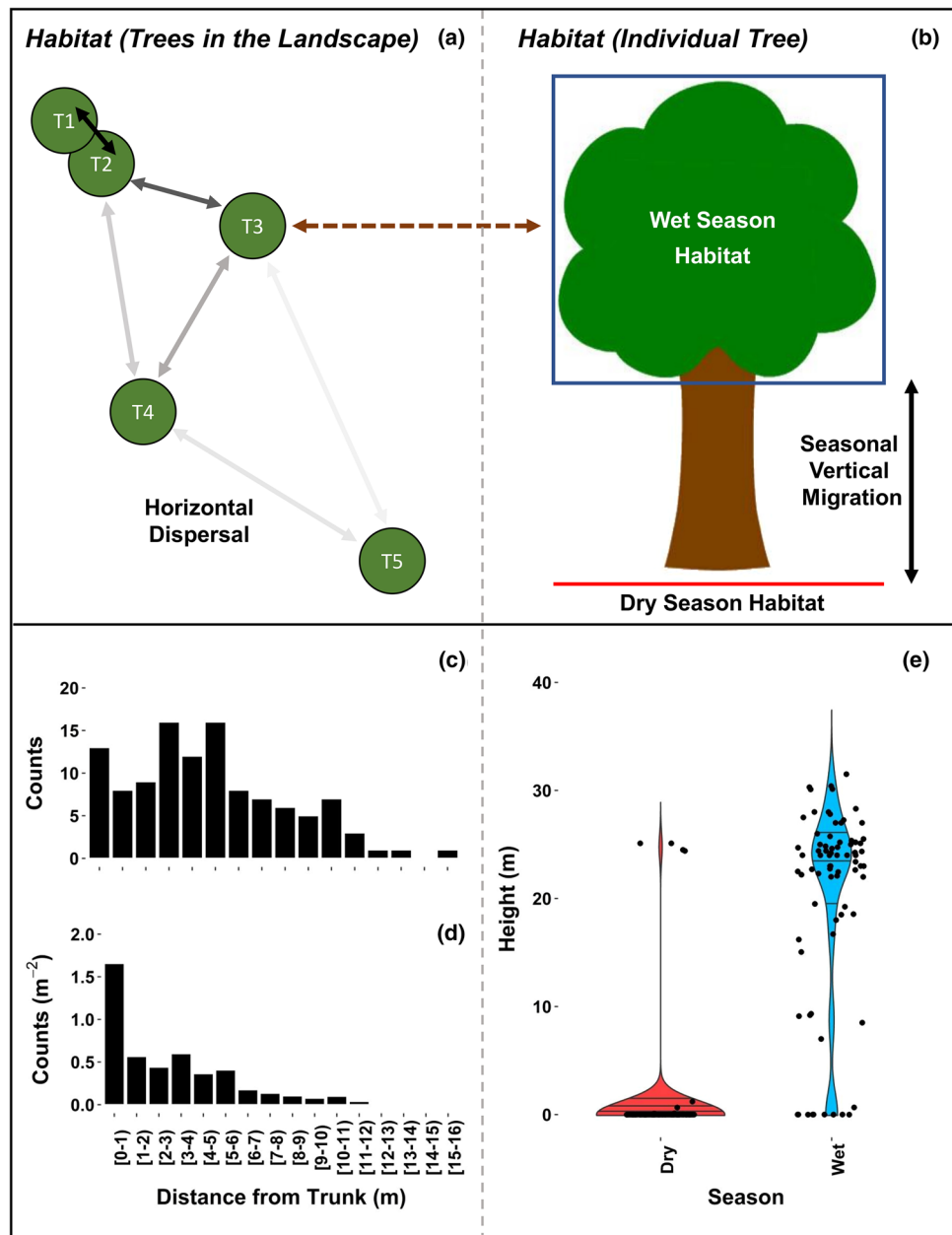
We conducted sequential surveys for frogs from 2017 to 2020 across three dry seasons (January–March) and three

wet seasons (April–December), starting in the wet season of 2017. During the 2017 and 2018 field seasons, we observed *A. fulguritus* primarily on *Anacardium excelsum* trees (henceforth, “Espavé”). To ensure recapture rates were sufficient to provide accurate estimates of *A. fulguritus* density, sampling effort was focused on Espavé trees. However, we also sampled trees of other species to assess the occurrence of *A. fulguritus* across a random sample of adult canopy trees. Our selection criterion for trees was the presence of a safe anchor point in the high canopy able to support a full vertical survey; thus we did not discriminate by microhabitat or tree characteristics and attained a random sample of adult canopy trees. We conducted 1-h vertical, ground-to-canopy surveys for frogs using methods detailed in Scheffers et al. (2013). At each tree, we conducted ground-to-canopy surveys with 10 min of survey time on the ground (in a 4 × 4 m square), as well as in the understory (1–4 m), sub-canopy (approx. half of the max. height climbed) and canopy (max. height climbed). We used the remaining 20 min to opportunistically survey from understory to canopy, resulting in a total survey time of 1 h. During arboreal surveys, we searched for arboreal amphibians in tree holes, moss, epiphytes, and other microhabitat structures (Heyer et al. 1994). We also conducted ground-only surveys at the base of each tree, which consisted of searching through leaf litter, logs, and other microhabitats within a 15-m radius around the tree for 1 h (Heyer et al. 1994). In total, we completed 237 ground-to-canopy surveys and 415 ground-only surveys, representing 652 survey man-hours. When captured, the vertical height of tree-based individuals and the horizontal distance from the tree trunk of ground-based individuals was recorded with a laser distance meter. Though it was not our express intent to study the specific breeding ecology of *A. fulguritus*, we also noted all observations of breeding/reproductive activity (e.g. the presence of tadpoles being carried by adults). Ventral photographs of each individual *A. fulguritus* were used to determine unique ventral patterns and manually compile a capture history for each individual.

Tree surveys were repeated within and across seasons, however, due to logistical constraints in some seasons, trees were not surveyed evenly. For example, some trees were consistently sampled within and across all seasons, while others were sampled in only a single season. In total we surveyed 107 trees (41 Espavé and 66 trees comprising 37 other species, Table S1). In the 2019 and 2020 dry seasons, additional ground surveys were conducted without paired canopy surveys. Basham and Scheffers (2020) determined that *A. fulguritus* almost exclusively occurs on the ground during the dry season, and thus surveys were effective at sampling the majority of individuals present without a paired canopy survey.

*A. fulguritus* is known to utilise ground and canopy habitat, therefore we recorded variables that may facilitate

**Fig. 1** **a** Conceptual figure showing the distribution of trees, which represent “ponds” (in classical literature; e.g., Semlitsch 2008), in the landscape on a horizontal scale. Arrows between trees are shaded to represent the likelihood of movements between sites, darker being more likely. **b** Conceptual figure showing the seasonal horizontal and vertical habitat distribution of *A. fulguritus* on individual trees. **c, d** The distribution of *A. fulguritus* away from the trunk when found on the ground in either the dry season. Mean distance from trunk values were calculated for each individual in each year, with the number of individuals in each 1 m interval representing the raw values shown in (c). In (d), the relative density of individuals was calculated as the number of individuals in each 1 m interval divided by the area in square meters of that 1 m interval (representing 1 m wide circular bands with the trunk at the centre). **e** Violin plot showing the empirical vertical distribution of captured *A. fulguritus* in the wet and dry seasons. To account for repeated catches of the same frog, each point represents the mean height of a specific individual in each season. Only data collected during paired ground and canopy surveys are included here. Paired surveys: dry season  $n=95$ , wet season  $n=97$



vertical habitat use, serve as or influence microhabitats, or retain moisture ( $N=13$  habitat variables, Table S2). Therefore, we recorded tree species, diameter at breast height (DBH), canopy height, presence or absence of moss on the trunk, canopy size (calculated using the area of a polygon formed by measuring the distance away from the trunk that branches extended to in the cardinal directions), and number of vines greater than 5 cm in diameter. We recorded the relative area of visible surface tree roots, epiphyte density, and density of *Ludovia* epiphytes on a categorical scale from low to high (integers 0–5). We include a separate measure of *Ludovia* epiphytes because *A. fulguritus* were often observed within them during arboreal surveys and we hypothesized

a specific microhabitat affinity to *Ludovia*. Epiphyte density may include, non-exclusively, the presence of *Ludovia*, and therefore may be correlated but each metric describes different levels of epiphyte specificity (general epiphyte affinities versus a specific affinity to *Ludovia*). We also measured additional habitat variables within two transects (10 m length  $\times$  2 m width) on opposite sides of each tree. We recorded small stems less than 8 cm in diameter and large stems greater than 8 cm within the transects, which we used to calculate a small and large stem density. At 10 m, 5 m, and 0 m on each transect we recorded three measures of canopy density, with the first using a Spherical Densiometer (left, right, and forward, facing away from the trunk;



Forestry Suppliers Spherical Crown Densiometer, defined as % light blocked by overhead vegetation) and two additional measures of percentage of ground cover vegetation below 50 cm (1 m<sup>2</sup> quadrat to the left and right side of transect).

## Data analysis

All analyses were conducted using R (R Core Team 2020). First, we scaled each continuous variable to a mean of zero and unit variance by subtracting the mean and dividing by the standard deviation. Tree species were reduced to a binomial variable of Espavé or “non-Espavé” due to the high number of tree species (37 “non-Espavé” species) with a small number of representative individual trees (Table S1). We then quantified variation in tree habitat characteristics across 107 trees and compared those characteristics between Espavé and non-Espavé trees using a Principal Components Analysis (PCA; implemented with the “prcomp” function from the R package “stats”; Fig. 2). To inform our analytical approach, we then calculated the collinearity of variables using the pairwise nonparametric Spearman correlations function “corr.test” from the R package “psych” (Revelle 2015; Fig. S2). We also compared variable means between Espavé and “non-Espavé” trees using *t*-tests.

To determine how habitat characteristics influence the distribution and abundance of *A. fulguritus*, we used Generalized Linear Mixed-Effects Models (GLMMs) to model presence/absence and count data resulting from repeated surveys. Presence/absence data were fitted using binomial GLMMs with a logit link function via the “glmer” function in the R package “lme4” (Bates et al. 2015). We fitted the count data with negative binomial GLMMs with a log link function, implemented via the R package “glmmTMB” (Brooks et al. 2017). To determine the influence of each habitat variable, we created candidate model sets for both model types. These model sets were constructed first by specifying a base model, which contains parameters that will be featured in every model. This base model featured tree ID as a random intercept, which accounted any for spatial dependencies resulting from repeated surveys. Recognizing that the spatial distribution of trees in the landscape may explain some variation in the data, we also included a scaled spatial variable of Latitude + Longitude as a fixed effect in the base model. Finally, the candidate model sets were built by specifying each habitat variable as a fixed effect, however due to multicollinearity, models only featured a single habitat variable (Figs. 2, S2). Lastly, models were duplicated with an interaction term for the Espavé/non-Espavé, because initial observations of *A. fulguritus* showed habitat affinities towards Espavé. However, due to the inherent complexity of interactive models, some models were removed due to non-convergence. To evaluate each

candidate model in its respective model set, we employed an information theoretic approach with Akaike’s Information Criteria (AIC) as our operative criterion for determining relative explanatory power (Burnham and Anderson 2004). Additionally, to determine the objective explanatory power of each variable used in our candidate sets, we derived marginal and conditional pseudo R<sup>2</sup> metrics for fixed and random effects, respectively (Nakagawa and Schielzeth 2013; Johnson 2014).

The density of pond-breeding amphibians inhabiting overwintering terrestrial habitat decreases with distance away from their breeding pond (Smith and Green 2005). To determine if this phenomenon exists in our data, we calculated the relative density of *A. fulguritus* with increasing distance from the trunk of the surveyed tree, whereby the mean distance values were calculated for each individual in each year. The count of individuals within each 1 m band extending 15 m outwards from the tree trunk was then divided by the area in square meters in that 1 m circular band around the tree, to give a relative density of *A. fulguritus* per square meter in each band.

To assess tree-wise population sizes we used the basic Lincoln–Petersen method (Seber 1974).

Lincoln–Petersen Method

$$\hat{N}_i = \frac{M_i \times T_i}{R_i},$$

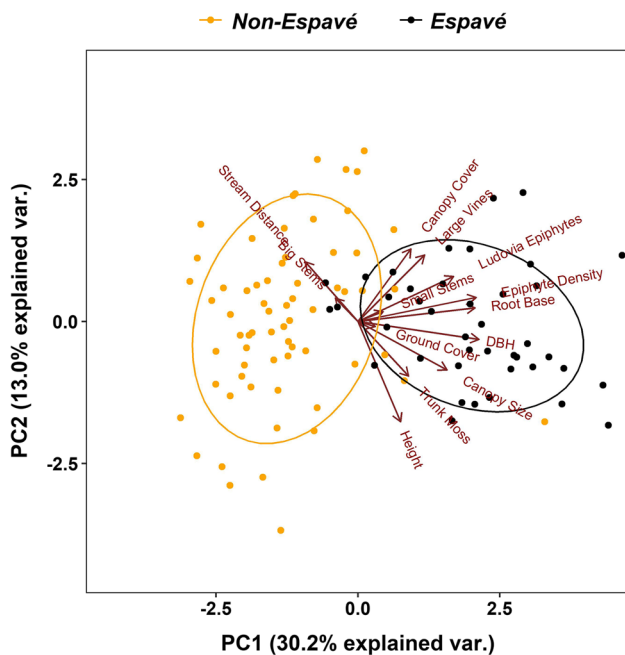
where  $\hat{N}_i$  is the total estimated population size,  $R_i$  is the sum of marked recaptures in the last sample,  $M_i$  is the sum of previously marked individuals, and  $T_i$  is the total individuals in the last sample, for tree  $i = 1, \dots, n$ .

We were only able to conduct this analysis on trees with sufficient recapture rates to calculate reliable population estimates (i.e. trees surveyed on 3 or more occasions in the same year, with recaptures of at least 5 individuals). Thus, these estimates represent the upper bounds of frog abundance hosted by trees at the site.

Four main assumptions must be addressed for this analysis (Lindeman 1990):

(1) *Animals do not lose markings between sampling occasions* Of the 89 unique recaptured individuals, only two indicated minor changes in pattern. Colour patterns may change as juveniles and/or young adults develop, but here our analysis focused only on adults to reduce misidentification of individuals. Furthermore, recaptured individuals were strikingly consistent in pattern even across 1- to 2-year periods.

(2) *Markings are correctly noted and recorded for each sampling occasion* We relied on ventral colour pattern-matching by a human researcher. Due to some inconsistencies in photos we could not use pattern recognition technology (Gamble et al. 2008). Photo matching was repeated and no resulting mismatches were found.



**Fig. 2** Principal component analysis of the scaled habitat characteristic variables of trees, grouped by Espavé (41 trees), and all “Other” tree species (66 trees of 37 species)

(3) *The population is closed, i.e., there is no loss (death or emigration) or dilution (birth or immigration) between sample periods* We used sampling occasions from both the dry season and wet season of the same year to bolster the number of known marked individuals at a site. In the 3–5 month intervening period between seasons we expect the same death rate for marked and unmarked individuals, which may cause a slight overestimation of population size, but we expect very low recruitment of new adult individuals in the wet season sampling that immediately follows the less reproductive dry season. Regarding immigration, recorded movements between trees were very rare (2 of 89 individuals moved horizontally).

At two pairs of trees, we detected multiple movements of frogs between trees. Because these paired trees were also very close (approximately 9 m and 14 m, respectively; mean pairwise distance = 1030 m), they were likely spatially non-independent and thus, we combined data for these trees as they were considered single “breeding units” for the purposes of population and philopatry estimation (Semlitsch 2008). Population estimates for each tree pair across multiple years were halved for a “per tree” estimate.

(4) *All individuals in the population have an equal probability of capture during each sampling occasion* We surveyed sites thoroughly and recaptured individuals were found at varied locations on or beneath the host tree. However, some

frogs exhibited microhabitat fidelity (within a tree), which may lead to an underestimation in our estimates due to the favourable recapture of some marked individuals.

To estimate philopatry and migration, we summarised recaptures across trees, seasons, and years, and assessed the proportion of recaptures that involved horizontal movements between trees, recaptures at the same tree, and movement between vertical strata. Here, philopatry would be indicated by a low number of horizontal movements, a high number of recaptures at the same tree, and higher densities of frogs remaining close to the host tree in the dry season. Vertical migration would be indicated by recaptures between dry and wet seasons occurring at the ground and canopy, respectively. To assess population-level seasonal height shift, we also included a simple model of mean frog height by season (data presented in Fig. 1e) and report the estimated marginal means and standard deviations for both seasons.

## Results

Of the 41 Espavé trees sampled, 23 were inhabited by *A. fulguritus*, whereas of the 66 “non-Espavé” trees, representing 37 tree species, only two were inhabited. Across all surveys we found ten individual frogs carrying tadpoles in the canopy of Espavé during the wet season. Of these ten, five were found among epiphytic masses of *Ludovia* epiphytes and the other five were found among mixed-species epiphyte masses of ferns and orchids with large accumulations of leaf litter. A single frog was found carrying tadpoles on the ground, among leaf litter during the dry season, underneath an Espavé. In the dry season the mean height of individuals was 0.632 m (SD = 3.88) (Fig. 1e), and in the wet season mean height was 19.8 m (SD = 9.4) (Fig. 1e). Dry season mean height and standard deviation were strongly influenced by the 4 recordings of individuals found in the canopy, as the majority were found at 0 m.

Our mixed-effect presence models suggest DBH was the best predictor of *A. fulguritus* occurrence (Table 1, Fig. 3a). There was, however, competing support from the interaction model of DBH and Espavé (representing the binomial factor of Espavé/non-Espavé; Fig. 3b) and the interaction model of stream distance and Espavé (Fig. 3c). The top three models cumulatively explain approximately 95% of the overall variance in our analysis of *A. fulguritus* presence (Table 1). Mixed-effects models of *A. fulguritus* counts suggest their abundance was best explained by the interaction of stream distance and Espavé (Fig. 3d), followed by Espavé (Fig. 3e), and the interaction model of DBH and Espavé (Fig. 3f). The top three models cumulatively explain approx. 63% of the variance in our analysis of *A. fulguritus* abundance (Table 1).

Our t-tests showed that Espavé trees significantly differed in most structural and habitat features from the mixed-species community. Specifically, Espavé were distributed closer to streams and had greater DBH, root base size, epiphyte density, and *Ludovia* epiphytes (Table S2). Several structural and habitat features were strongly correlated, e.g. DBH, Epiphytes, and Roots (Figs. 2, S2).

Population sizes averaged approximately 12 frogs per tree, with 2 trees supporting populations of over 20 individuals (Table 2). Because 16 of the 25 inhabited trees (of 107 total sampled trees) did not have sufficient captures/recaptures for reliable population estimates, it is likely that a small number of trees host a disproportionately large proportion of the total population within our study area.

Excluding movements which occurred between two close pairs of trees determined as individual breeding units, the vast majority (98%) of recaptures occurred at the same tree, with only two individual frogs having moved between trees (63 m and 204 m horizontal movements; Table 3). Frogs were recaptured at the same trees over multiple seasons

and years, and during the dry season, frog density declined rapidly away from the trunk of surveyed trees (Fig. 1c, d), thus providing strong evidence of philopatry in adult *A. fulguritus*.

## Discussion

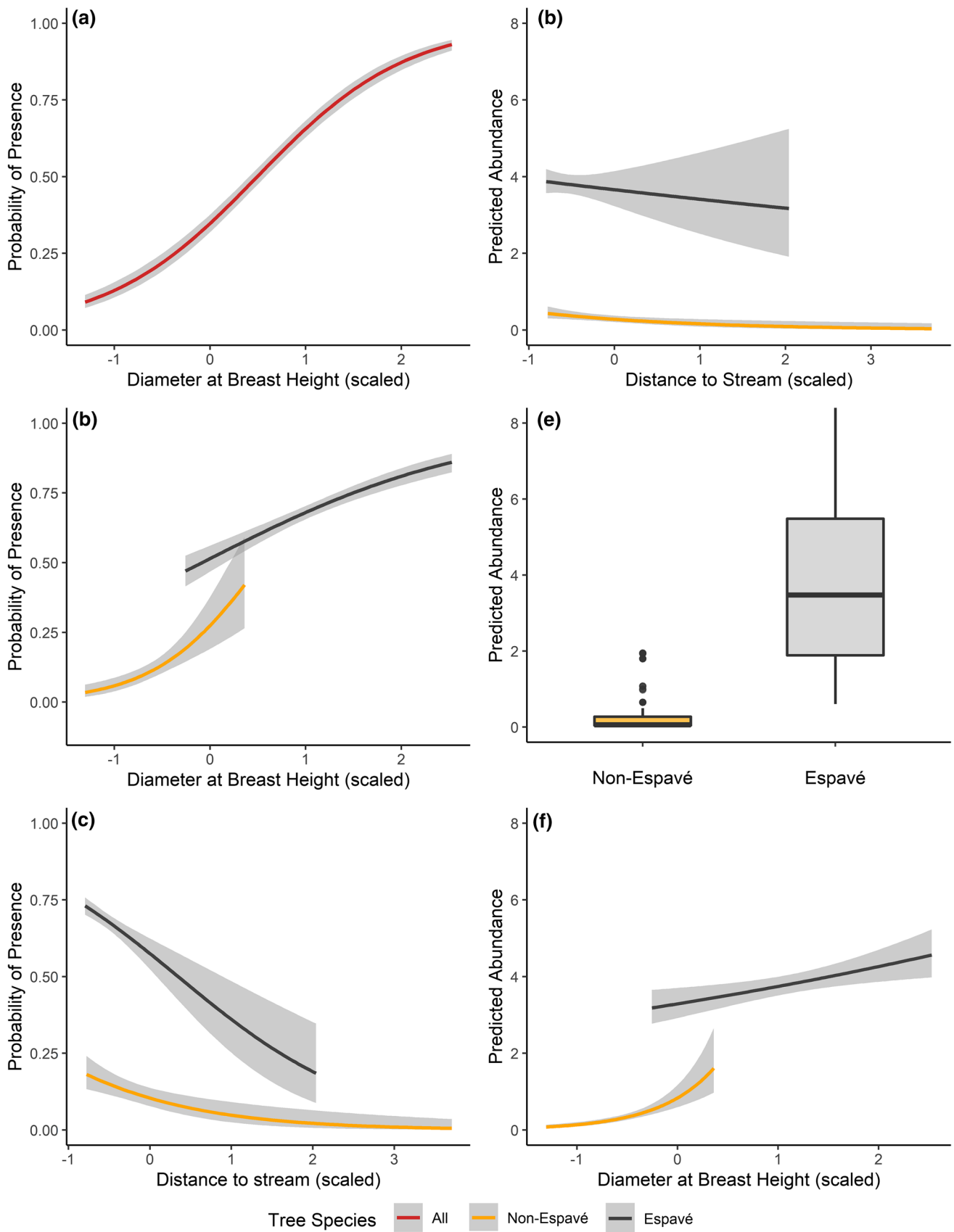
We observed that *A. fulguritus* had a strong preference for the largest trees, which in this forest were primarily Espavé (Fig. 3a, b). At our sampling location, Espavé trees were larger in girth, had greater root bases, grew closer to streams, and hosted more epiphytes than a random sample of adult canopy trees. We demonstrate that *A. fulguritus* undergoes a seasonal migration from the epiphyte-laden canopy in the wet season to the root and leaf litter microhabitats at ground level in the dry season. Indeed, migration is typically driven by resource utilization and life-cycle processes (Chapman et al. 2011; Pittman et al. 2014). Interestingly, the vertical migration of arboreal amphibians mirrors the well-studied

**Table 1** Generalized Linear Mixed Model results ranked by AICc for presence and count data, respectively

Fixed effects	<i>K</i>	$\Delta AICc$	$\omega_i$	$\sum \omega_i$	Marginal $R^2$	Conditional $R^2$
Presence						
DBH	4	0.000	0.704	0.704	0.463	0.692
DBH*Espavé	6	2.823	0.172	0.875	0.496	0.677
Stream Distance*Espavé	6	4.944	0.059	0.935	0.444	0.672
Espavé	4	6.959	0.022	0.956	0.462	0.693
Ground Cover	6	7.263	0.019	0.975	0.486	0.702
Moss*Espavé	6	8.954	0.008	0.983	0.465	0.694
Tree Height*Espavé	6	9.576	0.006	0.989	0.474	0.689
Canopy Cover*Espavé	6	10.032	0.005	0.994	0.525	0.669
Vines*Espavé	6	10.062	0.005	0.998	0.517	0.675
Stream Distance	4	13.383	0.001	0.999	0.504	0.669
Counts						
Stream Distance*Espavé	7	0.000	0.223	0.223	0.567	0.836
Espavé	5	0.004	0.223	0.446	0.621	0.807
DBH*Espavé	7	0.435	0.179	0.625	0.553	0.824
Ground Cover*Espavé	7	0.741	0.154	0.779	0.567	0.836
Moss*Espavé	7	1.286	0.117	0.896	0.574	0.840
Canopy Cover*Espavé	7	2.288	0.071	0.968	0.565	0.833
Tree Height*Espavé	7	4.121	0.028	0.996	0.578	0.827
DBH	5	8.063	0.004	1.000	0.615	0.816
Roots	9	16.985	0.000	1.000	0.633	0.814
Stream Distance	5	18.001	0.000	1.000	0.586	0.816

Each fixed effect covariate was used as a predictor variable to model *A. fulguritus* presence and counts, the response variables, with 'tree ID' as a random effect. Each model also featured a scaled geographical variable (Latitude + Longitude) as a single fixed effect. The top 10 models are included here. In the counts model set, the interaction models of *Ludovia*\*Espavé, Roots\*Espavé, and Epiphytes\*Espavé did not converge and were not included

*K* # parameters, *AICc* Akaike's Information Criteria corrected for small sample sizes,  $\Delta AICc$   $AIC_i - \min(AIC)$ ,  $\omega_i$  model weight,  $\sum \omega_i$  cumulative model weight, *Marginal R*<sup>2</sup> proportion of variance explained by fixed effects alone, *Conditional R*<sup>2</sup> proportion of variance explained by random effects alone





**Fig. 3** Top ranked model predictions for frog presence (**a–c**) and abundance (**d–f**) by habitat variables. **a** Model predictions of frog presence probability as a function of tree diameter at breast height (DBH), **b** an interaction between DBH and a binomial factor, Espavé and non-Espavé, and **c** model predictions of frog presence probability as a function of an interaction between distance to stream, and an Espavé/non-Espavé factor. **d** Model predictions of frog abundance as a function of an interaction between distance to stream and an Espavé/non-Espavé factor, and **e** the binomial factor, Espavé and non-Espavé; and **f** model predictions of frog presence probability as a function of an interaction between DBH and the binomial factor, Espavé and non-Espavé. Model predictions were obtained from the three top ranked models in Table 1 (presence and counts); solid lines and shaded areas represent a line of best fit and standard error, respectively, using a binomial smoothing function

seasonal horizontal movement patterns of pond-breeding amphibians, with individuals migrating between terrestrial and aquatic habitats (Linsenmair and Spieler 1998; Pechmann et al. 2001; Elewa 2005; Semlitsch 2008; Pittman et al. 2014). For pond-breeding species, migration distances between the terrestrial and aquatic habitats are often at the scale of hundreds to thousands of meters, radiating away from the breeding habitat (Smith and Green 2005; Rittenhouse and Semlitsch 2007; Pittman et al. 2008). However, we record migratory distances of *A. fulguritus* to be limited to approximately 30 vertical meters. Such short movement distances are likely correlated with small home ranges of dendrobatid frogs, which generally show strong patterns of philopatry and territoriality (Brown et al. 2009; Meuche et al. 2011; Werner et al. 2011). Although frogs of diverse families, including Dendrobatidae (Pašukonis et al. 2016), Hylidae (Donnelly and Guyer 1994; Schiesari et al. 2003; Roznik and Alford 2015), Microhylidae (Vences et al. 2003), Rhacophoridae (Kam et al. 1996; Khongwir et al. 2016), among others, have been observed to move vertically for reproduction, this study represents the first comprehensive quantification of vertical movements by unique individuals across multiple seasonal cycles, thus providing sufficient data to assess the presence of vertical migratory behaviours. Our efforts provide a unique insight, but the nature of vertical movement by frogs requires further study and characterization that can be achieved by combining individual tracking and extensive vertical surveying of animals in forests globally.

Semlitsch (2008) offers a discussion of the evolutionary pressures driving dispersal and philopatry in amphibians. Philopatry may confer greater fitness advantages through the utilization of stable, high-quality sites (habitat), as individuals may simply return to known sites and utilize the high-quality habitat repeatedly. However, if individuals do not obtain knowledge of new sites in the landscape,

any degradation of sites over time will eventually reduce advantages gained through philopatry (Gamble et al. 2007). Thus, an equilibrium between philopatry and dispersal may be reached by combining the benefits of repeatedly utilizing high quality sites, with discovering and dispersing to new sites that may replace those that are deteriorating (Semlitsch 2008; Sinsch 2014). We see here that *A. fulguritus* conforms to at least part of this equilibrium by demonstrating strong patterns of interannual philopatry, migration between aquatic and terrestrial habitats, and successful (albeit limited) movements between distant sites (trees). Unfortunately, we were unable to determine if movements were to unknown (random) or known (non-random) trees. It must also be noted that movements between trees are more likely to occur in the dry season, when frogs are on the ground and able to move horizontally. However, the physiological demands of the dry season may limit horizontal movement, and therefore could also be a driver of philopatry in this system. Our study gives further evidence that philopatry in frogs can originate in any circumstance where life-cycle processes are tied to discrete use of resources in space.

The breeding habitat of pond-breeding amphibians is relatively distinct and clearly defined in a landscape. Similarly, the reproductive locations of *A. fulguritus* seem to be delineated as single trees containing high densities of epiphytes and microhabitats. Thus, a single tree may function similarly to a “pond”, and so the philopatry that we describe here is at the scale of tree, which supports the phytotelmata where larval development occurs. While we did not observe the specific event of tadpole deposition in phytotelmata, we did observe ten individuals carrying tadpoles in the canopy. The preference for trees with a high density of epiphytes and phytotelmata, however, is not surprising for a phytotelm-breeder, especially considering that males of this species are known to carry larvae (soon after hatching) to phytotelmata including water-filled bromeliads (Kahn and Montoya 2016). Furthermore, sites that contain many phytotelmata within a small area, or on a tree, are more feasibly defended and monitored (Pröhl 2005; Werner et al. 2011). For example, the home range size of male Amazonian *Ranitomeya reticulata* were strongly correlated with the number of bromeliad phytotelmata in proximity (Werner et al. 2011).

Interestingly, the majority of individuals caught in the wet season were found in the canopy, including 10 of 11 individuals observed transporting tadpoles. Observations of *A. fulguritus* at other localities (Kahn and Montoya 2016) and studies of other closely related dendrobatids have documented egg laying occurring on the ground, with hatched tadpoles then transported to above-ground phytotelmata (Lötters et al. 2007; Wells 2007). With so few occurrences

**Table 2** Lincoln-Petersen population estimates for *A. fulguritus* across trees and years

Tree	2018	2019	Year Mean	Per Tree
#67/#69	23.3	27	25.15	12.6
#89	12	18.6	15.3	15.3
#90	10	6	8	8
#103		12	12	12
#111/#114		44.8	44.8	22.4
#119		12	12	12
#121		6	6	6
Mean				12.6
SD				4.9
Max				22.4

Of 107 trees, seven (here considering trees #67 and #69, and #111 and #114 as two separate combined sites) had sufficient sampling coverage and recaptures to produce population estimates. All seven were Espavé

seen at ground level in the wet season (Fig. 1e), it is possible that *A. fulguritus* are undertaking their entire reproductive cycle in the canopy, through the stages of mating, egg laying, hatching, tadpole transport, and maturation. This hypothesis requires further investigation, but may be a common strategy for arboreal dendrobatids residing in locations where resources are concentrated in the canopy. Thus, while philopatry is observed at small scales in many dendrobatids (Ringler et al. 2009; Werner et al. 2011; Pašukonis et al. 2014; Beck et al. 2017; Nothacker et al. 2018), we highlight the impact that uniquely large keystone trees may have on frogs with life-cycle processes tied to vertical habitats.

While we see here that Espavé trees may act as keystone structures at our study location, this role may be filled by other tree species in other forests, because *A. fulguritus* distributions are likely driven by the quality of epiphytes and habitat that grow on the tree, not the tree species itself. We

suggest that this biological phenomenon is widespread and can originate anywhere, regardless of phylogenetic origins, so long as resource limitation is coupled with life-cycle processes in space. Indeed, similar relationships between frogs and trees may play out across vertical and horizontal space in many forests, driving novel patterns of philopatry and seasonal vertical migration which have yet to be documented due to a lack of vertical sampling.

As such, further targeted research is needed to fully characterize the importance of LOTs, in addition to Espavé, for frogs that breed in phytotelmata or other arboreal microhabitats of forest canopies. However, systems with LOTs are quite rare owing to widespread land-use change (urbanization and conversion to agriculture) and natural resource extraction (mining, silviculture). In Panama, large trees, including the Espavé, are sought after in silvicultural practices (Santander and Albertin 1980) and degradation has already severely impacted the region's forests (Condit et al. 2001). Our study clearly shows the potential impact of selective or single tree logging on individual species where strong commensalism exists, as we show in the relationship of *A. fulguritus* and Espavé trees. If large, old Espavé trees were logged in this forest, we predict the likely extirpation of *A. fulguritus* populations owing to the removal of its primary reproductive habitats. Trees as keystone structures are often highlighted in degraded or sparse landscapes where their impact is disproportionate to the surrounding landscape (Manning et al. 2006; Le Roux et al. 2015). Yet, in this primary growth forest, Espavé trees likely provide habitat and resources to a wide variety of other plant and animal species, as well as sequester carbon, improve habitat connectivity, and supplement soil nutrients (Manning et al. 2006). Here, by quantifying the relationship between *A. fulguritus* and large trees, we provide supporting evidence for the importance and conservation value of LOTs as keystone structures within contiguous primary growth forests.

**Table 3** Summary of captures and recaptures across trees (here considering trees #67 and #69, and #111 and #114 as two separate combined sites)

Statistic	Count
Total Captures	374 (200)
Dry season	259 (160)
Wet season	115 (78)
Total Recaptures	174 (89)
Recaptures at the same site (philopatry)	172 (87)
Recaptures at the same tree in the same season and year	121 (76)
Dry season	86 (55)
Wet season	35 (25)
Recaptures at a different tree—i.e. horizontal movement (emigration)	2 (2)
Vertical movements across seasons at the same tree (migration)	35 (29)
Vertical movements at the same tree in the same season and year	2 (2)

Unique individuals recorded in parentheses

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00442-022-05108-9>.

**Acknowledgements** Financial support was generously provided by the American Museum of Natural History's Theodore Roosevelt Memorial Grant and the American Philosophical Society's Lewis and Clark Fund. We thank Noel Rowe for his logistical support and permission for use of his research station facilities. We also thank Heikki Rissanen, 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 Permits SE/A-26-2018, SC/A-26-2018, and SE/A-14-2020.

**Author contribution statement** EB and BRS secured funding, conceptualised the study and wrote the manuscript. EB and JAB conducted data analysis. EB, MG-P, AR-M, and NC conducted field investigations and curated data.

**Data availability** Data available via GitHub repository: [https://github.com/schefferslab/Basham\\_et\\_al\\_2021](https://github.com/schefferslab/Basham_et_al_2021)

## References

- Adams BJ, Schnitzer SA, Yanoviak SP (2017) Trees as islands: Canopy ant species richness increases with the size of liana-free trees in a Neotropical forest. *Ecography* (cop) 40:1067–1075. <https://doi.org/10.1111/ecog.02608>
- Ashton LA, Barlow HS, Nakamura A, Kitching RL (2015) Diversity in tropical ecosystems: the species richness and turnover of moths in Malaysian rainforests. *Insect Conserv Divers* 8:132–142. <https://doi.org/10.1111/icad.12090>
- Basham EW, Scheffers BR (2020) Vertical stratification collapses under seasonal shifts in climate. *J Biogeogr* 47:1888–1898. <https://doi.org/10.1111/jbi.13857>
- Basham EW, Seidl CM, Andriamahohatra LR et al (2019) Distance-decay differs among vertical strata in a tropical rainforest. *J Anim Ecol* 88:114–124. <https://doi.org/10.1111/1365-2656.12902>
- Basham EW, Saporito RA, González-Pinzón M et al (2021) Chemical defenses shift with the seasonal vertical migration of a Panamanian poison frog. *Biotropica* 53:28–37. <https://doi.org/10.1111/btp.12842>
- Basset Y, Cizek L, Cuénoud P et al (2015) Arthropod distribution in a tropical rainforest: tackling a four dimensional puzzle. *PLoS ONE* 10:e0144110. <https://doi.org/10.1371/journal.pone.0144110>
- Bates D, Mächler M, Bolker BM, Walker SC (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48. <https://doi.org/10.18637/jss.v067.i01>
- Beck KB, Loretto M-CC, Ringler M et al (2017) Relying on known or exploring for new? Movement patterns and reproductive resource use in a tadpole-transporting frog. *PeerJ* 5:e3745. <https://doi.org/10.7717/peerj.3745>
- Brooks ME, Kristensen K, van Benthem KJ et al (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J* 9:378–400. <https://doi.org/10.32614/RJ-2017-066>
- Brown JL, Morales V, Summers K (2009) Home range size and location in relation to reproductive resources in poison frogs (*Dendrobatidae*): a Monte Carlo approach using GIS data. *Anim Behav* 77:547–554
- Burnham KP, Anderson DR (2004) Multimodel inference understanding AIC and BIC in model selection. *journals.sagepub.com* 33:261–304. doi: <https://doi.org/10.1177/0049124104268644>
- Cascante-Marín A, Wolf JHD, Oostermeijer JGB et al (2006) Epiphytic bromeliad communities in secondary and mature forest in a tropical premontane area. *Basic Appl Ecol* 7:520–532. <https://doi.org/10.1016/j.baee.2005.10.005>
- Cayuela H, Valenzuela-Sánchez A, Teulier L et al (2020) Determinants and consequences of dispersal in vertebrates with complex life cycles: a review of pond-breeding amphibians. *Q Rev Biol* 95:1–36. <https://doi.org/10.1086/707862>
- Chambers JQ, Negron-Juarez RI, Marra DM et al (2013) The steady-state mosaic of disturbance and succession across an old-growth Central Amazon forest landscape. *Proc Natl Acad Sci* 110:3949–3954. <https://doi.org/10.1073/pnas.1202894110>
- Chapman BB, Brönmark C, Nilsson JÅ, Hansson LA (2011) The ecology and evolution of partial migration. *Oikos* 120:1764–1775. <https://doi.org/10.1111/j.1600-0706.2011.20131.x>
- Cockle KL, Martin K, Robledo G (2012) Linking fungi, trees, and hole-using birds in a Neotropical tree-cavity network: Pathways of cavity production and implications for conservation. *For Ecol Manag* 264:210–219. <https://doi.org/10.1016/j.foreco.2011.10.015>
- Comita LS, Engelbrecht BMJ (2009) Seasonal and spatial variation in water availability drive habitat associations in a tropical forest. *Ecology* 90:2755–2765. <https://doi.org/10.1890/08-1482.1>
- Condit R, Robinson WD, Ibáñez R et al (2001) The status of the Panama canal watershed and its biodiversity at the beginning of the 21st century. *Bioscience* 51:389–398. [https://doi.org/10.1641/0006-3568\(2001\)051\[0389:TSOTPC\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0389:TSOTPC]2.0.CO;2)
- D'Angelo SA, Andrade ACS, Laurance SG et al (2004) Inferred causes of tree mortality in fragmented and intact Amazonian forests. *J Trop Ecol* 20:243–246. <https://doi.org/10.1017/S0266467403001032>
- Donnelly MA, Guyer C (1994) Patterns of reproduction and habitat use in an assemblage of Neotropical hyliid frogs. *Oecologia* 98:291–302. <https://doi.org/10.1007/BF00324217>
- Elewa AMT (2005) Migration of organisms: climate geography ecology. Springer, Berlin
- Franklin JF, Spies TA, Van PR et al (2002) Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *For Ecol Manag* 155:399–423. [https://doi.org/10.1016/S0378-1127\(01\)00575-8](https://doi.org/10.1016/S0378-1127(01)00575-8)
- Gamble LR, McGarigal K, Compton BW (2007) Fidelity and dispersal in the pond-breeding amphibian, *Ambystoma opacum*: Implications for spatio-temporal population dynamics and conservation. *Biol Conserv* 139:247–257. <https://doi.org/10.1016/j.biocon.2007.07.001>
- Gamble L, Ravela S, McGarigal K (2008) Multi-scale features for identifying individuals in large biological databases: An application of pattern recognition technology to the marbled salamander *Ambystoma opacum*. *J Appl Ecol* 45:170–180. <https://doi.org/10.1111/j.1365-2664.2007.01368.x>
- Heyer R, Donnelly M, Foster M, McDiarmid R (1994) Measuring and monitoring biological diversity: standard methods for amphibians. Smithsonian Institution, Washington, D.C.
- Hillers A, Veith M, Rodel MO (2008) Effects of forest fragmentation and habitat degradation on West African leaf-litter frogs. *Conserv Biol* 22:762–772. <https://doi.org/10.1111/j.1523-1739.2008.00920.x>
- Janzen DH (1970) Herbivores and the number of tree species in tropical forests. *Am Nat* 104:501–528. <https://doi.org/10.1086/282687>
- Johnson PCD (2014) Extension of Nakagawa & Schielzeth's R2GLMM to random slopes models. *Methods Ecol Evol* 5:944–946. <https://doi.org/10.1111/2041-210X.12225>
- Kahn TR, Montoya N (2016) Yellow-bellied Poison Frog *Andinobates fulguritus* (Silverstone, 1975). In: Kahn TR, La Marca E, Lotters S et al (eds) Aposematic Poison Frogs (*Dendrobatidae*) of the Andean Countries: Colombia, Bolivia, Ecuador, Peru and Venezuela. Conservation International Tropical Field Guides, Arlington

- Kam YC, Chuang ZS, Yen CF (1996) Reproduction, oviposition-site selection, and tadpole oophagy of an arboreal nester, *Chirixalus eiffingeri* (Rhacophoridae), from Taiwan. *J Herpetol* 30:52–59. <https://doi.org/10.2307/1564706>
- Khongwir S, Hooroo RNK, Dutta SK (2016) Breeding and nesting behaviour of *Rhacophorus maximus* (Anura: Rhacophoridae) in Meghalaya, North East India. *Curr Sci* 110:1102–1105. <https://doi.org/10.18520/cs/v110/i6/1102-1105>
- Kitching RL, Ashton LA, Nakamura A et al (2013) Distance-driven species turnover in Bornean rainforests: Homogeneity and heterogeneity in primary and post-logging forests. *Ecography* (cop) 36:675–682. <https://doi.org/10.1111/j.1600-0587.2012.00023.x>
- Le Roux DS, Ikin K, Lindenmayer DB et al (2015) Single large or several small? Applying biogeographic principles to tree-level conservation and biodiversity offsets. *Biol Conserv* 191:558–566. <https://doi.org/10.1016/j.biocon.2015.08.011>
- Lindeman PV (1990) Closed and open model estimates of abundance and tests of model assumptions for two populations of the turtle, *Chrysemys picta*. *J Herpetol* 24:78–81
- Lindenmayer D (2016) The importance of managing and conserving large old trees: a case study from Victorian mountain ash forests. *Proc R Soc Vic* 128:64. <https://doi.org/10.1071/RS16006>
- Linsenmair KE, Spieler M (1998) Migration patterns and diurnal use of shelter in a ranid frog of a West African savannah: a telemetric study. *Amphibia-Reptilia* 19:43–64. <https://doi.org/10.1163/156853898X00322>
- Lötters S, Jungfer K, Henkel FW, Schmidt W (2007) Poison frogs. In: *Biology, species & captive husbandry*. Edition Chimaira, Frankfurt
- MacArthur RH, Wilson EO (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton
- Magnusson WE, Lima AP, De Lima O (1996) Group lightning mortality of trees in a Neotropical forest. *J Trop Ecol* 12:899–903. <https://doi.org/10.1017/S0266467400010166>
- Mahmoud T, Gairola S, El-Keblawy A (2015) Large old trees need more conservation attention: A case of *Tamarix aphylla* in the arid deserts of the United Arab Emirates. *J Asia-Pac Biodivers* 8:183–185. <https://doi.org/10.1016/j.japb.2015.04.006>
- Manning AD, Fischer J, Lindenmayer DB (2006) Scattered trees are keystone structures—implications for conservation. *Biol Conserv* 132:311–321. <https://doi.org/10.1016/j.biocon.2006.04.023>
- Manning AD, Gibbons P, Fischer J et al (2013) Hollow futures? Tree decline, lag effects and hollow-dependent species. *Anim Conserv* 16:395–403. <https://doi.org/10.1111/acv.12006>
- McCracken SF, Forstner MRJ (2014) Herpetofaunal community of a high canopy tank bromeliad (*Aechmea zebrina*) in the Yasuní Biosphere Reserve of Amazonian Ecuador, with comments on the use of “arboreal” in the herpetological literature. *Amphib Reptile Conserv* 8:65–75
- McDowell N, Allen CD, Anderson-Teixeira K et al (2018) Drivers and mechanisms of tree mortality in moist tropical forests. *New Phytol* 219:851–869
- Méndez-Castro FE, Bader MY, Mendieta-Leiva G, Rao D (2018) Islands in the trees: a biogeographic exploration of epiphyte-dwelling spiders. *J Biogeogr* 45:2262–2271. <https://doi.org/10.1111/jbi.13422>
- Meuche I, Linsenmair KE, Pröhl H (2011) Female territoriality in the strawberry poison frog (*Oophaga pumilio*). *Copeia* 2011:351–356. <https://doi.org/10.1643/ce-08-135>
- Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R<sup>2</sup> from generalized linear mixed-effects models. *Methods Ecol Evol* 4:133–142. <https://doi.org/10.1111/j.2041-210x.2012.00261.x>
- Neckel-Oliveira S, Gascon C (2006) Abundance, body size and movement patterns of a tropical treefrog in continuous and fragmented forests in the Brazilian Amazon. *Biol Conserv* 128:308–315. <https://doi.org/10.1016/j.biocon.2005.09.037>
- Nothacker JA, Neu CP, Mayer M et al (2018) Homing behavior in the neotropical poison frog *Ameerega trivittata*. *Salamandra* 54:30–36
- Parker GG, Lowman MD, Nadkarni NM (1995) Structure and microclimate of forest canopies. In: Lowman MD, Nadkarni NM (eds) *Forest canopies*. Academic Press Inc, Cambridge, pp 73–106
- Part T (1991) Philopatry pays: a comparison between collared flycatcher sisters. *Am Nat* 138:790–796. <https://doi.org/10.1086/285252>
- Pašukonis A, Warrington I, Ringler M, Hödl W (2014) Poison frogs rely on experience to find the way home in the rainforest. *Biol Lett*. <https://doi.org/10.1098/rsbl.2014.0642>
- Pašukonis A, Trenkwalder K, Ringler M et al (2016) The significance of spatial memory for water finding in a tadpole-transporting frog. *Anim Behav* 116:89–98. <https://doi.org/10.1016/j.anbehav.2016.02.023>
- Pašukonis A, Loretto MC, Rojas B (2019) How far do tadpoles travel in the rainforest? Parent-assisted dispersal in poison frogs. *Evol Ecol* 33:613–623. <https://doi.org/10.1007/s10682-019-09994-z>
- Pechmann JHK, Estes RA, Scott DE, Gibbons JW (2001) Amphibian colonization and use of ponds created for trial mitigation of wetland loss. *Wetlands* 21:93–111. [https://doi.org/10.1672/0277-5212\(2001\)021\[0093:ACAUPJ\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2001)021[0093:ACAUPJ]2.0.CO;2)
- Penone C, Allan E, Soliveres S et al (2019) Specialisation and diversity of multiple trophic groups are promoted by different forest features. *Ecol Lett* 22:170–180. <https://doi.org/10.1111/ele.13182>
- Pittman SE, Jendrek AL, Price SJ, Dorcas ME (2008) Habitat selection and site fidelity of cope’s gray treefrog (*Hyla chrysoscelis*) at the aquatic-terrestrial ecotone. *J Herpetol* 42:378–385. <https://doi.org/10.1670/07-1702.1>
- Pittman SE, Osbourn MS, Semlitsch RD (2014) Movement ecology of amphibians: A missing component for understanding population declines. *Biol Conserv* 169:44–53
- Pröhl H (2005) Territorial behavior in dendrobatid frogs. *J Herpetol* 39:354–365. <https://doi.org/10.1670/162-04A.1>
- R Core Team (2020) R: A language and environment for statistical computing. R Found. Stat. Comput
- Ranius T, Niklasson M, Berg N (2009) Development of tree hollows in pedunculate oak (*Quercus robur*). *For Ecol Manag* 257:303–310. <https://doi.org/10.1016/j.foreco.2008.09.007>
- Revelle W (2015) Package “psych”—procedures for psychological, psychometric and personality research. R Packag, p 1–358.
- Ringler M, Ursprung E, Hödl W (2009) Site fidelity and patterns of short- and long-term movement in the brilliant-thighed poison frog *Allobates femoralis* (Aromobatidae). *Behav Ecol Sociobiol* 63:1281–1293. <https://doi.org/10.1007/s00265-009-0793-7>
- Rittenhouse TAG, Semlitsch RD (2007) Distribution of amphibians in terrestrial habitat surrounding wetlands. *Wetlands* 27:153–161. [https://doi.org/10.1672/0277-5212\(2007\)27\[153:DOATHJ\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2007)27[153:DOATHJ]2.0.CO;2)
- Robinson D, Warmsley A, Nowakowski AJ et al (2013) The value of remnant trees in pastures for a neotropical poison frog. *J Trop Ecol* 29:345–352. <https://doi.org/10.1017/S0266467413000382>
- Roznik EA, Alford RA (2015) Seasonal ecology and behavior of an endangered rainforest frog (*Litoria rheocola*) threatened by disease. *PLoS ONE* 10:e0127851. <https://doi.org/10.1371/journal.pone.0127851>
- Santander C, Albertin W (1980) *Anacardium excelsum*, especie forestal de los tropicos americanos. *Turrialba* 30:17–23
- Scheffers BR, Phillips BL, Laurance WF et al (2013) Increasing arborescence with altitude: a novel biogeographic dimension. *Proc R Soc B Biol Sci* 280. <https://doi.org/10.1098/rspb.2013.1581>
- Schiesari L, Gordo M, Hödl W (2003) Treeholes as calling, breeding, and developmental sites for the amazonian canopy frog,



- Phrynohyas resinifictrix* (Hylidae). Copeia 2003:263–272. [https://doi.org/10.1643/0045-8511\(2003\)003\[0263:TACBAD\]2.0.CO;2](https://doi.org/10.1643/0045-8511(2003)003[0263:TACBAD]2.0.CO;2)
- Seber GAF (1974) The estimation of animal abundance and related parameters. J Anim Ecol 43:603. <https://doi.org/10.2307/3397>
- Seidl CM, Basham EW, Andriamahohatra LR, Scheffers BR (2019) Bird's nest fern epiphytes facilitate herpetofaunal arboreality and climate refuge in two paleotropical canopies. Oecologia 192:297–309. <https://doi.org/10.1007/s00442-019-04570-2>
- Semlitsch RD (1998) Biological delineation of terrestrial buffer zones for pond-breeding salamanders. Conserv Biol 12:1113–1119. <https://doi.org/10.1046/j.1523-1739.1998.97274.x>
- Semlitsch RD (2008) Differentiating migration and dispersal processes for pond-breeding amphibians. J Wildl Manag 72:260–267. <https://doi.org/10.2193/2007-082>
- Semlitsch RD, Bodie JR (1998) Are small, isolated wetlands expendable? Conserv Biol 12:1129–1133. <https://doi.org/10.1046/j.1523-1739.1998.98166.x>
- Sinsch U (2014) Movement ecology of amphibians: from individual migratory behaviour to spatially structured populations in heterogeneous landscapes. Can J Zool 92:491–502. <https://doi.org/10.1139/cjz-2013-0028>
- Sist P, Mazzei L, Blanc L, Rutishauser E (2014) Large trees as key elements of carbon storage and dynamics after selective logging in the Eastern Amazon. For Ecol Manag 318:103–109. <https://doi.org/10.1016/j.foreco.2014.01.005>
- Smith MA, Green DM (2005) Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? Ecography (cop) 28:110–128. <https://doi.org/10.1111/j.0906-7590.2005.04042.x>
- Spruch L, Hellwig J, Zotz G, Blasius B (2019) Modeling community assembly on growing habitat “islands”: a case study on trees and their vascular epiphyte communities. Theoret Ecol 12:513–529. <https://doi.org/10.1007/s12080-019-0425-4>
- Stacey PB, Ligon JD (1991) The benefits-of-philopatry hypothesis for the evolution of cooperative breeding: variation in territory quality and group size effects. Am Nat 137:831–846. <https://doi.org/10.1086/285196>
- Tews J, Brose U, Grimm V et al (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J Biogeogr 31:79–92. <https://doi.org/10.1046/j.0305-0270.2003.00994.x>
- Vences M, Raxworthy CJ, Nussbaum RA, Glaw F (2003) New microhylid frog (*Plethodontohyla*) from Madagascar, with semi-arboreal habits and possible parental care. J Herpetol 37:629–636. <https://doi.org/10.1670/258-01A>
- Wells KD (2007) The ecology & behavior of amphibians. The University of Chicago Press, Chicago
- Werner P, Elle O, Schulte LM, Lötters S (2011) Home range behaviour in male and female poison frogs in Amazonian Peru (*Dendrobatiidae*: *Ranitomeya reticulata*). J Nat Hist 45:15–27. <https://doi.org/10.1080/00222933.2010.502257>
- Woods CL, Cardelús CL, Dewalt SJ (2015) Microhabitat associations of vascular epiphytes in a wet tropical forest canopy. J Ecol 103:421–430. <https://doi.org/10.1111/1365-2745.12357>
- Yanoviak SP (2001) The macrofauna of water-filled tree holes on Barro Colorado Island, Panama. Biotropica 33:110–120. [https://doi.org/10.1646/0006-3606\(2001\)033\[0110:TMOWFT\]2.0.CO;2](https://doi.org/10.1646/0006-3606(2001)033[0110:TMOWFT]2.0.CO;2)
- Yanoviak SP (2013) Shock value: are lianas natural lightning rods? In: Lowman M, Devy S, Ganesh T (eds) Treetops at risk: challenges of global canopy ecology and conservation. Springer International Publishing, New York, pp 147–153. [https://doi.org/10.1007/978-1-4614-7161-5\\_15](https://doi.org/10.1007/978-1-4614-7161-5_15)