



Bird's nest fern epiphytes facilitate herpetofaunal arboreality and climate refuge in two paleotropic canopies

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Abstract

In tropical forests, epiphytes increase habitat complexity and provision services rare to canopy environments, such as water retention, nutrient cycling, and microclimate refuge. These services facilitate species diversity and coexistence in terrestrial ecosystems, and while their utility in forest ecosystems is appreciated for the *Bromeliaceae* of the Neotropics, fewer studies have examined the role of Paleotropic epiphytes in ecological niche theory. Here, we compare herpetofaunal presence, abundance, and diversity of in bird's nest fern (*Asplenium nidus complex*; BNF) to other microhabitats in Madagascar and the Philippines. We measure BNF fern microclimates, examine temporal use of canopy microhabitats, and test models of fern characteristics hypothesized to predict herpetofaunal use. In both countries, one in five BNFs were occupied by herpetofauna, mostly amphibians, and species using BNFs were highly dissimilar from those in other microhabitats. Herpetofaunal presence and abundance were greater in BNFs than in other canopy microhabitats and were most commonly used during the day when fern temperatures were highly buffered. Finally, BNF area was the best predictor of herpetofaunal presence and abundance, compared to canopy cover and BNF height. Importantly, these patterns remained consistent despite the distinct phylogenetic histories of our two communities (Asian versus African). Our results suggests that BNFs and their microclimate services play a critical role in the ecology of two Paleotropic forests, and facilitate the use of canopy habitats by climate-sensitive species. However, future studies are needed to assess the consistency of BNFs' utility as a microclimate refuge across their large range.

Keywords Ecosystem function and services · *Asplenium nidus* · Canopy · Epiphytes · Microclimate · Arboreality

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This manuscript presents a combination of ecological observations and empirical comparisons in two biodiverse forests and highlights a testable phenomenon for how epiphytes create critical habitat for canopy herpetofauna. The results show that a particular epiphyte, the *Asplenium* bird's nest fern, is a preferentially occupied canopy habitat in two geographically divergent forests by phylogenetically distinct species. The paper presents a novel microclimate-area relationship theory for the use of canopy habitats, suggesting that the driver of preferential herpetofaunal use and facilitator of herpetofaunal arboreality is the epiphyte's microclimate buffering services. These work positions bird's nest ferns as a keystone canopy habitat in parts of the Paleotropics, in need of further study and conservation protection.

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Extended author information available on the last page of the article

Introduction

Tropical rainforest canopies are among the world's most species-rich habitats (Hammond et al. 1997; Ozanne et al. 2003; Nakamura et al. 2017), within which canopy epiphytes can be significant biodiversity facilitators (Watson 2001; Ellwood and Foster 2004; Gonçalves-Souza et al. 2010; Francisco et al. 2018). Epiphytes add both landscape and fine-scale structural complexity to forests, increasing vertical habitat availability and allowing for niche partitioning and diversification of ecological communities (Romero and Vasconcellos-Neto 2005; Gonçalves-Souza et al. 2010; Díaz et al. 2012; Pritchard et al. 2016). While over 30,000 species of epiphyte exist, those with architecture capable of holding water, amassing soil, cycling nutrients, and creating microclimatic refuges in the otherwise hot and dry canopy are some of the best facilitators of biodiversity (Fish 1983; Benzing 1998; Winchester 2003; Grippa and Hoeltgebaum 2007; Beaulieu et al. 2010; Scheffers et al. 2014b). Epiphytes with

these characteristics are used by animal taxa across the forest's vertical strata, and often support unique ecological communities, including species evolved to thermally and hydricly buffered microclimate conditions (Stork and Grimbacher 2006; Scheffers et al. 2014a).

Among the water-retaining and service-providing epiphytes, South America's tank bromeliads in the *Bromeliaceae* family are the most well studied. Tank bromeliads play a critical role in the life cycles of many animal taxa and facilitate forest biodiversity through their provisioning of phytotelmata (water bodies held within vegetation) and services such as nutrient cycling and soil creation (Fish 1983; Benzing 2000; Rocha et al. 2000; Gonçalves-Souza et al. 2010). Notably, a large number of amphibian and invertebrate species are evolved to use bromeliad phytotelmata for breeding and as microclimate refuges (Lannoo et al. 1987; Peixoto 1995; Rocha et al. 2004; Araújo et al. 2007). Tank bromeliads; however, are conspicuously restricted to the Neotropics, so what epiphyte species or groups fill their role in the Paleotropics? For Asian and Australian tropical forests, the cosmopolitan and abundant bird's nest fern (*Asplenium nidus* complex [BNF]) is a good candidate (Holtum 1976). BNFs provide near analogous services to tank bromeliads: they retain water, create soil, cycle nutrients, act as breeding habitat, and provide microclimate buffering, all of which are expected to facilitate biodiversity and are associated with increased canopy invertebrate diversity in Borneo and Japan (Online Resource 1; Ellwood and Foster 2004; Turner and Foster 2006; Karasawa et al. 2008; Díaz et al. 2012; Scheffers et al. 2014b). These and most other studies on BNF biodiversity have focused on select locations in Asia and Australia, with a few or no studies in its Afro-tropical range, raising the question: how comparable are BNF microhabitats in the Paleotropics? BNFs have largely been examined through studies of invertebrate communities, but services such as microclimate buffering are attractive to temperature-sensitive herpetofauna, such as amphibians (Scheffers et al. 2013a). Convergent habitat usage of BNFs by amphibian species of marked phylogeographic difference would demonstrate their importance as a microhabitat and biodiversity facilitator. Furthermore, assessing BNFs' ecological utility for herpetofauna of different regions provides valuable life-history data for the conservation of threatened and declining amphibian populations (Houlahan et al. 2000; McCarty 2001).

We compare the herpetofaunal use of BNFs in two geographically distinct Paleotropic locations that are hotspots of herpetofaunal endemism—Madagascar as part of the Afro-tropical zone and the Philippines as part of the Asian-tropical zone. Madagascar and the Philippines contain outstanding herpetofaunal diversity (354 and 114 amphibian species and 380 and 204 reptile species, respectively) and endemism (amphibians: 99% and 80%, reptiles: 90% and 70%), and

are considered biodiversity hotspots of critical conservation priority (Myers et al. 2000; Groombridge and Jenkins 2002; Brown et al. 2013). To date, 40% (145/354) of Madagascar's amphibian and 35% (132/380) of its reptile species are listed as IUCN threatened, and the same applies to 42% (48/114) of the amphibian and 34% (69/204) of reptiles species in the Philippines (Goodman et al. 2005; Andreone et al. 2005; IUCN 2018; Amphibiaweb 2013). In both hotspots, *A. nidus* BNFs are a common forest epiphyte, and thus, we investigated whether BNFs function as a critical microhabitat for these herpetofauna despite their unique phylogenetic and spatially explicit origins. We test a range of hypotheses relating to the microhabitat and climate niche space provisioned by BNFs (see Flow Chart: Online Resource 2). We predict that BNFs will have greater herpetofaunal presence and abundance when compared to other canopy microhabitats and will support different diversity (species richness and community similarity) relative to other microhabitats. Next, we test whether patterns of BNF use by herpetofauna are related to microclimate buffering. We hypothesize that BNFs will function as a microclimate buffer against daytime heat extremes and that herpetofaunal use of buffered canopy habitats will be greater during the day than at night. Finally, we predict that herpetofaunal presence and abundance inside BNFs will be positively predicted by greater fern size and lower canopy cover, as larger epiphytes provide more habitat space and retain moisture longer (Zotz 1999; Scheffers et al. 2014b), and low canopy cover coupled with increasing height increases dependence on microclimate refuges (Fayle et al. 2009; Silva et al. 2011; Scheffers et al. 2014b). We test these predictions by determining which herpetofauna use BNFs relative to other forest microhabitats, measuring BNF temperatures relative to canopy temperatures, comparing patterns of diurnal and nocturnal herpetofaunal presence in buffered microhabitats, and by measuring habitat characteristics that predict BNF usage.

Methods

Study locations

We conducted surveys within Ranomafana National Park (here after RNP; 21°15'S, 47°27'E), a 41,600 ha reserve in southeastern Madagascar with an elevation range of 600–1500 m, in 2015–2016 (Wright and Andriamihaja 2002). RNP encompasses a range of habitats including primary and secondary lowland and pre-montane tropical rainforest as well as a 3 km buffer of mixed remnant forest and agricultural land (Balko and Underwood 2005). Precipitation in the region is highly seasonal; an average annual rainfall of 2830 mm is defined by a peak-wet season in January–March (average monthly rainfall: 508 mm) and dry

season in June–October (average monthly rainfall: 143 mm; (Dunham et al. 2011).

Surveys were also conducted on Mt. Banahaw in central Luzon, Philippines in 2011. This site is defined by primary rainforests: lowland dipterocarp forest below 800 m, dipterocarp and *Pinus* montane forest from 900 to 1700 m, and mossy and *Pinus* forest beyond 1700 m. Lacking a distinct dry season, annual rainfall in the area amounts to 3100 mm yr. with an average relative humidity of 85% (Banaticla and Buot 2005).

Bird's nest fern surveys

To determine how herpetofauna use of BNFs in comparison to surrounding forest microhabitats, we utilized ground-based and canopy survey techniques to access and examine the species using BNF microhabitats in Madagascar ($n = 50$) and the Philippines ($n = 150$; Jepson 2000). Surveyed BNFs were selected along three random 100 m linear transects as encountered within 15 m of either transect side. Any BNFs on the ground or in trees safely accessible by climbing techniques and at least 2 m apart to allow for sufficient diversity of paired microhabitats (see below) were included in the survey (height: range 0–32 m). A given BNF was surveyed three times from November 2015 to January 2016 with a minimum 10-day window between resurveys in Madagascar and four times in May–September, 2011 in the Philippines with a 3-week window between resurveys. Surveys were diurnal, as this is the time when a BNF's role in creating a climate-mitigating refuge is most important to temperature-sensitive and nocturnal species (Scheffers et al. 2014b). Each fern was thoroughly searched using the techniques of Scheffers et al. (2014a). In summary, we explored all leaf axils and debris starting at the epiphyte's base and working up towards the center of the fern. A BNF's height above ground in meters, area (length \times width of the fern base), and the above canopy cover were measured immediately following its first survey (see below).

Following each BNF survey, we searched 2–5 additional paired microhabitat sites to compare the importance and use of other non-BNF microhabitats by herpetofauna. Paired microhabitat sites were selected as the nearest comparable potential microhabitat and were equal in area (length \times width of the fern base) and survey duration with their associated BNF. One paired site was always ground leaf litter, referred to hereafter as a “paired-ground” site, which is a habitat known to buffer temperature and dehydration rates in amphibians (Seebacher and Alford 2002). Paired-ground sites were selected using a random bearing and distance within 5 m of the associated fern and were manually searched by overturning the top 10 cm of leaf litter and inspecting crevices and root cavities. Our other 1–4 paired sites were aboveground (AG) microhabitats, referred

to hereafter as “paired-AG microhabitats,” which were sites deemed capable of providing similar climate buffering or other services as BNFs to herpetofauna. Paired-AG microhabitats consisted of tree cavities, moss mats on tree trunks, decaying logs or snags, *Pandanus* palms, non-*Asplenium* epiphytes, or suspended dense leaf clusters, and were selected as encountered by the surveyor in alternating directions from the BNF. These sites were examined in a fashion similar to BNFs by carefully inspecting leaf axils, lifting accumulated debris, sieving water pockets, and/or removing loose bark.

Although we attempted to standardize microhabitat sampling units and search area to overcome the challenges of multidimensionality, each microhabitat type represents a volume rather than a surface area, complicating standardization across types. As such, we attempted to derive conservative estimates of BNF utility to herpetofauna by penalizing BNFs via oversampling paired-AG and paired-ground microhabitats. In total, we surveyed 150 paired-ground and 300 paired-AG microhabitats in Madagascar, and 183 paired-ground and 770 paired-AG microhabitats in the Philippines.

Bird's nest fern characteristics to predict use

For each fern in our BNF surveys, we quantified the physical BNF traits (i.e., size, height) and habitat characteristics (i.e., canopy cover) likely to affect herpetofaunal use. For example, a BNF's height and size influence its water retention and may, therefore, influence herpetofaunal occupancy and abundance within. Indeed, studies show both vertebrate abundance and occupancy and invertebrate biomass increase with fern size (Ellwood and Foster 2004; Scheffers et al. 2014b). For our purposes, we defined fern size as the area of the fern's base (length \times width), as the base is the part of the fern that retains water, provides sheltered habitat, and creates microclimate refuge. We recorded BNF height in meters from the ground. Height may influence the accessibility of a fern as well as the above canopy cover. Greater height and less canopy cover increases exposure to solar radiation, thereby influencing a BNF's interior and surrounding microclimate (Silva et al. 2011; Scheffers et al. 2013b). Canopy cover measurements (CC) were collected directly above each fern using a spherical densitometer.

Bird's nest fern microclimates

BNF's have been shown to buffer local air temperature in the Philippines (Scheffers et al. 2013a). To test whether BNFs function similarly in Madagascar, we compared daily within-fern temperatures to the ambient canopy temperature by placing temperature loggers (Maxim Hygrochron ibutton Model DS1923; <http://www.maxim-ic.com/>) within the

center of five randomly selected BNFs and the upper canopy of two trees. The ambient canopy loggers were suspended under a plastic funnel to shelter them from direct solar radiation (as per Scheffers et al. 2013a). Loggers recorded temperature every 15 min and data were recorded from December 2015 to February 2016.

Day vs. night–ground-to-canopy tree surveys of buffered habitats

To test whether herpetofaunal use of BNFs aligns with the provisioning of buffered microclimates in time, we conducted a set of ground-to-canopy tree surveys to examine herpetofaunal day versus night use of sheltering microhabitats. Sheltered microhabitats can provide buffered microclimates, so we expect the probability of finding temperature-sensitive herpetofauna in these habitats will be higher during the day, when ambient conditions are hot and dry and thermal refuges are needed, than at night when temperatures are cool and moist and thermal refuges are needed less. To test this microclimate-use alignment, a focal tree (Madagascar $n=70$; Philippines $n=37$) was surveyed twice within 24 h, once diurnally from 8 AM to 3 PM and once nocturnally from 8 PM to 12 AM. In each 60 min. survey, a surveyor searched for herpetofauna while climbing to conduct a set of four searches, starting at the ground (base of tree), moving into the understory (1–4 m), then to the sub-canopy (~half of the maximum. height climbed), and finishing in the canopy (maximum. height climbed). We searched all accessible microhabitats during these tree surveys and recorded where all captured or encountered herpetofauna were found. The BNFs and microhabitats encountered during this survey were different from those studied in our BNF-specific surveys.

Data analysis

Analysis of herpetofaunal presence and abundance

We calculated and compared the probability of herpetofaunal presence in BNFs and in other microhabitats by tallying the number of times herpetofauna were recorded in a given microhabitat and dividing by the total number of microhabitats of that type surveyed. We compared the magnitude and direction of the resulting numbers through pair-wise division and tested whether the presence/absence distributions in each microhabitat were different using a Chi-squared two-sample test and the null hypothesis that herpetofaunal presence does not differ between sites.

To analyze the relative abundance of herpetofauna in each microhabitat type, we derived a catch-per unit-effort (CPUE) for each BNF survey as the average number of herpetofauna caught within the microhabitat (BNF, paired-ground, and

paired-AG microhabitat) divided by the total number of times that habitat type was surveyed (i.e., animals/survey). This CPUE allowed us to standardize our effort per survey across the differing sample sizes for our microhabitat sites. We then tested whether CPUE in BNFs was greater than CPUE in other microhabitat types using Welch's *t* tests, which compare samples with unequal variances and samples sizes (Welch 1947).

Analysis of herpetofaunal diversity

We looked for differences in species richness between our microhabitat sites by analyzing observed and estimated herpetofaunal richness for each microhabitat type with sample-based rarefaction and extrapolation curves (Chao et al. 2014; Hsieh et al. 2016), and we assessed the similarity of our microhabitat species assemblages through pair-wise comparisons of the Jaccard Similarity Index (*J*; Jaccard 1912):

$$J = \frac{a}{a + b + c},$$

where *a* is the number of species in common, *b* and *c* are the number of species unique to either site, and *J* values are reported from 0 to 1 with increasing values reflecting higher similarity between sites. We chose the Jaccard Similarity Index over other similarity coefficients that more heavily weigh 'a' cases (i.e., Sørensen Index) to preserve differences between species communities from adaptations to canopy versus ground microhabitat sites. Modeled richness was estimated as the mean of 200 bootstrap replications with 95% confidence intervals. Modeled curves were drawn in R version 3.3.2 (R Core Team 2017) using the "iNEXT" package (Hsieh et al. 2016) and graphed using ggplot2 (Wickham 2016). *J* values were calculated using the "vegan" package (Oksanen et al. 2014).

Analysis of BNF climate data

We measured BNFs microclimate-buffering potential in Madagascar by comparing the daily minimum and maximum temperatures of BNFs to ambient temperatures in the forest canopy using a one-way Fisher Pitman permutation test based on 1000 Monte Carlo resamplings in the R package *coin*.

Analysis of day vs. night, ground-to-canopy tree surveys of buffered habitats

We summarized the total number of herpetofauna found across 11 common aboveground microhabitats and documented whether they were found during the day or night. Four of these microhabitats provide a buffered shelter from ambient climate (referred to as *buffered*; e.g., BNFs, moss

mats, tree cavities, *Pandanus sp.*) and seven did not (e.g., bamboo, branch, exposed leaves, exposed non-BNF ferns, tree trunk, vine, and others). We used paired t tests to determine if the proportion of herpetofauna found within buffered microhabitats during the day differed from the proportion using buffered microhabitats at night. Our a priori expectation is that buffered microhabitats are used comparatively more during the day than at night, because they offer refuge against hot and dry daytime conditions.

Analysis of BNF characteristics that predict herpetofaunal use

We used a generalized linear regression model (GLM) with a binomially distributed error term and a logit link function to determine which BNF characteristics best predict herpetofaunal presence in Madagascar and the Philippines. In total, we tested eight models consisting of three univariate models (fern height, canopy cover, and fern area) (see 2.2.1 *Bird's nest fern characteristics to predict use* for justification of variable inclusion in our models), one null model (intercept only), three multivariate models, and one global model (all variables combined). Our three multivariate models included: (1) fern height and canopy cover (e.g., a fern high in the canopy under sparse vegetation might be exposed to high levels of solar radiation resulting in hot and dry microclimates), (2) fern height and fern area (e.g., large ferns might mediate the effects of increased solar radiation at greater heights in the canopy), and (3) canopy cover and fern area (large ferns might mediate the effects of increased solar radiation from low canopy cover). We ran a second analysis using generalized mixed-effect models in the R package *lme4* for both locations combined. Here, the model structures remained the same, but we added location to our models as a random effect. We reran our model sets for abundance using GLMs with a negative binomial error

structure to account for count data with large numbers of zeros. Because of the relatively small physical size of BNFs, our zeros are likely true zeros rather than zeros resulting from omission error, and therefore, a negative binomial distribution was the best option for our modeling needs. Our single exception was in our Madagascar-only models where our negative binomial models suffered from poor model convergence, likely due to small numbers of counts in our data. We used a Gaussian model as indicated by McDonald and White (2010), which performs satisfactorily in cases where small counts lead to failure in multinomial distributions.

We chose the most parsimonious model using Akaike's Information Criterion adjusted for small samples (AICc) to identify variables that best predicted occurrence and abundance (Anderson and Burnham 2002). The top models were chosen from those models with the smallest ΔAICc (difference between AIC models; Anderson and Burnham, 2002). Models with $\Delta\text{AICc} < 2$ were considered top predictive models, and we used evidence ratios to derive the ratio of model weights between the top-ranked and second-ranked model. We further assessed the relative importance of each covariate in predicting presence and abundance of herpetofauna by model-averaged coefficients, with the 50% and 95% unconditional standard error to assess uncertainty in parameter estimates (Anderson and Burnham 2002; Galipaud et al. 2017). All models were assessed for over-dispersion, and we developed all models using R version 3.4.4 (R Core Team 2018).

Results

Herpetofaunal presence and abundance

Our BNF surveys found that herpetofauna in both Madagascar and the Philippines use BNF microhabitats (Tables 1 and

Table 1 Presence, abundance, and richness of herpetofauna in the microhabitats of bird's nest fern (BNF) surveys

	Madagascar			Philippines		
	BNFs	Paired AG	Paired ground	BNFs	Paired AG	Paired ground
Total sites sampled	50	300	150	150	770	183
Richness	7	5	5	4	1	4
Richness (unique to location)	4	2	2	3	0	2
Abundance	11	7	14	37	1	8
Proportion of total herpetofauna	0.34 (11/32)	0.22 (7/32)	0.44 (14/32)	0.80 (37/46)	0.02 (1/46)	0.17 (8/46)
Occupancy (abundance/sites sampled)	0.22 (11/50)	0.02 (7/300)	0.09 (14/150)	0.25 (37/150)	0.001 (1/770)	0.04 (8/183)
Presence (presence/sites sampled)	0.2 (10/50)	0.02 (7/300)	0.09 (13/150)	0.2 (30/150)	0.001 (1/770)	0.04 (8/183)

Each BNF survey is composed of one BNF search and 2–5 paired-microhabitat searches of sites equal in size to the associated fern. One paired site was always ground leaf litter; the remaining were paired-aboveground (AG) microhabitats, which included non-ground tree cavities, moss mats, snags, *Pandanus* palms, non-*Asplenium* epiphytes, and dense leaf clusters. Abundance and richness calculations are totaled across all samples

2; Fig. 1, Online Resource 3). BNFs contained approximately 30% of our surveyed abundance in Madagascar and 80% of the abundance in the Philippines. In both countries, amphibians were the dominant occupiers of BNFs, and BNF residing taxa in Madagascar included six frog species: *Anodonthyla boulengeri*, *A. moramora*, *Boophis madagascariensis*, *Gephyromantis tchenki*, *Platypelis grandis*, one unidentified frog species, and one skink species: *Phelsuma quadriocellata*. In the Philippines, four frog species were found in BNFs: *Platymantis luzonensis*, *P. banahao*, *P. montanus*, and *Philautus surdus* and no reptiles; however, a single *Sphenomorphus* spp. skink was found in a paired-AG microhabitat survey.

Addressing our first prediction, we found that the probability of herpetofaunal presence was higher in BNFs than in other microhabitats sites for both Madagascar and the Philippines. In Madagascar, the presence in BNFs was 10 times higher (0.20/0.02; $p < 0.001$) in BNFs than in paired-AG microhabitats, 2.2 times higher (0.20/0.09; $p = 0.05$) in BNFs than in paired-ground microhabitats, and 4 times higher (0.08/0.02; $p < 0.005$) in paired-ground versus paired-AG microhabitat sites (Tables 1 and 2). In the Philippines, herpetofaunal presence was 200 times (0.2/0.001; $p < 0.001$) higher in BNFs than in paired-AG microhabitats, 5 times higher (0.2/0.04; $p < 0.001$) in BNFs than in paired-ground microhabitats, and 34 times higher (0.043/0.00130; $p < 0.005$) in paired-ground compared to paired-AG microhabitats.

Comparing CPUEs, we found that abundance was higher in BNFs than in all other paired microhabitats from the Philippines; however, BNF abundance was only higher than paired-AG microhabitats in Madagascar (Table 2). Specifically, abundance in Madagascar's BNFs

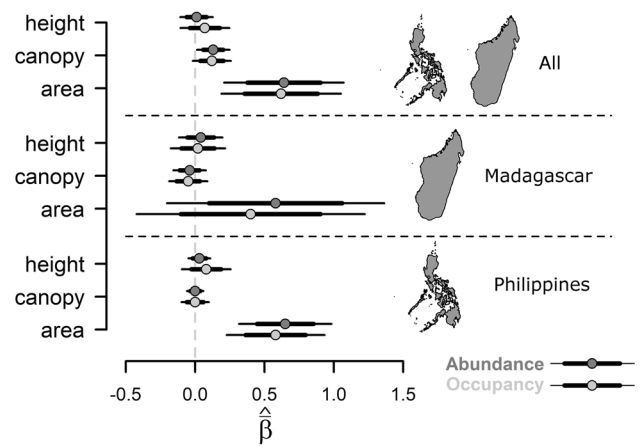


Fig. 1 Model-averaged estimates of effect sizes, β , of covariates derived from contrasting eight models with bird's nest fern characteristics and the habitat variable canopy cover (CC) as predictors of total herpetofaunal presence or occupancy (light gray) and abundance (dark gray) (Madagascar $N=50$, Philippines $N=150$, Combined=200). Models were fitted using a generalized linear model for Madagascar and the Philippines and a linear mixed-effects model for All (Madagascar and the Philippines held as a random effect). To assess uncertainty in parameter estimates, we provide the probability distribution of each parameter estimate with thick and thin lines the 50% and 95% unconditional standard error, respectively

($\bar{x} = 0.073$, $SD = 0.15$) was similar to abundance in paired-ground microhabitats (0.073/0.093; $\bar{x} = 0.093$, $SD = 0.17$; $p = 0.53$), but 3.2 times greater than abundance in paired-AG microhabitats (0.073/0.023; $\bar{x} = 0.023$, $SD = 0.06$; $p = 0.037$). We also found abundance in paired-ground microhabitats was four times greater than that of paired-AG microhabitats (0.093/0.023; $p = 0.006$). In the Philippines, we found abundance was 2.4 times greater in BNFs

Table 2 Outputs for pair-wise and statistical comparisons of herpetofaunal species similarity, abundance, and presence/absence for microhabitats in bird's nest fern (BNF) surveys

Comparison	Measure	Madagascar	Philippines
BNF-ground	J	0.091	0.143
	CPUE	$df=1; t=0.62; p=0.53$	$df=1; t=2.370; p=0.018^*$
	P/A	$df=1; X^2=3.68; p=0.05^*$	$df=1; X^2=18.40; p<0.001^*$
BNF-paired AG	J	0.20	0
	CPUE	$df=1; t=2.14; p=0.036^*$	$df=1; t=4.445; p=0.0001^*$
	P/A	$df=1; X^2=25.25; p<0.001^*$	$df=1; X^2=146.19; p<0.001^*$
Ground-paired AG	J	0.25	0.25
	CPUE	$df=1; t=2.28; p=0.006^*$	$df=1; t=2.077; p=0.039^*$
	P/A	$df=1; X^2=8.01; p<0.005^*$	$df=1; X^2=8.012; p<0.005^*$

Significant p values are ≤ 0.05 and *; test statistics calculated using Welch's t tests for CPUE (individuals/survey) and Chi-squared two-sample tests (X^2) of presence/absence distributions; Jaccard Similarity Index (J), Catch-per-Unit-Effort ($CPUE$) abundance, and presence/absence (P/A) from bird's nest fern (BNF), paired-aboveground (AG), and paired-ground (Ground) microhabitats

BNFs microhabitats better support herpetofaunal presence and abundance than other canopy (paired-AG) microhabitats in both Madagascar and the Philippines. BNF species are unique and the species similarity between BNFs and all other paired microhabitats was on average (15%) in Madagascar and (6.3%) in the Philippines

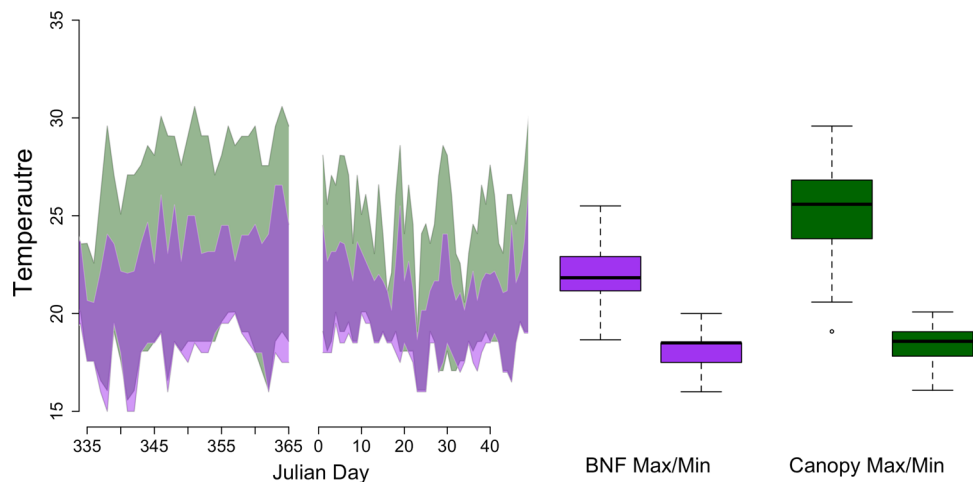
(\bar{x} = 0.097, SD = 0.24) than in paired-ground microhabitats (0.097/0.040; \bar{x} = 0.040, SD = 0.18; p = 0.018) and 16 times greater than in paired-AG microhabitats (\bar{x} = 0.006, SD = 0.08; p = 1.5e-5). Abundance in paired-ground microhabitats was 6.7 times greater than abundance in paired-AG microhabitats (0.040/0.006; p = 0.039).

Herpetofaunal diversity

Species richness did not strongly differ between BNFs and other microhabitat sites. While raw richness was 1.4 times higher in BNFs than other microhabitat sites (7:5:5; Table 1; Online Resource 3), the confidence intervals of all modeled curves either overlapped, with the exception of paired-AG microhabitats richness in the Philippines where only one individual was observed, or were under-saturated, with the exception of BNF richness in the Philippines (sample coverage = 1.0; Online Resource 3; CI reported in Online Resource 4). In Madagascar, observed (interpolated) to estimated (extrapolated) richness ratios were 7:20 species in BNFs (s.e. = 12.27), 5:9 species in paired-ground (s.e. = 6.70), and 5:7 (s.e. = 2.96) species in paired-AG microhabitats. In the Philippines, observed-to-estimated ratios were 5:5 (s.e. = 0.37) in BNFs, 4:6 (s.e. = 3.31) in paired-ground, and 1:1 (s.e. = 0.31) in paired-AG microhabitats.

As for the similarity of species assemblages, we found low similarity between BNF communities and other microhabitat sites (Table 2). BNF and paired-ground species composition in Madagascar was the least similar (9.01%), while BNF and paired-AG microhabitat species were 20.0% similar. BNF communities in the Philippines were 14.7% similar to those of paired-ground sites, but shared no species in common (0.0%) with paired-AG microhabitat sites. Paired-AG and paired-ground sites were 25% similar in both countries.

Fig. 2 Epiphytes are cooler with lower variability than surrounding canopy temperatures. Box and whisker plots indicate the upper and lower quartiles of data with the dark horizon line indicating the median of data. Data loggers were placed in the canopy of two trees and five BNFs



Bird's nest fern vs. canopy climate

Bird's nest fern do buffer diurnal temperature extremes. The median minimum and maximum daily temperature within BNFs ranged from 18.5 to 22.7 °C, respectively (Fig. 2), whereas the median minimum and maximum daily ambient temperature within the canopy ranged from 18.6 to 27.1 °C, respectively (Fig. 2). Our permutation tests indicated that minimum temperatures were comparable between BNFs and ambient (Z = -1.1633, p = 0.250), whereas maximum temperatures significantly differed by 4.4 °C (Z = -6.3602, p < 0.001). The variance in minimum and maximum daily temperature was 1.4 and 8.6 for BNFs and 1.4 and 9.5 for the canopy, respectively.

Day vs. night use of buffered habitats

In our day vs. night, canopy-to-tree surveys of buffered microhabitats, we found that herpetofaunal species used buffered habitats more often during the day than at night (Table 3; t = 1.84, df = 9, p = 0.049). Specifically, herpetofauna in Madagascar were eight times more likely to be diurnally sheltered (19/38) than nocturnally sheltered (9/145). Additionally, we found six species using BNFs as shelters that were not previously documented in our primary BNF surveys. In the Philippines, herpetofauna were also more likely to use buffered habitats during the day than at night, where they were ten times more likely to be diurnally sheltered (10/10) than nocturnally sheltered (4/41; Table 3).

Predictors of herpetofaunal presence and abundance in BNFs

Our analysis of model averaged, standardized coefficients and effect sizes supported BNF area as the most influential predictor of herpetofaunal occupancy and abundance (Table 4; Fig. 1). In both Madagascar and the Philippines,

Table 3 Diurnal vs. nocturnal abundance of sheltered vs. non-sheltered (N/S) herpetofauna in buffered and non-buffered habitats

Habitat type	Madagascar					Philippines				
	Day sheltered	Day N/S	Night sheltered	Night N/S	Total	Day sheltered	Day N/S	Night sheltered	Night N/S	Total
Buffered habitats										
Non-BNFs	15	0	8	0	23	4	0	2	2	8
BNF	4	0	1	2	7	6	0	2	1	9
Total	19	0	9	2	30	10	0	4	3	17
Non-buffered habitats	0	19	0	134	153	0	0	0	34	34
All habitats	19	19	9	136	183	10	0	4	37	51

Herpetofauna in Madagascar were 8× more likely to be found sheltered in a buffered habitat during the day (19/38) than at night (9/145), and in the Philippines, they were 10× more likely sheltered in a buffered habitat during the day (10/10) than at night (4/41). Herpetofauna were found in above-ground habitats during day vs. night vertical canopy surveys. Those denoted “buffered” were found within the habitat and not exposed to moving ambient air

Table 4 Model comparison (AICc & Δ AICc) of bird's nest fern parameters for predicting the presence (occupancy) and abundance of herpetofauna in the Philippines and Madagascar

	Rank	Model	LL	AICc	Δ AICc	R^2	ω	Evidence ratio
Occupancy								
Philippines	1	~Area + CC	-61.55	129.1	0	0.16	0.57	2.87
	2	Global	-61.55	131.4	2.11	0.16	0.20	
	8	Null	-73.65	149.3	20.07		0.00	
Madagascar	1	~Area	-23.81	51.8	0	0.05	0.28	1.13
	2	Null	-25.02	52.1	0.24		0.25	
All	1	~Area	-88.84	183.8	0	0.21	0.51	2.26
	2	~Area + Height	-88.62	185.4	1.63	0.21	0.23	
	8	Null	-98.68	201.4	17.60		0.00	
Abundance								
Philippines	1	~Area + CC	-145.15	298.6	0	0.12	0.39	1.46
	2	~Area	-146.59	299.3	0.75	0.10	0.27	
	3	Global	-145.13	300.7	2.11	0.12	0.14	
	8	Null	-153.62	311.3	12.73		0.00	
Madagascar	1	~Area	-85.76	178.0	0	0.05	0.28	1.17
	2	Null	-87.051	178.4	0.31		0.24	
All	1	~Area	-195.20	398.6	0	0.08	0.47	1.94
	2	~Area + Height	-194.81	399.9	1.31	0.09	0.24	
	8	Null	-202.61	411.3	12.72		0.00	

All models with a Δ AICc < 0.2 were considered substantial predictors of occurrence and abundance and provided in the table. We provide the model rank for the null model (intercept only) relative to the eight models for our analyses. The global model includes fern height, fern area, and canopy cover. Also shown are the log likelihood (LL) and the difference in AICc of each model from the highest ranked model (Δ AICc). R^2 indicates the proportion of the variance in the dependent variable that is predictable from the independent variable. Evidence ratio indicates the ratio of model weights between the top-ranked and second-ranked model

BNF area had a positive effect on presence and abundance (Fig. 1). The best-supported model for predicting occupancy or abundance of herpetofauna included BNF area and/or BNF area plus canopy cover. In the Philippines, canopy cover had an influential effect on herpetofauna presence,

whereas BNF height was not supported as an influential predictor of presence or abundance (Fig. 1). For the combined analysis of BNFs in Madagascar and the Philippines, area again remained the most influential predictor of presence and abundance (Table 4; Fig. 1).

Discussion

Our study reveals that *Asplenium nidus* bird's nest ferns are a cosmopolitan habitat and microclimate refuge for herpetofauna in the canopies of two geographically and phylogenetically distinct forests in the Paleotropics (Scheffers et al. 2014a, b). We draw this conclusion following observations of high herpetofaunal presence, abundance, and of unique communities in BNFs relative to other aboveground microhabitats, as well as from differences in buffered microhabitat use between day and night, buffered canopy temperature extremes inside BNFs, and through our models, revealing BNF area is the best predictor of herpetofauna presence and abundance. Importantly, area is also a key characteristic that influences microclimate buffering and hydration in BNFs (Scheffers et al. 2014b). We acknowledge that our study was limited to extensive sampling at only two sites, one in each of two countries, we broadly considered the Asian (the Philippines) and African (Madagascar) Paleotropics. As such, low replication of sites across geography means that we cannot fully generalize our findings across the Paleotropics. Nonetheless, the corroboration in patterns between geographically and phylogenetically disjunct lineages of herpetofauna provides compelling evidence for BNF utility in tropical rainforests. We encourage further studies of BNFs' role as canopy biodiversity facilitators and as a climate-buffering habitat to more thoroughly assess the generality of our conclusions both within Madagascar and the Philippines, as well as in other Paleotropical forests.

Use of bird's nest ferns and the facilitation of arboreality

In our study of two Paleotropical rainforest canopies where we kept all surveyed habitats equal in size and duration of search, the most reliable location to find herpetofauna was inside BNFs (Table 1). Here, 20% of the BNFs in both our Madagascar and Philippines study sites contained herpetofauna, and BNFs were more likely to be occupied by herpetofauna than all other comparable paired microhabitats. In terms of abundance, we found that even though BNFs are effectively 'floating' islands in space, their herpetofaunal abundance was more similar to ground microhabitats (high spatial connectivity), than to other 'floating' canopy microhabitats. These observations suggest that BNFs represent a unique aboveground microhabitat that is preferentially occupied relative to other canopy habitats.

While our study did not find strong statistical support for higher species richness inside BNFs compared to other paired microhabitats, we found that BNFs may facilitate

a unique portion of the forest canopy's biodiversity. Our estimated total species richness inside BNFs in Madagascar (20 species; Online Resource 3 & 4) aligned with the published estimate of canopy species richness in the same forest from Basham et al. (2018) (19 species), suggesting that BNF richness may be indicative of overall canopy richness. Interestingly, our Jaccard Similarity indices found very little community overlap between BNFs and both paired-AG microhabitats and paired-ground sites. Basham et al. (2018) found that species assemblages and life-history adaptations in Madagascar are mostly delineated between ground and canopy habitats with high niche conservatism; however, low similarity between the species in BNFs and other paired-AG microhabitats may indicate obligate BNF associations. Indeed, Scheffers et al. (2013b) concluded that some of their observed amphibian species are likely obligate BNF breeders. Adaptations for arboreal life strategies have been linked to productive and structurally complex ecosystems, wherein species evolve to exploit additional niche space within the forest canopy (Simard et al. 2011; Oliveira and Scheffers 2019). Arboreality, therefore, can increase species richness and coexistence within an ecosystem (MacArthur and MacArthur 1961; Scheffers et al. 2013b, 2017; Ashton et al. 2016; Oliveira and Scheffers 2019). Given that BNFs add structural complexity to the forest canopy and are a widely occupied canopy microhabitat by unique canopy species, it follows that BNFs likely facilitate arboreality as a behavioral strategy and in doing so increase a forest's capacity for overall biological richness.

Importance of bird's nest fern microclimate services

The frequent use of *Asplenium nidus* BNFs by temperature-sensitive animal groups in multiple Paleotropical locations, combined with our results, furthers the assertion that BNFs are microclimate refuges (Fig. 2; Turner and Foster 2006; Scheffers et al. 2014b). Our microclimatic data support a 4 °C differential between the maximum temperature inside and outside of BNFs (Fig. 2), and other epiphytes have been shown to create cooler, moister, and less variable canopy microclimates (Online Resource 1; Benzing 1998; Freiberg 2001; Stuntz et al. 2002). Thus, BNFs not only provide physical habitat space, but also a buffered microclimate. The combined observations of this study and others suggest that thermal buffering in conjunction with water availability is the driving factors of many animals' BNF use (Feder 1982; Cohen et al. 1996; Spieler and Linsenmair 1998; Seebacher and Alford 1999; Freiberg and Turton 2007; Scheffers et al. 2014b; Ruano-Fajardo et al. 2014). BNFs retain water (Kluge et al. 1989; Freiberg and Turton 2007), and here, we see a water-sensitive taxon utilizing that critical resource (Table 3). Furthermore, our models show that BNF

area is the best predictor of presence and abundance (Fig. 1). Although our models from Madagascar performed poorly compared to the Philippines, indicated by confidence intervals that overlap with zero, area was the sole variable with larger-than-zero coefficients and coefficients that we equivalent in size to that of the Philippines—suggesting corroboration across data sets. Importantly, when combined with the Philippines data, area remained a strong positive predictor of presence and abundance. Large ferns can stay hydrated and buffer microclimate for multiple days to weeks (Scheffers et al. 2014b). This climate–area relationship allows BNFs to meet the physiological demands of temperature- and hydration-sensitive animals, such as amphibians (Scheffers et al. 2013a). BNFs may, therefore, play an important role in facilitating arboreality, and should be investigated as a keystone canopy habitat—as has been done with other water-retaining epiphytes (Online Resource 1; Watson 2001; Cooney and Watson 2008).

Bird's nest ferns, the bromeliad of the paleotropics

In a review of the literature, we found that Neotropical bromeliads and Paleotropic *Asplenium nidus* ferns similarly provision services to diverse ectothermic vertebrate and invertebrate species in forest canopies (Online Resources 1; González del Pliego et al. 2016). These services include water retention, soil creation, microclimate buffering, temporal shelter, nutrient cycling, and breeding habitat (Online Resource 1), many of which are rare or non-existent in the absence of epiphytes. For example, by gathering atmospheric nutrients and mineralizing canopy organic matter into their own biomass (Benzing 1989), epiphytes cycle a significant proportion of the canopy's mineral capital (Nadkarni 1984; Coxson and Nadkarni 1995) and form suspended soils with high nutrient concentrations (Paoletti et al. 1991). Perhaps, the most important service, water retention, is linked to other services such as nutrient cycling rates, type and quantity of food resources, breeding habitat, and microclimate buffering (Lannoo et al. 1987; Scheffers et al. 2014a, b). BNFs do differ from bromeliads in their method of water retention; they maintain moisture in their root masses and small pools of water at the base of their leaves (Scheffers et al. 2013b), whereas tank bromeliads pool relatively large volumes of water in rosette-shaped phytotelmata (Fish 1983; Frank 1983). These structural differences have consequences for the types of species and their life-history strategies supported. For example, BNFs do not facilitate the same levels of aquatic biodiversity observed in bromeliads, and cannot support amphibian species with a truly aquatic tadpole life-stage (Kitching 2000). Scheffers et al. (2013b), however, did find numerous frog egg clutches inside BNFs in the Philippines, suggesting that some species are capable of overcoming strict reliance on aquatic resources. As

for microclimate buffering, in both epiphytes, size remains the most important factor influencing buffering capability (Zotz and Thomas 1999; Stuntz et al. 2002; Scheffers et al. 2014b). All together, we believe that by revealing the similarity of these two epiphytes in terms of the services which they provide for a diversity of organisms in their respective ranges, we support the label of “keystone species” for BNFs, as already given to tank bromeliads. We also believe that this form of service comparison could become a paradigm for the assessment of other epiphyte species.

Conclusion

Epiphytes are an emblematic component of biodiverse tropical rainforests, and a growing literature shows that they facilitate the use of the forest canopy for diverse taxa (Rocha et al. 2000; Watson 2001; Ellwood and Foster 2004; Silva et al. 2011; Scheffers et al. 2014b). By providing critical habitat services in the otherwise harsh and dry canopy environment, epiphytes can create additional vertical niche space and enable greater species coexistence and opportunity for diversification (MacArthur and MacArthur 1961; Pearson 1971; Gonçalves-Souza et al. 2010; Ruano-Fajardo et al. 2014). Our study in two geographically distinct rainforests found that *Asplenium nidus* bird's nest ferns are preferentially and abundantly occupied by arboreal-adapted species assemblages, and provide an important microclimate-buffering service to temperature-sensitive occupants. A loss of this microhabitat resource could, therefore, negatively affect a large portion of the forest's canopy biodiversity, including species that are or will be using BNFs as microclimate refuge in response to climate change (Ellwood and Foster 2004; Scheffers et al. 2013a). These species are particularly vulnerable, because at least in our surveys, no other canopy microhabitat contained similar levels of herpetofaunal presence and abundance. In these locations, BNF function would not easily be replaced by other native epiphytes. While currently listed as an IUCN Species of Least Concern, *Asplenium nidus* is particularly sensitive to prolonged droughts (Freiberg and Turton 2007; IUCN 2019), which are forecasted to increase in the tropics as a result of climate change (Duffy et al. 2015; Corlett 2016). Focusing conservation and research efforts on protecting and restoring BNFs may be an underappreciated yet crucial step for mitigating biodiversity loss in parts of the Afro-Asian tropics.

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