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Asplenium bird's nest ferns in rainforest canopies are climate-contingent refuges for frogs



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ABSTRACT

Epiphytes are important for canopy dwelling organisms because they provide a cool and moist microhabitat in the relatively hot and dry canopy. Here we examine whether epiphytic *Asplenium* ferns act as important habitats for arboreal frogs. We conducted extensive fern and habitat surveys for frogs in the Philippines, and complimented these surveys with roaming day and night canopy surveys to identify the full extent of habitat use across the vertical strata. We artificially dried ferns of various sizes to identify relationships between water and temperature buffering. Ferns are the preferred diurnal microhabitat and breeding habitat for arboreal frogs. A strong positive relationship exists between fern size and frog usage and abundance. Our drying experiments show that large ferns buffer maximum temperatures and reduce variability in temperatures, and buffering is directly linked to their hydration. Frogs are likely using large ferns for their moist, cool, environments for breeding and daytime retreat, which supports the buffered microhabitat hypothesis—these plants promote species coexistence through habitat creation and amelioration of physical stress. However, drying experiments suggest that this buffering is contingent on regular rainfall. Altered rainfall regimes could lead to the unexpected loss of the functional capacity of these important fern habitats.

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1. Introduction

Tropical rainforests harbor most of the world's terrestrial biodiversity, and they do so in a structurally complex environment, providing niches that span from canopy down to the understory (Ozanne et al., 2003). Many of these niches are physical structures derived from plants and therefore serve as living features that promote species coexistence through fine-scale habitat creation and amelioration of physical stress—buffered microhabitats (Angelini et al., 2011). Unfortunately under climate change, altered climate may render these foundational niches uninhabitable through the direct death of living keystone species or through the loss of their ecophysiological functionality. The interplay between keystone species,

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their dependent communities and the abiotic environment that they create is an underappreciated aspect of climate change science (Koh et al., 2004).

Epiphytes are a non-trivial component of forest structural complexity. Epiphytes represent a prominent above-ground structure in rainforests and appear to provide shelter for a significant proportion of the invertebrate biodiversity in rainforest canopies (Hietz, 1999; Ellwood and Foster, 2004; Díaz et al., 2012; Fayle et al., 2012). One group of epiphytes that are especially noteworthy are *Asplenium* bird's nest ferns (BNF), a widespread and abundant epiphyte found throughout the Paleotropics (Holtum, 1976). Suspended-soil habitats such as bird's nest ferns appear to be strongly associated with above-ground biodiversity (Ellwood and Foster, 2004; Beaulieu et al., 2010; Gonçalves-Souza et al., 2010; Díaz et al., 2012). Indeed, bird's nest ferns may support species in over 27 orders of Arthropods (Ellwood and Foster, 2004) and have distinct suspended-soil invertebrate communities from those on the ground (Beaulieu et al., 2010). Impressively, a single fern in a Bornean rainforest contained twice the invertebrate biomass as its entire host tree (Ellwood and Foster, 2004). Thus, these ferns likely represent one of the most important epiphyte groups and above-ground habitats throughout the Paleotropics (Ellwood and Foster, 2004).

Although a modest body of research has highlighted the importance of *Asplenium* ferns to arboreal invertebrates and local canopy microclimate, only post-hoc hypotheses have been proposed to explain these patterns. These hypotheses are that ferns provide canopy space for retreat and nesting, buffer temperature and moisture, and absorb and therefore serve as a source of moisture (Ellwood et al., 2002; Freiberg and Turton, 2007; Fayle et al., 2012; Scheffers et al., 2013a, 2014). For example, ferns in one hectare of forest can contain over one ton of dry biomass (Ellwood et al., 2002), invertebrate biomass is related to fern size (Ellwood and Foster, 2004), and ferns are consistently moister than the air that surrounds them (Freiberg and Turton, 2007), respectively. With the exception of bats (*Cynopterus horsfieldi*), which use ferns as roosting sites (Tan et al., 1999), not a single study we know of examines whether ferns are used by vertebrates (a fundamental question posed by Ellwood and Foster (2004)) and none explicitly examine why these ferns are the real estate of choice in tropical rainforest canopies.

Here, we demonstrate that bird's nest ferns appear to function as a critical canopy microhabitat for a vertebrate group – arboreal frogs – for which almost nothing is known (they are highly cryptic, nocturnal, and located in the hard-to-access rainforest canopy, Kays and Allison (2001)). We surveyed for frogs within bird's nest ferns throughout the canopy in a Philippine montane rainforest to explore whether bird's nest ferns function as arboreal refuges for adult frogs, and if they serve as critical breeding habitat for these frogs. We compare fern usage to the surrounding rainforest environment to determine whether ferns are disproportionately used by frogs and therefore may function as buffered microhabitats that expand the utility of canopy environments (Dayton, 1972; Tews et al., 2004). We further examined which fern and surrounding habitat characteristics best predict frog occurrence and abundance within ferns. Last, we test whether ferns provide a more consistent climate than the surrounding rainforest and therefore expand the biotic potential of inhospitable canopy environments. In total, our research suggests that *Asplenium* provide strong protection from temperature extremes and act as critical sources of moisture in the canopy. Further, experimental drying of ferns indicates that the thermal buffering they provide is strongly contingent on their state of hydration, a state that can change very rapidly in the absence of rain.

2. Materials and methods

2.1. Study area

We surveyed bird's nest ferns on Mt. Banahaw in southern Luzon, Philippines. The full systematics of ferns at this site have not been conducted but a study by Banaticla and Buot (2005) suggests that they are *Asplenium cymbifolium*. We do not provide species name due to this uncertainty. The site is characterized by lowland dipterocarp forest up to 800 m elevation, dipterocarp and montane forest from 900–1700 m elevation, and mossy and *Pinus* forest above 1700 m elevation. Our study was not conducted below 900 m because at lower elevations (<800 m) agriculture has replaced forest. We allowed 100 m of elevation to buffer any potential effects from these disturbances. The climate is marked by the absence of a distinct dry season with annual rainfall of around 3100 mm yr⁻¹ and 85% relative humidity on average (Banaticla and Buot, 2005).

2.2. Bird's nest fern and paired sampling surveys

We established two 100 m transects at 900, 1100, 1300, 1500, 1700 m (across the altitudinal distribution of bird's nest ferns; Figure S1 (see Appendix A)) and used canopy access techniques to access and survey 150 canopy ferns (Jepson, 2000).

Each fern was surveyed for frogs and eggs four times during the day starting from May–September, 2011. We sampled during the day as daytime refuges are most important in mediating hot temperatures. All ferns sampled were of sufficient size to contain frogs (fern area; mean: 837 cm²; range: 12–5933 cm²). During each survey, we thoroughly searched each fern, starting at the bottom, working up along its sides, and lastly searching the debris filled bowl located at the top of each fern. During surveys, we also had an observer on the ground watching for frogs that may jump out during searches.

To determine other microhabitats that may be important to frogs and to determine frog usage of these microhabitats relative to ferns we sampled for frogs in other near-by microhabitats for each surveyed fern. We sampled 953 paired microhabitats in total. Paired sampling occurred on the same day as ferns surveys. Two to five locations were sampled

for each fern, and sample size area was, at a minimum, of equal size to the associated fern. The number of samples varied due to availability of suitable habitats for paired samples. For each paired survey, we sampled the closest available habitat type of similar size and structure. Of the 953 paired random samples, 381 were other non-*Asplenium* epiphytes, 229 were tree microhabitats (e.g., under bark), 183 were ground microhabitats (e.g., rocks and litter mats), 71 were stumps and decaying logs, 29 were vine mats, 11 were moss mats, 15 were *Pandanus*, 14 were saddles of trees filled with detritus, 9 were suspended detritus mats, 6 were phytotelmata, and 4 were branches with structures.

We also conducted ground-to-canopy tree surveys for frogs to examine day and night usage by frogs and to explore whether frogs use alternative arboreal habitats (see Scheffers et al., 2013a,b for more details). From May–October 2011, we conducted 74 ground-to-canopy tree surveys at each elevation band where populations of *Asplenium* ferns occur (see Supporting Information for more details). In total, we sampled approximately $75\% \pm 9$ SD of the total tree height across elevations.

2.3. Bird's nest fern characteristics

For each fern we collected fern and local habitat characteristics that may affect frog use of ferns. Fern size may influence its ability to stay cool and wet and has been linked to increased richness and abundance of invertebrates (Ellwood and Foster, 2004). We measured two metrics that are indicative of fern size. We determined its area by multiplying the width of the organic mass by its height and measured the length of the five longest fronds (LL). We quantified local habitat characteristics that may influence frog usage of ferns. We measured the canopy cover (CC) above each fern using a spherical densitometer. For each bird's nest fern located within a tree, we recorded tree height and its diameter-at-breast-height (DBH). We also recorded the total epiphyte cover (EPI) for each tree by assigning a score from 0–4 (0: 0%, 1: 1%–25%, 2: 26%–50%, 3: 51%–75%, and 4: 76% and above). We recorded the average moss cover (MOSS) at breast height by recording percent cover within a square, averaged from measurements taken on three sides of the fern's host tree. Justification for the inclusion of fern variables and descriptive statistics are provided in Tables S1 and S2 in Supporting Information (Appendix A).

2.4. Garden experiments—link between temperature buffering and precipitation

We assessed the relationship between thermal buffering and precipitation in bird's nest ferns through drying experiments. At 1100 m a.s.l., we removed nine ferns of varying sizes, from small to large, and wrapped the root mass in nylon mesh (to retain all roots, humus, and other debris) and suspended the ferns approximately 1.5 m above the ground with rope. We derived a semi-dry mass for each fern by drying them until mass plateaued with time. A true dry mass would not be possible without killing the fern. We then continuously watered each fern until water leaked through the sides and bottom of the root mass. Ferns were protected with a clear plastic tarpaulin that was elevated a few meters above the ferns to allow normal transpiration and drying, and to prevent rain from re-wetting the ferns. Ferns were weighed three times daily for 20 days. The dry mass was subtracted from wet mass recorded on each day to determine the total volume of water in each fern. We considered the total mass lost since initial wetting to be equal to the total volume of water lost from each fern, by assuming the weight change due to photosynthesis and respiration during the experiment to be negligible.

During the drying experiment, we also examined within-fern temperatures relative to ambient temperature directly above the fern. We did so by placing a single temperature logger (Maxim Hygrochron ibutton Model DS1923; <http://www.maxim-ic.com/>) in the central bowl of each fern. Paired loggers were placed approximately 0.5 m above each fern and suspended under a plastic funnel to shelter them from direct solar radiation. Loggers recorded temperature every 15 mins.

2.5. Analysis—predictors of frog abundance

We derived a total frog abundance metric by summing the total number of frogs with the total number of egg masses found in ferns and dividing by the total number of surveys. Path analysis was used to explore the relationships among predictor variables and total abundance in ferns. We designated bird's nest fern area (BNF AREA), height of fern (BNF HGHT), canopy cover above fern (CC), diameter at breast height of fern's tree (TREE DBH), tree height (Tree HGHT) and epiphyte cover of fern's tree (EPI) as predictors of abundance. Prior to analysis, we standardized all variables to a mean of zero and standard deviation of approximately 1. We created a four “layer” multiple regression analysis; “layer 1” had DBH, CC, EPI, and TREE HGHT as predictors and BNF HGHT as the response variable; “layer 2” had BNF HGHT predicting AREA; “layer 3” had AREA predicting total abundance and “layer 4” had AREA, BNF HGHT, CC, DBH, EPI, and TREE HGHT as predictors and total abundances as the response variable. Leaf length (LL) and moss cover (MOSS) were removed from analysis due to their correlation with other variables (Table S3 Appendix A). We provide a summary of variables that best predict occurrence in Table S1 (Appendix A).

2.6. Predictors of frog occurrence

We used random forest analysis to examine which variables best predict frog occurrence in ferns. The relative importance of each variable in predicting occurrence (frog and egg occurrence combined) was determined using regression tree analysis.



Fig. 1. (A) A pair of bird's nest ferns in the rainforest canopy on Mt. Banahaw, the Philippines; (B) an exposed male *Platymantis luzonensis* sitting on the frond of a fern; (C) a sheltered female and male *Platymantis banahao* in amplexus within a bird's nest fern; and (D) a clutch of eggs (marked by the arrow) within a bird's nest fern (subset photo shows a single egg).

We used Breiman's random forest algorithm from the package *randomForest* in R stats version 2.15.1 (R Project for Statistical Computing, <http://www.r-project.org>). We chose random forest analysis because it is robust to interactions and correlations among variables, and does not over fit the data (Ranganathan and Borges, 2010). For random forest analysis, the prediction error on the out-of-bag portion of the data is determined and then repeated for each predictor variable. In other words, we record the changes in mean square error that is realized by leaving a variable out of the model. The difference between the two are then averaged over all trees, and normalized by the standard deviation of the differences. The node impurity is measured by the Gini index. We designated bird's nest fern area (AREA), height of fern (BNF HGHT), canopy cover above fern (CC), diameter at breast height of fern's tree (TREE DBH), and epiphyte cover of fern's tree (EPI) as predictors of occurrence (justification and statistics for each variable is provided in Tables S1 and S2 (Appendix A)).

2.7. Water retention and temperature buffering in ferns

For all nine ferns, we plotted the total water remaining and the proportion of water remaining for each day. Water remaining is derived by subtracting fern dry weight from total weight (wet and dry). For six of the nine ferns, we determined the difference in maximum temperature and difference in the coefficient of variation in temperature from the paired ambient loggers. Coefficient of variation (CV) is a normalized measure of dispersion that was calculated as the ratio of the standard deviation to the mean. Positive numbers that result from subtracting the ambient CV from fern CV indicate a more stable temperature within the fern relative to ambient. We used analysis of covariance (ANCOVA) to model differences in temperature maximums and CV with fern as a factor and days since watering as a covariate. We used pairwise comparisons of means via Tukey contrasts on the variables in order to determine which groups of ferns differ from each other significantly. Fern were placed into four groups based on their overall wet weight (0–1000 g, 1000–3000 g, 3000–4000 g, >4000 g).

3. Results

3.1. Frog abundance and richness in bird's nest ferns

Adult frogs use ferns as microhabitats and breeding habitats (Fig. 1 and Table 1). Five frog species, *Philautus surdus*, *Platymantis luzonensis*, *P. banahao*, *P. montanus*, and *Polypedates leucomystax*, were found within 150 ferns surveyed. Ferns were occupied by *P. luzonensis* at 900 m, *P. luzonensis* and *P. surdus* at 1100 m, *P. surdus* and *P. banahao* at 1300 m, *P. banahao*, and *P. montanus* at 1500 m, and *P. montanus* at 1700 m. Abundance was on average $0.25 (\pm 0.05 \text{ SE}; \text{range: } 0\text{--}5)$ and $0.41 (\pm 0.08 \text{ SE}; \text{range: } 0\text{--}6)$ for adults and egg clutches, respectively. The proportion of ferns occupied by adult frogs and eggs remained relatively constant across elevation (adults: 0.29, 0.07, 0.24, 0.26, 0.50 and eggs: 0.21, 0.33, 0.29, 0.13, 0 for 900 m, 1100 m, 1300 m, 1500 m and 1700 m a.s.l., respectively).

Table 1

The occurrence of frog adults and egg clutches (combined) in BNFs was 53%. Conversely, the occurrence of frog adults and egg clutches (combined) in paired random samples was 9%. BNF and paired habitats were sampled from 900 to 1700 m on Mt. Banahaw the Philippines from May to September, 2011. For each BNF, areas of equal size (minimum) to the associated fern were sampled at two to five locations (i.e., paired random samples). Paired samples consisted of ground leaf litter, tree branches and hollows, non-*Asplenium* fern species, vines, moss and epiphytic mats, decaying logs, and *Pandanus* palms, among others. Adult and egg clutch abundance are the total number of individuals observed across all samples. Occupied indicates the number of habitats (i.e., fern or pair) which were occupied by adults, egg clutches or adults and egg clutches.

	BNF total	Paired random sample total
Total sampled	150	953
Total adult abundance	39	9
Total egg clutch abundance	62	0
# Occupied (adults)	30	9
# Habitats occupied (egg clutches)	35	0
Total # habitats occupied (adults and egg clutches)	53	9
	(avg.)	(avg.)
Adult proportion	(0.20)	(0.006)
Egg proportion	(0.23)	0
Combined proportion	(0.35)	(0.006)

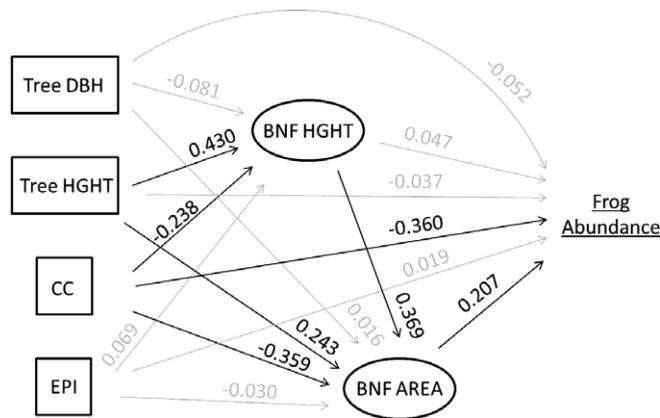


Fig. 2. Path analysis showing relationships between habitat variables and total frog abundance (eggs and adults) within bird's nest ferns ($N = 150$). Variables are defined in Table S1 (Appendix A). Dark arrows indicate significant relationships (p -value < 0.5) and gray arrows indicate non-significant relationships. Numbers along arrows represent the coefficients and the direction of the relationship.

Assuming that frog detectability is constant across survey locations, our data suggest that BNFs are on average 58 times more likely to have frogs and/or their eggs present during the day than a random sample of equivalent area from the surrounding forest (Table 1). BNFs serve as refuge for adults but also serve as breeding sites for arboreal frogs. Of the two species of frogs for which eggs could be located, *P. luzonensis* (distribution below 1100 m) and *P. banahao* (distribution from 1100 to ~1600 m), we found that eggs were present in approximately one in five ferns, whereas no eggs were found in randomly sampled microhabitats adjacent to BNFs (Table 1).

3.2. Predictors of frog abundance

The path analysis suggests that canopy cover is negatively related to abundance, even after accounting for its negative impact on BNF height and area (Fig. 2). BNF area positively predicted abundance with tree and BNF height influencing frog abundance indirectly through their positive effect on BNF area (Fig. 2). Tree diameter-at-breast height (Tree DBH) and surrounding epiphyte cover (EPI) had no effect on frog abundance or fern size (Fig. 2). Fern size, canopy cover and fern height were all correlated (Table S3, see Appendix A). Larger BNFs are found higher up in the forest stratum and under sparser canopy cover (Table S3, see Appendix A).

3.3. Predictors of frog occupancy

We examined six predictors of frog and egg occurrence (combined) within BNFs using random forests models. Our analyses suggest that fern size and height in the forest stratum positively predict frog occurrence whereas canopy cover negatively predicts frog occurrence (Figure S2, see Appendix A). Epiphyte cover has a small effect on frog occurrence within ferns (Figure S2, see Appendix A).

Table 2

The number of adults found during canopy surveys (day and night) in 37 trees from 900 to 1500 m (14 trees at 900 m, 5 at 1100 m, 13 at 1300 m, 5 at 1500 m elevation). Sheltered indicates that individuals were found within the habitat and therefore not exposed to ambient air.

Habitat type	Night	Night sheltered	Day	Day sheltered
Broad leaf	14	0	0	0
Vine	7	0	0	0
Tree bark	5	0	0	0
Other epiphyte	4	0	0	0
BNF	3	2	6	6
Crevice with Detritus	2	2	3	3
Branch	1	0	0	0
Moss	1	0	1	1
Pandanus	1	0	0	0
Other	3	0	0	0
Total	41	4	10	10

3.4. Complementary arboreal surveys—day versus night

To explore whether frogs use other habitats in the rainforest canopy, we conducted canopy surveys (day and night) in 37 trees for adult frogs across the elevation range of bird's nest ferns. During these extensive broad area surveys, we found 51 frogs in the forest canopy. Of 41 frogs found at night, 34 were found in exposed habitats and four (11%) were found in sheltered habitats (Table 2). Three individuals did not have habitat data recorded. Conversely, 10 frogs were found during the day, all of which were in sheltered habitats (Table 2). Two (5%) frogs from night surveys were sheltered within BNFs compared to six during the day (60%). The remaining frogs were found on broad leaves, within or on moss and epiphytic mats, crevices and organic detritus, among others (Table 2).

3.5. Garden experiments

Bird's nest ferns have a large capacity to absorb water: water increased fern weight by around 52% (± 7 SD) across all fern sizes. Ferns retained over 30% of their water for 8–13 days (Fig. 3). The ability of ferns to buffer maximum temperatures and reduce variability in temperatures is directly linked to their hydration (Fig. 3). The slope of the relationship between delta Tmax or delta CV and days since watering was similar among ferns despite their varying mass (delta Tmax: $df = 5$, $F = 1.074$, $P = 0.379$; delta CV: $df = 5$, $F = 1.498$, $P = 0.197$). Removal of the interaction term did not significantly affect the fit of either model ($F = 1.0729$, $P = 0.379$ and $F = 1.498$, $P = 0.196$ for delta Tmax and delta CV, respectively). The more parsimonious models with the interaction term removed revealed a significant effect of days since watering and fern on both delta Tmax and delta CV (in both cases, days since water $P < 0.001$ and fern $P < 0.001$). Post-hoc Tukey tests indicated that the main difference was between two of the three largest ferns (> 4000 g) and all other ferns, the former approaching ambient conditions more slowly.

4. Discussion

4.1. Frogs and ferns in the rainforest canopy

Bird's nest ferns are one of the most widely distributed and ecologically important epiphytes in the Paleotropics (Ellwood and Foster, 2004). Yet, much of their importance is understood from only a few key studies that are focused on invertebrate communities. Our study documents a novel frog–fern relationship: bird's nest ferns serve as important above-ground refuges and a highly used breeding habitat for arboreal frogs in our system. The results of our study complement a growing literature showing ferns support a diverse fauna (not just invertebrates) and substantial animal abundance (Ellwood and Foster, 2004; Karasawa et al., 2008; Beaulieu et al., 2010).

Knowledge of arboreal habitat use by frogs is limited due to the cryptic nature of frogs as well as the difficulty in accessing canopy habitats (Kays and Allison, 2001). Canopy surveys in our study area show that almost 80% of all frogs in our rainforest site are found above-ground (Scheffers et al., 2013b). Yet, frogs are temperature sensitive and hydrophilic which begs the question: how are such high abundances maintained in the relatively hot, dry canopy environment?

The most likely mechanism for this frog–fern relationship and for why ferns promote the utility of rainforest canopies is that ferns create small-scale temperature and moisture refuges and so buffer sensitive ectotherms from excesses of heat and desiccation (Scheffers et al., 2014). In our study, this micro-refugia interpretation was supported in three ways: (1) patterns of occurrence in day versus night surveys (see Table 2); (2) through the environmental characteristics that best predict occupancy and abundance of frogs in BNFs, and (3) by direct observation and experimental data on the microclimates fostered by BNFs.

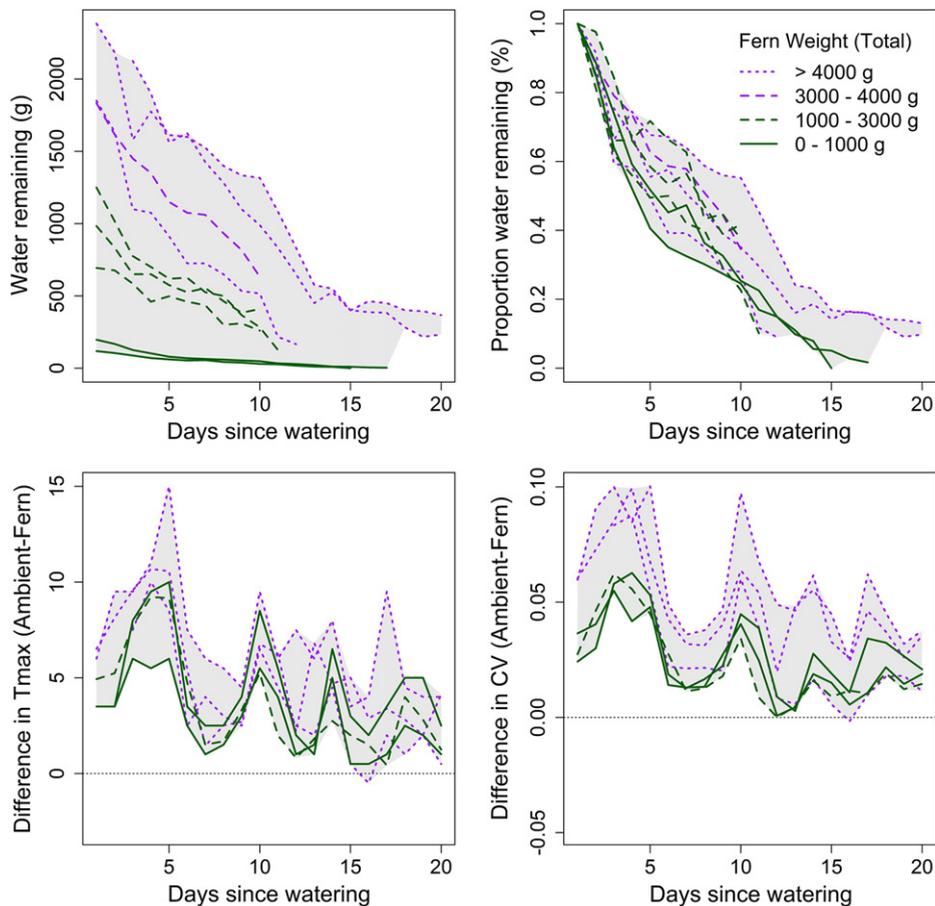


Fig. 3. The total water weight (top left), proportion of water remaining (top right) and thermal buffering of bird's nest ferns (lower left and right). Water weight was monitored in nine ferns over a 20 day period of no exposure to rain following complete saturation. Temperature was monitored in six of the nine ferns. Difference in maximum temperature and the coefficient of variation from ferns and paired ambient are shown as ferns dry. Positive differences in maximum temperature and the coefficient of variation (y -axis) indicate that ferns had cooler and less variable temperature than ambient. The bigger the difference in coefficient of variance the greater the fern's capacity to buffer temperature. Ferns are grouped and colored by total fern weight (dry and wet).

4.2. Day versus night

Ours is the first study for any taxon to examine the use of *Asplenium* between night and day, and the results are revealing. Our day/night comparisons clearly show that ferns function as diurnal retreat sites in the canopy: 60% of all frogs found in our daytime ground to canopy surveys were located within ferns with the remainder located in crevices with detritus or moss. When we further examined daytime use of ferns using a paired sampling design, ferns surveyed along transects during the day were on average 58 times more likely to be used by frogs than a paired random sample in the forest. Moreover, all five arboreal frog species from our study area used ferns as diurnal retreats and two of these (*P. luzonensis* and *P. banahao*) species may be obligate bird's nest fern breeders: we did not locate a single clutch of eggs outside of BNFs during our fern transect surveys nor during canopy surveys. Despite this high fern usage in the day, adult frogs clearly move out of BNFs at night: only 5 % of frogs in the nighttime surveys were found in ferns. Given that the extremes of heat and desiccation occur mostly during the day, these observations suggest that the disproportionate use of BNFs by adult frogs during the day provides strong circumstantial evidence in support for our microhabitat hypothesis. This evidence is strengthened further when we examine the microhabitat characteristics that predict frog usage.

4.3. Fern characteristics that best predict frog usage

Ferns occurring at greater heights tend to be larger and occur under less canopy cover (similar patterns were found by Fayle et al., 2009). Bigger ferns had the highest abundances and occupancy of frogs. These results mirror those of Ellwood and Foster (2004) who show a strong positive relationship between the number of leaves on a fern (i.e., indicative of size) and invertebrate biomass. As canopy cover above ferns increased, frog abundance and occupancy decreased. This pattern

remains applicable even after accounting for canopy cover's negative impact on BNF area. A similar pattern was observed in Brazil, where epiphytic bromeliads located in habitats exposed to the sun were more frequently occupied by anurans than habitats located in the shade (Silva et al., 2011). Higher canopy cover may lower temperature and evaporation, thereby diminishing dependence on the buffering effect afforded by BNFs. Alternatively, places that are warmer in the afternoon and evening (i.e., places with low canopy cover) may be favorable, but these places, without the buffering provided by ferns may also be inhospitable during the middle of the day. We also examined other possible factors that might impact the abundance of frogs within ferns, such as surrounding epiphyte cover and tree diameter size, but none of these were found to play a significant role.

4.4. *Micro-climatic environment within ferns*

By monitoring fern climate within the rainforest canopy as well as directly manipulating ferns' abiotic conditions, we show that BNFs reduce temperature variation (also see Turner and Foster (2006); Scheffers et al. (2013a)) and that BNFs within our study area can store water for almost two weeks. These results are consistent with those of others: bird's nest ferns in Australia and Singapore have also been shown to retain water (see Kluge et al. (1989); Freiberg and Turton (2007)). Importantly, however, our experiment shows that this capacity to retain water is strongly contingent on the size of the fern (in turn, the major predictor of frog occupancy/abundance). Thus, we suspect frogs developed a proclivity for laying eggs in ferns because they not only provide ample above-ground space (Fayle et al., 2012) for laying eggs but also provide a climate controlled environment for development that is more stable than external conditions. In this respect, bigger ferns provide a better buffer than their smaller conspecifics.

Further, our experiment clearly demonstrated that the temperature buffering ability of ferns is strongly contingent on their hydration status, and big ferns dry out more slowly than small ferns. But ferns in our study area likely remain moist almost constantly (the longest consecutive time without precipitation in our study area was 9 days over the course of 7 months: Scheffers, unpub. data). Thus while temperature buffering and shelter from desiccation serve as the most likely explanations for why ferns harbor significant biodiversity in the canopy, these capacities are strongly dependent on regular rainfall.

5. Conclusion

5.1. *The role of bird's nest ferns in thermal ecology, arboreality, and species distributions*

Our work identifies a direct link between fern size (the primary predictor of abundance) and temperature and moisture. This link suggests that the presence of smaller scale climate controlled epiphytes collectively expand the availability of usable space in the harsh rainforest canopy. The relatively hot, dry canopy is unsuitable for most species of frog unless they are behaviorally or physiologically well-adapted (Tracy et al., 2010). We show that the use of BNFs by frogs as daytime refuges is one such adaptation: frogs that utilize BNFs can evade the daytime canopy environment while minimizing the energetic costs of daily movements between suitable daytime refuges and optimal night time foraging areas (Stewart, 1995; Vickers et al., 2011). Levels of arboreality in many organisms may prove to be strongly linked to the presence of suitable arboreal habitats such as bird's nest ferns.

5.2. *Bird's nest ferns as climate refuges*

The buffering capacity of ferns expands the thermal habitat tolerances of fern-obligate frogs in our study area by 8.5 °C (Scheffers et al., 2013a) and reduces their exposure to climate extremes by over 30 fold (Scheffers et al., 2014), yet our study suggests that this expansion in tolerance and reduction in vulnerability will largely be dependent on precipitation. This link indicates that warming is not required to threaten canopy communities because changes in precipitation alone can remove the buffering capacity of canopy ferns making even contemporary temperatures inhospitable in the rainforest canopy. This is an important consideration because current climate models project extreme warming as well as strong reductions in or increased stochasticity of rainfall in some areas (Meehl and Tebaldi, 2004; Fischer and Knutti, 2013). Changes in precipitation can increase extirpation risk of montane species by 10-fold (McCain and Colwell, 2011). Therefore, although ferns effectively serve as thermal buffers, these buffering properties are only applicable if minimum inputs from precipitation are maintained. Two possible scenarios might occur if extreme changes occur in weather: (1) the ferns themselves die (periods longer than eight weeks of no rain can kill ferns: Freiberg and Turton (2007)); or (2) the ferns survive but lose their buffering capabilities from sporadic small drought events. The loss of these biotic amplifiers would result in an overall attrition in canopy biodiversity as organisms would likely need to shift towards the ground (Scheffers et al., 2013b) as has been observed for frog communities during El Niño events in Papua New Guinea (Bickford, 2005). This increased density at ground levels may lead to local population decline across animal communities from competition and density-dependent mortality (Patrick et al., 2008; Green and Middleton, 2013).

Bird's nest ferns effectively buffer contemporary climate and thus serve as a critically important species in rainforest canopies. The strong link between climate buffering and precipitation however suggests that fern dependent communities might be especially vulnerable under extreme weather events.

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Authors contributions BRS designed the research. BRS collected data. BRS, BP and LPS designed models, analyzed results and wrote the manuscript.

Appendix A. Supplementary data

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.gecco.2014.06.004>.

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