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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.

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 (Holttum, 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 cm^2; range: 12 –5933 cm^2). 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