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Coqui frog populations are negatively affected by canopy opening but not detritus deposition following an experimental hurricane in a tropical rainforest

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ABSTRACT

Hurricanes, cyclones, and typhoons are common disturbances in many island and coastal forests. There is a lack of understanding of the importance to forest biota of the two major physical aspects that occur simultaneously during a hurricane: canopy disturbance and detritus (debris) deposition onto the ground. Using a replicated factorial design, our study involved experimentally determining the independent and interactive effects of canopy opening and debris additions to the forest floor on densities of coqui frogs (*Eleutherodactylus coqui*). Coquies are the dominant amphibian, and second most common vertebrate species, in the Luquillo Experimental Forest (LEF), a montane, tropical rainforest in northeastern Puerto Rico that frequently experiences hurricanes. Frogs were sampled in all twelve 30×30 m plots at three periods prior to installing treatments (July 2003, January 2004, July 2004), and at months 1, 3, 6, and 12 post-treatment. The degree of canopy opening and amount of debris deposited onto the forest floor by our experimental treatments closely mimicked conditions resulting from Hurricane Hugo, a severe hurricane that passed over the LEF in 1989. Based on findings from past studies involving natural hurricanes in the LEF, we predicted that coqui densities would increase in response to debris additions, and decrease or remain unchanged in response to canopy disturbance. However, we found that debris deposition had no significant effect on coqui density and that the opening of the canopy was the dominant aspect affecting coqui by significantly reducing their densities. We identified several possible explanations for the decreased coqui densities in open-canopy plots, including decreased litter moisture and insect prey, and temporal and spatial scales associated with disturbance that may have influenced coqui behavior. Following natural hurricanes, and in light of our findings from experimental hurricane impacts, we expect that coquies benefit from patches of intact canopy while suffering reduced densities in open-canopy settings. Furthermore, based on our study and other experimental forest studies involving frogs, future forest practices that remove significant canopy should probably be viewed as having an initially (up to 1 year) negative effect on the frog community.

1. Introduction

Hurricanes are among the most common large-scale disturbances in tropical forests (Lugo et al., 1983; Everham and Brokaw, 1996; Whitmore and Burslem, 1998; Lugo, 2008); they simultaneously create canopy gaps within predominately closed-canopy forests while adding large amounts of fresh, non-senesced biomass to the forest floor (Turton, 1992; Ostertag et al., 2003). While the dynamics of hurricane disturbance in tropical forests have been studied from the perspective of plant and animal community responses (Waide, 1991; Burslem et al., 2000; Angulo-Sandoval et al., 2004), no studies have attempted to decouple the effects of canopy opening and the concomitant changes in microclimate (e.g., light availability, temperature variation, drying and wetting cycles) from the effects of biomass addition (e.g., increased nutrient availability and energy to detrital food webs, increased forest floor structure). Such experimental decoupling of such prominent factors that occur simultaneously during a

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hurricane will help inform ecologists and forest managers about the mechanisms of forest change following large windstorms such as hurricanes.

Studies of amphibian population dynamics after canopy disturbance due to windstorms are relatively uncommon (but see Woolbright, 1991, 1996; Greenberg, 2001; Vilella and Fogarty, 2005), with most amphibian studies focused on the effects of canopy disturbance due to human land use (e.g., timber extraction activities; see Ash, 1988; Horn et al., 2005; Ernst and Rödel, 2005; Ernst et al., 2006; Popescu et al., 2012). The responses of amphibian species to canopy disturbance have ranged from populations increasing in abundance (Woolbright, 1991, 1996; Horn et al., 2005; Popescu et al., 2012), decreasing in abundance (Pough et al., 1987; Petranka et al., 1993; Popescu et al., 2012) or exhibiting no change (Greenberg, 2001; Vilella and Fogarty, 2005). The underlying drivers of these amphibian responses to canopy disturbance have been attributed to changes in microclimate (Pough et al., 1987; Woolbright, 1996; Popescu et al., 2012), prey availability (Horn et al., 2005), predator abundance (Woolbright, 1991, 1996), and habitat structure (Woolbright, 1991, 1996).

Most of the studies listed above were conducted in temperate regions where the focal amphibian group was Caudata (salamanders, broadly defined) and the type of disturbance was human land use related to timber extraction (Pough et al., 1987; Ash, 1988; Harpole and Haas, 1999; Petranka et al., 1993). Fewer studies concentrate on Anurans (frogs and toads) and/or natural canopy disturbances in tropical forests (Gardner et al., 2007; but see Woolbright, 1991, 1996; Vilella and Fogarty, 2005). In the Appalachian Mountains of North Carolina, U.S., Greenberg (2001) compared amphibian and reptile communities in undisturbed hardwood-dominated forest to those in forest gaps created by hurricane disturbance and found that lizard and snake species richness and abundance increased in gaps relative to the undisturbed forest. However, there were no differences between gaps and controls for amphibian species richness or in any measure of abundance, which Greenberg (2001) attributed to pre-adaptations of the amphibians to xeric conditions of the forest gaps. Also in a hardwood forest in the Southeastern U.S., the green tree frog (*Hyla cinerea*) abundance increased after formation of artificial gaps created by timber extraction, and such increases were positively correlated with insect abundance (Horn et al., 2005).

In Puerto Rico, the two vertebrate groups that numerically dominate most forests are lizards in the genus *Anolis* (family Polychrotidae) and tree frogs in the genus *Eleutherodactylus* (family Leptodactylidae). In the Luquillo Experimental Forest (LEF) of northeastern Puerto Rico, *Eleutherodactylus coqui* (hereafter, referred to as coqui or coquies (pl.)) has been estimated to reach densities of 20,570 frogs ha^{-1} (Stewart and Woolbright, 1996) while anoles (*Anolis gundlachi*, *A. stratulus* and *A. evermanni*) reach combined densities of 29,370 lizard ha^{-1} (Reagan, 1996). Because of their overall abundance, the dynamics of coqui populations have been the subject of many studies since 1980.

Coqui population size in the LEF increased following concomitant increases in forest floor structure (Stewart and Pough, 1983). In the same forest, Woolbright (1991) found that coqui populations increased 4-fold at 1 year after Hurricane Hugo. Such increases in coqui abundances were attributed to a variety of contributing factors, including increases in forest floor habitat structure that benefited coqui egg-laying and males guarding the egg masses (see Stewart and Pough, 1983), increases in forest floor humidity due to the emergence of dense understory vegetation, and the reduction of major invertebrate predators that probably competed for resources with coqui and served as potential predators of coquies (Formanowicz et al., 1983; Woolbright, 1991, 1996). Additionally, coqui abundances can shift dramatically due to relatively high fecundity, and reproduction can occur up to 9 times per year with clutches of 15–45 eggs (Rivero, 1978). Despite such high fecundity from frequent reproductive events, an increase in the adult coqui population was not detectable until 1 year after a severe hurricane (Hugo) passed over the LEF (Woolbright, 1991, 1996). Woolbright (1991) suggested low juvenile survivorship due to desiccation in the leaf litter as a possible explanation for the observed time lag in coqui population increase following the passing of Hurricane Hugo in 1989. Moreover, there was a pronounced drought that lasted nearly 3 months in the LEF immediately following the passage of Hurricane Hugo (Scatena and Larsen, 1991; Woolbright, 1991). Woolbright (1996), studying the same plot in the LEF, examined pre-Hurricane Hugo coqui population dynamics and found that in response to tree fall gaps that occurred in January 1988, the coqui population increased similarly to that after Hurricane Hugo but at an accelerated pace (5 months). In contrast, Vilella and Fogarty (2005) reported no changes in coqui populations at two sites in the western Cordillera Central of Puerto Rico following the passing of Hurricane Georges in 1998, but this lack of population change may have been due to their sampling occurring just 8 months following the storm.

Given the conflicting results from studies examining frog population dynamics following natural canopy disturbances and the variety of explanations for those dynamics, experiments designed to examine the underlying mechanisms affecting frog population fluctuations would be informative. Canopy disturbance and debris deposition to the forest floor are the two major physical aspects that occur simultaneously during a hurricane. In all previous studies of the response of coqui populations to hurricane disturbances, it has been impossible to separate the independent effects of canopy opening and concomitant changes in microclimate, from the deposition of canopy debris that alters microhabitat structure, humidity at the forest floor and/or nutrients and energy availability. In 2004, we implemented an experiment to separate the effects of these two major aspects of hurricane disturbance (canopy openness and debris deposition) on coqui populations. We tested the following hypotheses posed by Stewart and Pough (1983) and Woolbright (1991, 1996): (1) coquies are limited by the availability of understory nest sites, (2) nest site limitation is relieved by the addition of leaf litter to the forest floor, and (3) leaf litter compensation for nest site limitation will be independent of any microclimate changes that occurs as a result of canopy opening. We predict that coqui densities will increase in response to debris additions, and decrease or remain unchanged in response to canopy disturbance.

2. Methods

2.1. Study site

This study took place in the LEF of Puerto Rico, Western Atlantic, near the El Verde Field Station (EVFS; 18°20′N, 65°49′W; see map in Shiels and González, 2014). The LEF is a 11,000 ha tropical (18°N latitude) evergreen forest that spans elevations of approximately 100–1075 m. Mean annual rainfall at EVFS is 3500 mm, and monthly precipitation is variable, but May to December are usually the wettest months and January to April are typically slightly drier (Zimmerman et al., 2007). The study site is in tabonuco forest (subtropical wet forest in the Holdridge System; Ewel and Whitmore, 1973), which is the lowermost and dominant of four general vegetation zones along an altitudinal gradient across the LEF. The most common trees at the study site are *Dacryodes excelsa* (Burseraceae), *Prestoea acuminata* var. *montana* (syn. *Prestoea montana*; Arecaceae), *Sloanea berteriana* (Elaeocarpaceaea), and *Manilkara bidentata* (Sapotaceae). In 2003, prior to our treatments, the 135 tallest canopy trees at our study site averaged 18.1 ± 0.3 m (range: 13–30 m; A. Shiels, unpublished data).