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Experimental decoupling of canopy opening and debris addition on tropical gastropod populations and communities

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ABSTRACT

Climate-induced disturbances such as hurricanes affect the structure and functioning of many ecosystems, especially those in the Caribbean Basin, where effects are well documented with regard to biodiversity and biogeochemical dynamics. Because climate change will likely alter the frequency or intensity of such storms, it is increasingly important to understand the mechanistic bases for ecosystem responses. However, this is particularly difficult to do in the absence of manipulative experiments that decouple confounded factors such as canopy opening and debris deposition. To address this issue, we exploited a replicated factorial design to experimentally distinguish the effects of canopy opening and debris deposition on population- and community-level characteristics of gastropods in the Luquillo Experimental Forest of Puerto Rico. Despite considerable spatial variation, abundances of all gastropods (combined) as well as abundances of each of 3 species (i.e., *Alcadia striata*, *Platysuccinea portoricensis*, and *Polydontes acutangula*) responded significantly to canopy opening while abundances of each of 2 species (i.e., *Pl. portoricensis*, and *Po. acutangula*) responded significantly to debris deposition within two years of experimental manipulation. In contrast, two species (i.e., *Gaeotis nigrolineata* and *Nenia tridens*) did not respond to any experimental manipulations in the short term. Moreover, species composition did not differ between pre- and post-manipulation periods, in part because of considerable variation among replicated blocks. In contrast, canopy removal consistently affected species richness, Shannon diversity, and rarity, while debris deposition consistently affected species richness and Shannon diversity. Neither treatment affected species dominance or evenness. Longer-term responses of the gastropod fauna were more complex. Although considerable interspecific heterogeneity characterized responses of the gastropod fauna, temporal variation in mean abundance for each of the three manipulative treatments was similar to that of the non-manipulated treatment when abundances were combined for all species. In contrast, temporal variation in each of the manipulative treatments was unrelated to temporal variation in the non-manipulated treatment for species richness, evenness, dominance, and rarity. Moreover, temporal variation in abundance generally differed between at least two of the manipulative treatments for most species and temporal variation in components of taxonomic biodiversity generally differed between manipulative treatments as well. Temporal variation in species composition was considerable and comparable for each of the four treatment combinations. Species composition within each treatment combination varied over time in ways unrelated to temporal variation in the other treatment combinations, including the reference treatment (i.e., no canopy trimming and no debris addition). Manipulated treatments were surrounded by large areas of intact forest, and tabonuco forest generally exhibits appreciable spatial and temporal variation. Natural spatiotemporal variation in the study system likely overwhelmed many of the effects of experimental manipulations on gastropod populations or communities via edge effects and recruitment of individuals from nearby less disturbed portions of the landscape.

1. Introduction

The role of disturbance in molding the structure and function of ecosystems has emerged as a paradigm guiding much ecological research from both theoretical (Holling, 1973; Pickett and White,

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1985; Pickett et al., 1989; Willig and Walker, 1999; Vandermeer et al., 2004; Holt, 2006) and empirical (Walker et al., 1991, 1996a; Willig et al., 2007, 2010, 2011a) perspectives. Tropical forests in the Greater Caribbean Basin are hurricane mediated, as much of the spatiotemporal variation in the structure, physiognomy, and composition of these ecosystems arises as a consequence of intense storms (Walker et al., 1991, 1996a; Waide and Lugo, 1992). The ecological impact of these relatively infrequent but intense and large-scale disturbances has been well documented for plants (Brokaw and Greer, 1991; Boucher et al., 1994; Zimmerman et al., 1994; Grove et al., 2000; Lomascolo and Aide, 2001; Brokaw et al., 2004; Vandermeer et al., 2004), animals (Waide, 1991; Willig and Camilo, 1991; Secrest et al., 1996; Lopez et al., 2003; Schoener et al., 2004; Bloch and Willig, 2006; Schoener and Spiller, 2006; Bloch et al., 2007; Gannon and Willig, 2009), microbes (Willig et al., 1996; Miller and Lodge, 1997; Lodge et al., 1994), and ecosystem or biogeochemical processes (Walker et al., 1991; Zimmerman et al., 1994, 1995; Scatena et al., 1996; Silver et al., 1996; Ostertag et al., 2003). Nonetheless, the mechanistic bases of observed responses to hurricane-induced disturbance are poorly understood, in part because of the unpredictable timing of these disturbances and in part because of the interrelated suite of environmental characteristics that accompany hurricane impacts. Because the frequency of major hurricanes (Categories 3–5) in the Caribbean may increase (Landsea et al., 1999; Webster et al., 2005) in the near future as a consequence of climate change (but see Knutson et al., 2008), it is critical to understand the effects of these intense disturbances on the resistance, resilience, and vulnerability of biological systems (e.g., Holt, 2006; Gallopín, 2006; Schoener and Spiller, 2006).

Hurricanes have multifarious impacts on the environment. Severe hurricanes relocate the leaves and branches of the canopy to the soil surface, or to at least within a few meters of the soil surface (Brokaw and Greer, 1991; Lodge et al., 1994; Whigham et al., 1991; Wunderle et al., 1992, Wunderle, 1995; Rice et al., 1996). Several associated physical changes occur as a consequence of this canopy disturbance. Decreased canopy cover results in increased light levels at or near the soil surface (Fernández and Fetcher, 1991; Bellingham et al., 1995), and a corresponding increase in temperature. In terrestrial habitats, greater temperatures and increased air circulation at the ground surface lead to increased evaporation from litter and soils, and may decrease litter and soil moisture (Lodge, 1996), although reduced transpiration can offset soil moisture losses (Silver and Vogt, 1993). In addition, the deposition of debris from the canopy represents a significant alteration to the structure of the understory as well as a major change in the quantity and quality of carbon-inputs into detrital food webs. Thus, non-manipulative natural experiments cannot disentangle the various mechanistic bases of changes to the environment that arise from hurricane disturbance.

Considerable research in the Luquillo Mountains has documented the effects of different disturbances on plants, animals, and ecosystem processes over short (Frangi and Lugo, 1991; Walker et al., 1991; Scatena et al., 1993; Silver and Vogt, 1993; Wunderle, 1995; Zimmerman et al., 1994, 1995; Everham and Brokaw, 1996; Ostertag et al., 2005) and intermediate (Crow, 1980; Weaver, 1986; Gregory and Sabat, 1996; Walker et al., 1996a,b; Weaver, 2002; Willig et al., 2010) time scales. The documentation of changes in organismal, population, community, and ecosystem characteristics following disturbance has provided a rich context from which to explore fundamental mechanisms controlling the dynamics during recovery of strongly interconnected biotic systems. Nonetheless, many simultaneous and interacting attributes of disturbance make it difficult to distinguish the separate effects.

1.1. Objectives

We used a replicated factorial design to decouple the effects of canopy opening (increases temperature, alters moisture) from those associated with debris deposition (modifies structure, increases food resources, alters soil moisture) on population and community characteristics of gastropods in tabonuco forest in the Luquillo Mountains of Puerto Rico.

2. Methods

2.1. Study area

Situated within the hurricane-prone Caribbean (Fig. 1), the Luquillo Experimental Forest (LEF) comprises 11,300 ha in northeastern Puerto Rico (Fig. 1A). It is a Man and the Biosphere Reserve (Franklin, 1977) as well as a site in the U.S. National Science Foundation's Long-Term Ecological Research network (Hobbie et al., 2003). Sampling was conducted in tabonuco forest, approximately 1 km northeast of El Verde Field Station (18.321°N, 65.820°W; 340–470 m asl) (Fig. 1B). Tabonuco forest occurs at elevations up to 600 m asl, and is the most extensive and best studied portion of the LEF (Reagan and Waide, 1996; Brokaw et al., 2012a,b). It is a subtropical wet forest according to the Holdridge classification system (Ewel and Whitmore, 1973; Brown et al., 1983) and is characterized by a dominant hardwood species, *Dacryodes excelsa* (Burseraceae). Other common trees of the tabonuco forest canopy include *Manilkara bidentata*, *Sloanea berteriana*, *Guarea guidonia*, and *Prestoea acuminata* (Odum and Pigeon, 1970; Lawrence, 1996). Canopy height is >20 m, with emergent trees up to 35 m. Rainfall in tabonuco forest averages 346 cm per year (McDowell and Estrada-Pinto, 1988). Humidity is consistently high, and little seasonal or diurnal variation occurs in temperature (Odum and Pigeon, 1970).

2.2. Study organisms

Terrestrial gastropods are taxonomically diverse and numerically abundant in many ecosystems, making them useful species for biogeographic, macroecological, or conservation studies, including those focusing on community (Stanisic et al., 2007; Wronski and Hausdorf, 2010) or metacommunity structures (Presley et al., 2011; Willig et al., 2011b, 2013). Like most non-marine mollusks, terrestrial gastropods currently are suffering from global declines in abundance and diversity, and are in need of conservation management (Lydeard et al., 2004). In addition, gastropods are ectothermic, constrained in distribution and behavior by desiccation stress (Russell-Hunter, 1983; Cook, 2001), and are not particularly vagile. Consequently, changes in disturbance regimes combined with increased intensity of anthropogenic activities may put these faunas at even greater risk of local or regional extirpation.

In the LEF, terrestrial gastropods are well understood taxonomically (Garrison and Willig, 1996). Although forty-four species have been recorded from the LEF, only 26 of these forage above the leaf litter, and many are rare or maintain low population densities. Terrestrial gastropods in the LEF respond to small scale (Alvarez and Willig, 1993) and broad scale (Willig and Camilo, 1991; Secrest et al., 1996; Willig et al., 2007) disturbances. Moreover, the habitat associations of some species are well documented (Cary, 1992; Willig et al., 1998), as are the long-term spatiotemporal dynamics of many species (Willig et al., 1998, 2011a,b; Bloch and Willig, 2006; Presley et al., 2011).