

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., *Alcaldia striata*, *Platysuccinea portoricensis*, and *Polydortes 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.

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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,

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; Secret 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 north-eastern 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; Secret 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).

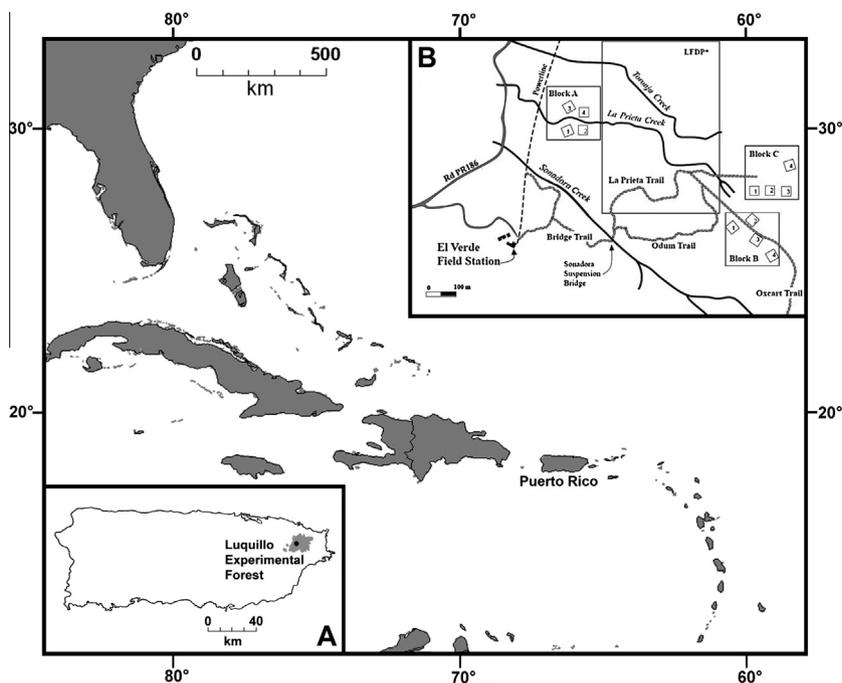


Fig. 1. Map of the Caribbean showing the location of Puerto Rico (labels on vertical borders are degrees north latitude and labels on horizontal borders are degrees west longitude) and the Luquillo Experimental Forest (LEF). Within the LEF (gray shading of Inset A), a solid circle (18.309° N, 65.796° W) indicates the location of the Canopy Trimming Experiment. Replicated blocks were located within the drainage of the Sonadora (Inset B) and in close proximity to the long-term forest dynamics plot (LFDP) in tabonuco forest. Road = gray, Trail = gray with dashed edge, Stream = solid line (after Richardson et al., 2010).

2.3. Field methods

2.3.1. The canopy trimming experiment (CTE)

A two-by-two factorial design (canopy trimming-by-debris deposition, Fig. 2) was deployed in each of three blocks (Blocks A, B, and C of Fig. 1B). Each block contained four plots (30 m by 30 m) chosen at random and assigned to one of the four treatment combinations (Fig. 2). Each plot was defined by 5 m wide perimeter (i.e., a buffer zone to reduce “edge effects” associated with non-manipulated forest) and an inner square (20 m by 20 m), subdivided into 16 sub-plots (5 m by 5 m), four of which were chosen at random and surveyed for gastropods. The four combinations (Fig. 2) of model I treatment factors (canopy trimming and debris deposition) are:

- (1) *Canopy not trimmed and debris not added (No Trim + No Debris)*: This represents the “reference” or “background” condition without any simulated hurricane effects.
- (2) *Canopy not trimmed and debris added (No Trim + Debris)*: This simulates the effect of a redistribution of canopy biomass by hurricanes, but decouples that effect from the consequences of canopy openings.
- (3) *Canopy trimmed and debris not added (Trim + No Debris)*: This simulates the effect of an altered microclimate that arises from hurricane-related canopy openings, but decouples that effect from the consequences of redistribution of resources.
- (4) *Canopy trimmed and debris added (Trim + Debris)*: This simulates the combined effects of hurricanes with respect to alteration of microclimate and redistribution of resources.

Full execution of experimental manipulations, including the trimming, weighing and redistribution of debris, extended from 26 October 2004 to 16 June 2005, and is described in detail elsewhere (Richardson et al., 2010; Shiels et al., 2010; Shiels and González, 2014), forming the basis for the following abbreviated summary. Treatment implementation was time-intensive

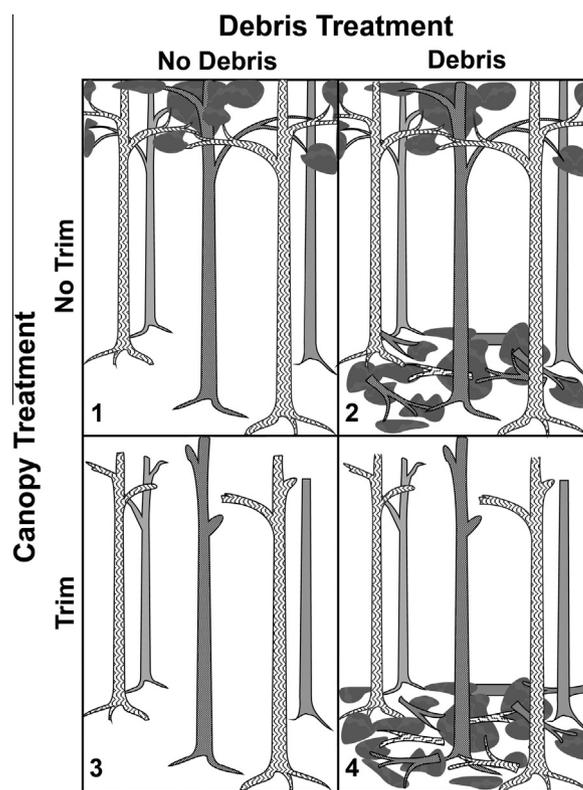


Fig. 2. The canopy trimming experiment employed a factorial design (canopy removal versus debris deposition treatments) to disentangle the interacting effects of increased inputs of organic matter associated with hurricane windfall (i.e., debris addition) and the effects of solar insolation and warming associated with canopy removal (canopy trimming): 1, reference (i.e., not trimmed and no debris addition [No Trim + No Debris]); 2, debris addition without canopy trimming (No Trim + Debris); 3, canopy trimming without debris addition (Trim + No Debris), and 4, canopy trimming with debris addition (Trim + Debris). See text for details.

and hampered by adverse weather and the large amount of plant material that had to be collected, weighed, and redistributed manually. Within plots designated for canopy trimming, limbs and stems smaller than 10 cm diameter were removed from all trees larger than 15 cm dbh. Trees between 10 and 15 cm dbh were trimmed at 3 m height. The leaves of palms that reached above 3 m were trimmed, being careful to preserve the apical meristem. All material removed from the canopy of each trimmed plot (i.e., debris) was collected, segregated as leafy twigs, wood, and palm, and weighed. Debris from one trimmed plot was returned to that plot, and distributed homogeneously. Debris from the other trimmed plot was removed and redistributed homogeneously to one of the two untrimmed plots. Approximately 10 t fresh weight of vegetation (111 t ha^{-1}) was removed from each plot ($\sim 39\%$ leafy twigs, 55% wood and 6% palm fronds). An unanticipated consequence of having mounds of leaf litter on the forest floor awaiting processing (from 1 week to 2 months) was that they were quickly colonized by invertebrate herbivores (mainly moth larvae). Thus, green leaves degraded rapidly, and mainly woody material was left for redistribution, with only small quantities of foliage. Although differences in litter quality existed among blocks, these differences were relatively small. The amount of detritus added to each of the six debris addition plots was approximately 5.4 t dry weight (60 t ha^{-1}).

2.3.2. Gastropod surveys

Annual (wet season) surveys of gastropods were conducted from 2004 to 2012. During each survey, each sub-plot was sampled for 3 nights, during which time one individual searched the sub-plot for snails and slugs. Sampling continued until all available substrates (surfaces of soil, leaf litter, vegetation, and rocks) were completely searched, or for a minimum of 15 min, whichever time was longer. To minimize alteration of long-term study plots, substrates were not manipulated while searching for gastropods (e.g., rocks or woody debris were not moved and leaf litter was not sifted). This limits the potential to detect small, litter-dwelling species.

In many terrestrial gastropod assemblages, most individuals and taxa dwell in the leaf litter (Tattersfield, 1996; Barker and Mayhill, 1999; Schilthuizen and Rutjes, 2001; Nekola, 2005), which can be problematic when attempting a complete taxonomic inventory of a region (Cameron and Pokryszko, 2005). In contrast, the gastropod fauna of the LEF comprises many large and arboreal taxa, and the density of gastropods in litter samples typically is quite low ($0.28 \text{ individuals/m}^2$; Richardson et al., 2005). In addition, estimates of population density by enumeration (minimum number known to be alive) correlate strongly with mark – recapture estimates of density for two arboreal species (*Caracolis caracolla* and *Nenia tridens*), suggesting that such estimates adequately reflect changes in relative density over time or space. Importantly, differences in detectability would only affect species-level analyses if such differences were treatment specific. Consequently, our inference space was constrained to include only macro-individuals that emerged above the soil or leaf litter (see Liew et al., 2010 for a similar approach), an assemblage for which we are confident that our visual sampling method was appropriate. Gastropods were identified to species in the field and never removed from the subplots in which they were found. All sampling was conducted at night (1900–0300 h) to correspond with peak gastropod activity (Heatwole and Heatwole, 1978).

2.4. Quantitative analyses

We estimated population- and community-level metrics for each sub-plot to evaluate responses to treatments in the CTE. The abundance of each species was estimated as the minimum number

known to be alive (MNKA) during three nights of survey (i.e., the maximum number of individuals of a species captured on any night) each year. We considered total gastropod abundance to be the sum of the MNKA for each species on each sub-plot each year. Because biodiversity is a multidimensional concept that comprises a number of interrelated aspects, we estimated five taxonomic metrics of biodiversity for each sub-plot each year. These aspects included: (1) richness (i.e., the number of captured species), (2) evenness (estimated as the Camargo index), (3) dominance (estimated as the Berger-Parker index), (4) diversity (estimated as the Shannon index), and (5) rarity (estimated as the number of species on a sub-plot whose overall relative abundance was less than $1/S$, where S is the number of species (13) obtained during both pre- and post-manipulation phases of the CTE). To ensure that metrics of biodiversity reflected desirable mathematical and biological properties, evenness, dominance, and diversity were converted to Hill numbers or numbers equivalents (Jost, 2006; Villéger et al., 2012) prior to all statistical analyses (this adjusts the index for dominance so that large values represent high biodiversity and low dominance). Species richness and species rarity are already numbers equivalents and do not require transformation. In a variety of contexts, these five metrics have been shown to effectively capture changes in biodiversity in response to geographic or environmental gradients (Stevens and Willig, 2002; Wilsey et al., 2005; Vance-Chalcraft et al., 2010; Willig et al., 2013).

2.4.1. Short-term responses to experimental manipulation

For population- or community-level characteristics, we used the difference over time (2006 post-manipulation value – 2004 pre-manipulation value) as the dependent variable, and conducted an analysis based on a linear mixed-effects model (Laird and Ware, 1982; Pinheiro and Bates, 1996, 2000). More specifically, we executed a two-factor (canopy trimming [trimmed or not trimmed] by debris deposition [added or not added]) analysis in a blocked design. Canopy trimming and debris deposition were Model I treatment factors, whereas block was a Model II treatment factor (3 levels). At the population level, we analyzed responses of a species only if the MNKA was at least 5 during both the pre-manipulation and post-manipulation phases of the CTE. Analyses were conducted in R using the lme function and the mass and nlme packages.

To assess short-term (i.e., 1–2 year) changes in species composition (i.e., the relative abundance and identity of species) in response to the various treatment combinations, we conducted a three-way log linear analysis (gastropod species identity by treatment [i.e., No Trim + No Debris versus Trim + No Debris versus No Trim + Debris versus Trim + Debris] by time [pre-treatment versus post-treatment]) using Program HILOGLINEAR in SPSS Release 20.0.0 (Sokal and Rohlf, 1995). Species abundance distributions for combinations of treatment and time were obtained by combining data from corresponding subplots and blocks. To assess the extent to which variation among random replicates (subplots within a block, or blocks within experimental treatment combinations) contributed to possible differences in species composition between 2004 (pre-treatment period) and 2006 (immediate post-treatment period), we conducted a hierarchical series of contingency g-tests (Sokal and Rohlf, 1995). To identify the experimental treatment combinations that evinced significant temporal differences (2004 versus 2006) in response to particular manipulations, we also conducted g-tests. To meet assumptions of g-tests and to facilitate comparison of results among treatments, rare taxa were combined into a single category, resulting in four species groups (i.e., *C. caracolla*, *Gaeotis nigrolineata*, *N. tridens*, and all other taxa combined) in all analyses. Because 0 abundance may characterize some species groups at smaller spatial scales (i.e., for particular subplots within blocks, or for particular blocks within an experimental treatment

combination), abundances of the four species groups were transformed by adding one to empirical counts prior to analyses at these scales. All *g*-tests were executed in R using the *likelihood.test* function from the *Deducer* package.

2.4.2. Long-term variation in responses to experimental manipulation

To evaluate temporal trajectories in population- or community-level characteristics of gastropods, we conducted two kinds of correlative analyses (Spearman Rank Correlation) based on annual mean characteristics for each combination of treatment and block (each datum was the mean value for four subplots). The first set of analyses evaluated the extent to which post-manipulation (2006–2012) temporal variation in each of the three manipulated treatments (i.e., No Trim + Debris; Trim + No Debris; and Trim + Debris) paralleled temporal variation in the non-manipulated or reference treatment (i.e., No Trim + No Debris). A non-significant correlation suggests that canopy trimming, debris addition, or both altered the way in which population or community characteristics of gastropods varied over time compared to background variation in the non-manipulated or reference treatment. The second set of correlative analyses evaluated the extent to which post-manipulation temporal variation differed between all possible pairs of the three manipulative treatments. Again, a non-significant correlation suggests that temporal trends in population- or community-level characteristics differed between experimental manipulations.

To assess temporal trajectories of species composition in response to the four different treatment combinations, we conducted a single Non-Metric Multidimensional Scaling (NMDS) ordination via Program ALSCAL in SPSS Release 20.0.0 for groups defined by combinations of treatment and time. To visualize changes in species composition over time, we plotted NMDS scores of Dimension 1 and Dimension 2 for each experimental treatment separately. Abundance estimates for gastropod species in these groups were obtained by combining data from corresponding subplots and blocks. Those species-specific abundances were then double-square-root transformed to enhance the ability of less abundant species to contribute to differences among treatments through time. Finally, ordination of groups defined by combinations of treatment and time was based on Euclidean distances.

To evaluate similarities in the temporal trajectories of compositional characteristics of gastropods, we conducted two kinds of correlative analyses (Spearman Rank Correlation) based on positions of the four treatment combinations in the two dimensional space defined by NMDS. The first set of analyses evaluated the extent to which temporal variation in each of the three manipulated treatments (i.e., No Trim + Debris; Trim + No Debris; and Trim + Debris) paralleled temporal variation in the non-manipulated or reference treatment (i.e., No Trim + No Debris). A non-significant correlation suggests that canopy trimming, debris addition, or both altered the way in which population or community characteristics of gastropods varied over time compared to background variation in the non-manipulated or reference treatment. The second set of correlative analyses evaluated the extent to which temporal trajectories of species composition differed between all possible pairs of the three manipulative treatments. Again, a non-significant correlation suggests that temporal trends in species composition differed between experimental manipulations.

3. Results

3.1. Short-term responses to experimental manipulation

We captured 9 species during the pre-manipulation (2004) phase and 13 species during the immediate post-manipulation (2006) phase (all 9 species from the pre-manipulation phase and

4 other rare species) of the CTE (Table 1). Regardless of phase, *C. caracolla*, *G. nigrolineata*, and *N. tridens* were the only common species.

Six species were captured in sufficient abundance to facilitate analyses at the population level (Table 2; Fig. 3). Block effects on abundance were common (4 species and all gastropods), indicating that considerable spatial heterogeneity characterized tabonuco forest, at least from the perspective of gastropod abundances. These block effects were either consistent regardless of canopy trimming and debris addition (*C. caracolla*), or emerged as interactions with the main treatment factors (*Alcaldia striata*, *Platysuccinea portoricensis*, *Polydotes acutangula*, and total gastropod abundance). Despite the variability in abundances induced by such spatial heterogeneity, 3 species responded significantly to canopy removal (*A. striata*, *C. caracolla*, *Pl. portoricensis*) and *Po. acutangula* responded to debris addition (Table 2; Fig. 3). Moreover, the effects of debris addition were predicated on canopy removal (i.e., a canopy trimming by debris removal interaction or a canopy removal by debris addition by block interaction) for *Pl. portoricensis*. The effect of debris addition depended on canopy removal from the perspective of total gastropod abundance as well. Two species (*G. nigrolineata* and *N. tridens*) did not respond to any treatments in the CTE.

Block effects were pervasive for all aspects of biodiversity (Table 2; Fig. 4). Canopy removal affected richness, diversity, and rarity. Debris addition affected richness and diversity. Dominance and evenness were not affected by canopy removal, debris addition, or their interaction. In contrast, short-term changes in species composition were non-significant for any of the three manipulative treatments and only approached significance for the reference treatment (Fig. 5).

Species composition did not differ between pre-treatment and immediate post-treatment periods (2004 versus 2006) regardless of the nature of the experimental manipulation, as evidenced by the absence of significant two- or three-way interactions involving species, treatment or time in hierarchical log-linear analyses (Table 3). This result is corroborated by contingency *g*-tests (Fig. 5) in that differences in species composition between pre-treatment and immediate post-treatment time periods were non-significant for all manipulative treatments and approached significance for the reference treatment. Non-significant contrasts between time periods could arise because of heterogeneity among subplots within blocks or among blocks within experimental treatment combinations. In fact, comparisons of species composition among subplots within blocks were non-significant in 11 of 12 contrasts during the pre-treatment time period (heterogeneity among subplots was only significant for Block C in the No Trim + Debris treatment combination) and for all 12 contrasts during the post-treatment time period (Fig. 5), suggesting that variation at this spatial scale was unimportant. In contrast, variation among blocks was significant or approached significance in three of the four treatments (i.e., No Trim + No Debris, No Trim + Debris, Trim + Debris) during the pre-manipulation period, and was significant for the reference treatment (i.e., No Trim + No Debris) during the post-manipulation period (Fig. 5), suggesting that variation at this spatial scale was important.

3.2. Long-term variation in responses to experimental manipulation

We captured 16 species during the entire post-manipulation phase (2006–2012) of the CTE (i.e., all species in Table 1 plus *Alcaldia alta*, *Diplosolenodes occidentalis*, and *Lamellaxis gracilis*). Regardless of phase, *C. caracolla*, *G. nigrolineata*, and *N. tridens* were the only common species.

Temporal variation in mean abundance for each of the three manipulative treatments was similar to that of the reference

Table 1
Gastropod abundance as measured by mean minimum number known alive per hectare for each of 13 species and for all gastropods combined, as well as the mean of each of five biodiversity indices (expressed as numbers equivalents) calculated separately for before (Pre; 2004) and after (Post; 2006) experimental manipulation for each combination of treatments. An asterisk denotes species for which population-level responses to experimental manipulations were conducted (Table 2).

Abundance (per ha)	No Trim + No Debris		No Trim + Debris		Trim + No Debris		Trim + Debris	
	Pre	Post	Pre	Post	Pre	Post	Pre	Post
<i>Alcadia striata</i> *	67	67	33	100	100	133	33	133
<i>Austroselenites alticola</i>	0	0	0	0	0	33	0	0
<i>Caracolus caracolla</i> *	1500	1533	1233	1200	900	467	533	933
<i>Caracolus marginella</i>	0	33	0	0	0	0	0	0
<i>Cepolis squamosa</i>	0	0	33	33	33	0	0	167
<i>Gaeotis nigrolineata</i> *	667	367	400	400	500	367	267	400
<i>Megalomastoma croceum</i>	0	33	0	0	0	0	0	0
<i>Nenia tridens</i> *	1133	1867	967	1167	567	767	833	1167
<i>Oleacina glabra</i>	33	100	0	100	33	0	67	0
<i>Oleacina playa</i>	0	0	0	0	0	33	33	0
<i>Platysuccinea portoricensis</i> *	100	167	233	100	100	0	67	0
<i>Polydotes acutangula</i> *	100	133	133	67	0	33	33	67
<i>Subulina octona</i>	0	0	0	67	0	0	0	0
All gastropods	3600	4200	3033	3267	2267	1833	1833	2933
Biodiversity								
Species richness	3.17	3.17	3.25	3.58	3.00	2.50	2.67	3.33
Shannon diversity	2.68	2.78	3.08	2.53	2.65	2.70	2.22	2.72
Camargo evenness	2.03	2.02	2.14	2.10	1.85	1.64	1.75	1.97
Berger-Parker dominance	2.38	2.34	2.66	2.19	2.39	2.30	1.92	2.47
Rarity	0.67	1.00	1.17	0.92	0.50	0.83	0.42	0.67

Table 2
Significance levels (exact *p*-values) from general linear mixed-effects models that quantified the effects of canopy trimming, debris removal, block, and their interactions on differences in abundances between pre (2004) and post (2006) experimental manipulation phases for each of 6 species of terrestrial gastropod, as well as for total gastropod abundance and for five metrics of biodiversity. Trim and Debris were model I between subjects factors, Block was a model II factor. Bold font indicates results that were significant (i.e., $p \leq 0.05$) or results that approached significance (i.e., $0.05 < p \leq 0.10$), and were interpretable (i.e. lower level effects are not interpreted if contained within higher level interactions; Sokal and Rohlf, 1995).

Abundance	Trim	Debris	Block	Trim × debris	Trim × block	Debris × block	Trim × debris × block
<i>Alcadia striata</i>	0.629	0.337	0.497	1.000	0.003	0.789	0.497
<i>Caracolus caracolla</i>	0.846	0.110	0.067	0.061	0.365	0.402	0.281
<i>Gaeotis nigrolineata</i>	0.407	0.125	0.501	0.926	0.294	0.398	0.196
<i>Nenia tridens</i>	0.659	0.659	0.224	0.464	0.552	0.296	0.800
<i>Platysuccinea portoricensis</i>	0.519	0.287	0.954	0.140	0.383	0.075	0.048
<i>Polydotes acutangula</i>	0.491	0.255	0.947	0.817	0.336	0.054	0.276
All gastropods	0.862	0.229	0.062	0.056	0.024	0.388	0.541
Biodiversity							
Species richness	1.000	0.087	0.173	0.245	0.021	0.449	0.889
Shannon diversity	0.580	0.062	0.135	0.478	0.031	0.548	0.991
Camargo evenness	0.787	0.513	0.044	0.395	0.258	0.985	0.108
Berger-Parker dominance	0.171	0.410	0.068	0.117	0.379	0.716	0.949
Rarity	1.000	0.228	0.372	0.684	0.030	0.274	0.722

treatment when abundances were combined for all species (Table 4). Nonetheless, interspecific heterogeneity in this regard was considerable (Fig. 6). For example, temporal variation in each of the manipulative treatments was unrelated to temporal variation on the non-manipulated treatment for three species (i.e., *A. striata*, *Po. acutangula*, and *Pl. portoricensis*) but was correlated with temporal variation in the non-manipulated treatment for *G. nigrolineata*. For five species (i.e., *A. striata*, *C. caracolla*, *N. tridens*, *Pl. portoricensis*, and *Po. acutangula*), temporal variation in the No Trim + Debris treatment was unrelated to that of the No Trim + No Debris treatment. For four species (i.e., *A. striata*, *N. tridens*, *Pl. portoricensis*, and *Po. acutangula*), temporal variation in the Trim + Debris treatment was unrelated to that of the No Trim + No Debris treatment. For three species (i.e., *A. striata*, *Pl. portoricensis*, and *Po. acutangula*), temporal variation in the Trim + No Debris treatment was unrelated to that of the No Trim + No Debris treatment.

Temporal variation in abundance generally differed between manipulative treatments (Table 4). Temporal variation on the

Trim + No Debris treatment was unrelated to temporal variation on the No Trim + Debris treatment for all but one species (*N. tridens*). Similarly, temporal variation on the No Trim + Debris treatment was unrelated to temporal variation on Trim + Debris treatment for all but one species (*C. caracolla*). Finally, temporal variation on the Trim + No Debris treatment was unrelated to temporal variation on the Trim + Debris treatment for all but two species (*C. caracolla* and *G. nigrolineata*).

Temporal variation in each of the manipulative treatments was unrelated to temporal variation in the non-manipulated treatment for each of four components of taxonomic biodiversity (species richness, evenness, dominance, and rarity; Table 4; Fig. 7). In contrast, temporal variation in each of the manipulative treatments was correlated to temporal variation in the non-manipulated treatment for diversity. Finally, temporal variation in components of taxonomic biodiversity generally differed between manipulative treatments. The only exceptions were for diversity and evenness, in which cases temporal variation in the Trim + No Debris treatment was correlated with that in the No Trim + Debris treatment.

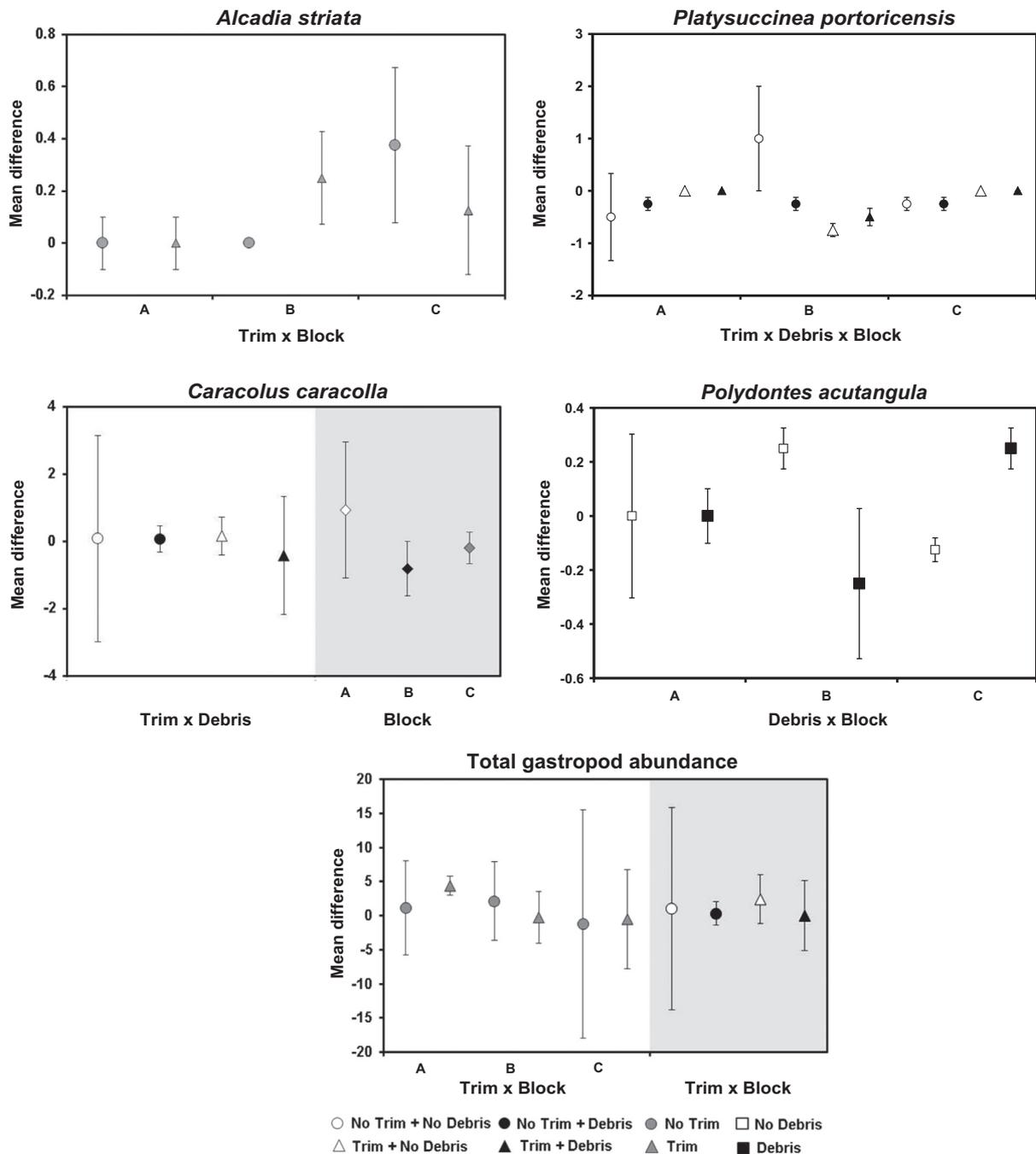


Fig. 3. Mean differences in gastropod abundance ($N_{2006} - N_{2004}$) per subplot (25 m²) associated with the application of treatments from the canopy trimming experiment (canopy trimming, debris deposition, and block) for each of 4 species that exhibited a significant response, as well as for all gastropods (13 species) as a group (Table 2). Data were pooled and plotted to represent only significant effects from linear mixed-effects models, with significant effects identified below each panel. For cases in which multiple effects were significant, background shading indicates data associated with different effects. The shading of diamonds distinguishes blocks when block effects were consistent regardless of other treatment effects. Error bars represent ± 1 SE.

Temporal variation in species composition was considerable and comparable for each of the four treatment combinations (compare the four panels in Fig. 8). Minimum convex polygons encompassing all post-manipulation compositional states within treatments were of similar size. Nonetheless, the amount of temporal variation within a treatment was not markedly different than the variation among sites designated for treatment prior to the application of the experimental manipulation (i.e., the variation among treatment combinations in 2004 before canopy was cut or debris deposited on the forest floor). Year-to-year changes in composition as quantified by the magnitude and direction of

change in location as defined by Dimensions 1 and 2 from NMDS (i.e., vectors connecting consecutive time periods) were quite distinctive for each of the four treatment combinations, and did not converge within 7 years of the initiation of the experiment (Fig. 8). Correlative analyses of dimension scores from NMDS (Table 4) revealed that (1) temporal trajectories of species composition in each of the three manipulative treatments were independent ($p > 0.05$) of that in the reference treatment, and (2) temporal trajectories of species composition for particular manipulative treatments were independent ($p > 0.05$) of temporal trajectories of any of the other manipulative treatments.

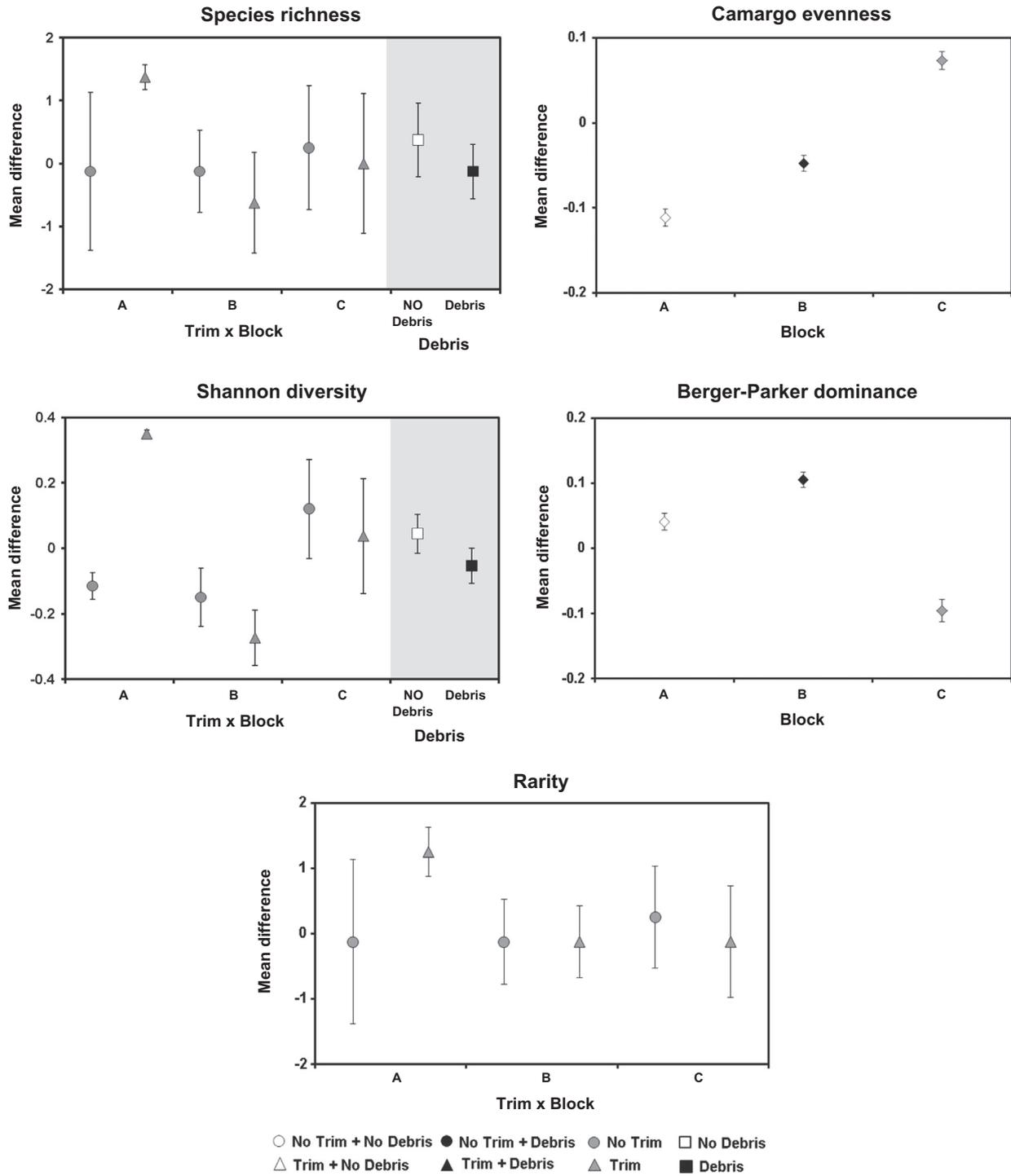


Fig. 4. Mean differences in five metrics of taxonomic biodiversity ($M_{2006} - M_{2004}$) per subplot (25 m²) for gastropods associated with the application of treatments from the canopy trimming experiment (canopy trimming, debris removal, and block; Table 2). Data were pooled and plotted to represent only significant effects from linear mixed-effects models, with significant effects identified below each panel. For cases in which multiple effects were significant, background shading indicates data associated with different effects. Each index of biodiversity was transformed into its numbers equivalent (this adjusts the index for dominance so that large values represent high biodiversity and low dominance). The shading of diamonds distinguishes blocks when block effects were consistent regardless of other treatment effects. Error bars represent ± 1 SE.

4. Discussion

Experimental manipulations in ecology, such as those incorporated into the CTE, represent excellent approaches for disentangling the effects of confounded factors and identifying the mechanisms that affect the distribution and abundance of organisms (Hairston, 1989; Resetarits and Bernardo, 1998). Nonetheless,

the interpretation of results of any manipulative experiment must be tempered by the extent to which experimental treatments effectively mimic natural phenomena at a variety of spatial and temporal scales (Maurer, 1999). This is particularly true of cyclonic storms and hurricanes, for which the frequency, intensity, and extent of such disturbances combine to determine the severity of response and subsequent trajectories of successional change in

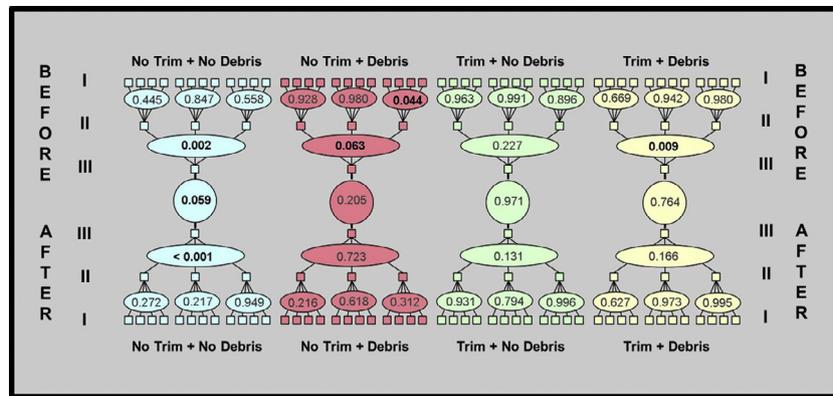


Fig. 5. Heterogeneity of species composition was evaluated based on a hierarchical execution of a series of *g*-tests (Sokal and Rohlf, 1995) for 2004 (before experimental manipulation) and 2006 (after experimental manipulation), separately. At level I in the hierarchy, each box represents a sub-plot within a block and treatment combination. At level II in the hierarchy, each box represents the combined data for all subplots within a block for a particular treatment combination. At level III in the hierarchy, each box represents the combined data for all subplots from all blocks that correspond to a particular treatment combination. Each ellipse represents a test of heterogeneity among randomized replicates (i.e., subplots within blocks [between levels I and II or blocks within treatment combinations [between levels II and III]). Each circle represents a test of heterogeneity between 2004 and 2006 (i.e., before and after experimental manipulation) for a particular experimental treatment combination. Exact *p*-values are reported for each test. Heterogeneity for a particular test that was significant ($p \leq 0.05$) or that approached significance ($0.05 > p \geq 0.10$) is indicated by bold text. Species composition for each test was based on the abundances of *Caracolus caracolla*, *Gaeotis nigrolineata*, *Nenia tridens*, and all other species combined (see text for details).

Table 3

Results of hierarchical log-linear analysis using a likelihood ratio test to evaluate the effect of treatment (combinations of canopy trimming and debris deposition) and time (before or after application of a specified manipulative treatment) on the species abundance distribution of gastropods (i.e., species effects) in the canopy trimming experiment (see text for details). Significant results ($p \leq 0.05$) are bold. df, degrees of freedom.

Statistical effects	df	Chi-square	<i>p</i> -value
<i>Multiple interactions</i>			
1-way and higher order effects	31	223.28	<0.001
2-way and higher order effects	24	30.99	0.154
3-way and higher order effects	9	7.20	0.616
<i>Single interactions</i>			
1-way effects	7	192.29	<0.001
2-way effects	15	23.79	0.069
3-way effects	9	7.20	0.616
<i>Partial associations</i>			
Species by treatment	9	11.25	0.259
Species by year	3	6.23	0.101
Treatment by year	3	4.86	0.183
Species	3	152.91	<0.001
Treatment	3	36.43	<0.001
Year	1	2.94	0.086

natural settings (Willig and Walker, 1999; Waide and Willig, 2012).

In the case of the CTE, a number of factors must be understood in the context of the manipulations and their spatial distribution within the landscape. First, tabonuco forest is quite heterogeneous in terms of topography (McDowell et al., 2012) and legacy of previous disturbance (Brokaw et al., 2012a,b; Scatena et al., 2012). This heterogeneity could enhance spatial variability and decrease the likelihood of detecting significant effects associated with canopy trimming or debris addition manipulations. Second, such heterogeneity could produce differences among randomly selected sites that have nothing to do with experimental manipulations. For example, significant differences in gastropod abundance and diversity were associated with “experimental treatments” in the CTE before the canopy was trimmed and before debris was deposited on the forest floor at any of the sites (Figs. 5–7). This necessitated a careful consideration of approaches that included repeated measures (at the plot level) for detecting responses of gastropods

to particular manipulations, beyond the statistical controls provided by blocking. Third, the landscape context for the CTE was much different than that associated with many hurricanes. For example, Hurricane Hugo caused widespread and extensive opening of the canopy and deposition of litter onto the forest floor (Walker et al., 1991) in many areas of tabonuco forest, such that the post-disturbance characteristics of any particular plot would be quite similar to the characteristics of the landscape within which it was embedded. In contrast, any particular plot that received an experimental manipulation in the CTE would be in close proximity to non-manipulated sites (i.e., the broader tabonuco landscape) or to plots receiving other experimental manipulations. Thus, short-term responses to the manipulations and longer-term trajectories of secondary succession could be strongly influenced by cross-scale interactions, including rescue effects for particular species (Peters and Havstad, 2006; Peters et al., 2006; Willig et al., 2007). Because of the configuration of treatment plots within the larger non-manipulated landscape of the tabonuco forest, we consider the CTE to more closely mimic the environmental context for canopy opening and debris deposition associated with Hurricane Georges, in which disturbed sites that experience canopy opening were small in area and surrounded by forest with intact canopies (Lomascolo and Aide, 2001; Ostertag et al., 2003). Finally, caution must be employed when evaluating experimental results from the CTE because of the degradation of leaves and branches after canopy cutting but before debris deposition, and the differences in the timing of debris deposition among blocks.

4.1. Complex responses to disturbance

4.1.1. Short-term effects

A non-manipulative natural experiment in tabonuco forest of Puerto Rico (Willig and Camilo, 1991) in the Bisley Watersheds documented short-term responses to Hurricane Hugo (1989) in which all of the non-rare gastropod taxa decreased by at least 50% (*C. caracolla*) and in a few cases (*G. nigrolineata*, *N. tridens*, and *Po. acutangula*) were undetected after the hurricane. Therefore, we predicted that these common gastropod species would decrease in abundance as a consequence of experimental manipulations involving canopy removal or debris deposition, as these treatments reflected the primary initial manifestations of

Table 4
Spearman rank correlations that evaluate correspondence in recovery trajectories for 7 years (2006–2012) after experimental manipulation between each possible pair of treatments for mean abundances of each of six species of gastropod and for mean total abundance regardless of species identity, for the mean of each of 5 indices of taxonomic biodiversity, and for Dimensions 1 and 2 from non-metric multidimensional scaling representing variation in species composition. Analyses are based on sample sizes of 21 (7 years \times 3 blocks); abundances are based on minimum number known alive; and indices of taxonomic biodiversity were transformed into numbers equivalents. Significant correlations ($p \leq 0.05$) are bold and indicate similarity in temporal trajectories in response to the pair of treatments.

Abundance	No Trim + No Debris vs. Trim + No Debris		No Trim + No Debris vs. No Trim + Debris		No Trim + No Debris vs. Trim + Debris		Trim + No Debris vs. No Trim + Debris		Trim + No Debris vs. Trim + Debris		No Trim + Debris vs. Trim + Debris	
	Rho	P	Rho	P	Rho	P	Rho	P	Rho	P	Rho	P
<i>Alcacia striata</i>	-0.292	0.198	0.179	0.438	0.115	0.621	0.238	0.299	0.102	0.661	0.191	0.407
<i>Caracolus caracolla</i>	0.897	<0.001	0.408	0.066	0.436	0.048	0.287	0.208	0.553	0.009	0.547	0.010
<i>Gaetotis nigrolineata</i>	0.595	0.004	0.548	0.010	0.680	<0.001	0.335	0.137	0.536	0.012	0.225	0.326
<i>Nenia tridens</i>	0.527	0.014	0.224	0.330	-0.012	0.960	0.497	0.022	0.171	0.460	0.269	0.238
<i>Platysuccinea portoricensis</i>	0.055	0.813	0.142	0.540	0.240	0.295	0.205	0.373	0.146	0.529	-0.108	0.640
<i>Polydontes acutangula</i>	-0.130	0.574	-0.072	0.755	-0.302	0.183	0.264	0.248	0.344	0.127	-0.097	0.676
All gastropods	0.773	<0.001	0.499	0.021	0.473	0.030	0.624	0.003	0.421	0.058	0.365	0.103
<i>Biodiversity</i>												
Species richness	-0.115	0.619	-0.349	0.121	0.160	0.490	0.099	0.669	-0.121	0.602	-0.057	0.808
Shannon diversity	0.475	0.030	0.511	0.018	0.442	0.045	0.516	0.017	0.365	0.104	0.401	0.071
Camargo evenness	0.314	0.166	0.382	0.088	0.344	0.127	0.541	0.011	0.350	0.120	0.424	0.056
Berger-Parker dominance	0.232	0.311	0.113	0.627	0.233	0.310	0.389	0.081	0.220	0.338	0.205	0.372
Rarity	0.290	0.202	-0.121	0.602	-0.017	0.941	0.193	0.403	-0.060	0.798	0.269	0.239
<i>Composition</i>												
Dimension 1	-0.127	0.582	0.100	0.665	-0.267	0.243	0.015	0.935	0.013	0.958	-0.421	0.058
Dimension 2	0.015	0.935	0.310	0.171	0.340	0.132	0.052	0.840	0.259	0.268	0.211	0.360

hurricane disturbances. The responses of these common gastropod species in the manipulative experiment were quite different than expected (Tables 1 and 2). More specifically, the abundances of *G. nigrolineata* and *N. tridens* did not respond significantly to any treatments, and sample mean abundances were actually higher after the manipulation on the Trim + Debris treatment. Although the abundance of *C. caracolla* responded significantly to the experimental manipulation, it did so by increasing in the Trim + Debris treatment while decreasing at least slightly in the No Trim + Debris and Trim + No Debris treatments. Indeed, such complex results were characteristic of population-level responses to the CTE as reflected in the predominance of significant interactive effects between treatment factors, including the fact that treatment effects were often predicated on block. Essentially, differences among blocks captured spatial variation in landscape context or the state of the ecological system prior to disturbance, and such differences in initial state played a large role in mediating immediate treatment effects in the CTE.

Context dependence provides a perspective from which to partially understand the contrast between the results from the non-manipulative experiment associated with Hurricane Hugo (Willig and Camilo, 1991) and those for the CTE, as well as to understand the differences in population-level responses between Hurricanes Georges (Bloch and Willig, 2006) and Hugo (Willig and Camilo, 1991). The environmental attributes of a site, the landscape that surrounds it, and the demographic characteristics of the species within it combine via cross-scale interactions (Peters and Havstad, 2006; Peters et al., 2006; Willig et al., 2007) to affect future population sizes based on births and deaths within a site, as well as based on the immigration to or emigration from the site. Hurricane Georges was less intense than Hurricane Hugo, producing less damage to the canopy, producing smaller canopy gaps, and depositing less debris on the forest floor (Lomascolo and Aide, 2001; Ostertag et al., 2003). From a landscape perspective, the damage from Hurricane Georges was more heterogeneous than was the damage from Hurricane Hugo. Thus, the abundances of gastropods at damaged sites after Hurricane Georges would be strongly affected by source-sink dynamics associated with the surrounding and less disturbed landscape. This parallels the situation that characterized the CTE in that much of the forest surrounding the experimental plots, as well as the proximity of reference plots to

manipulation plots within each block, would enhance the likelihood that gastropod populations would reflect the dynamics of the surrounding landscape (demographic inertia) in addition to dynamics associated with the specific treatment combination applied to the plot.

Treatment effects at the community level arose as a consequence of heterogeneity among blocks and as a consequence species-specific responses to canopy opening or debris addition. Indeed, characteristics of biodiversity reflecting the identity and relative abundances of species (i.e., species composition) evinced strong block effects prior to experimental manipulation (in the No Trim + No Debris, No Trim + Debris, and Trim + Debris treatments), some of which persisted into the post manipulation phase (No Trim + No Debris treatment) of the experiment (Fig. 5). Moreover, significant block effects characterized evenness and dominance, as well as the way in which species richness, diversity, and rarity responded to canopy trimming (Fig. 4). In contrast, the changes in species richness or diversity associated with debris addition were consistent regardless of block: debris deposition decreased richness and diversity, whereas both metrics increased over time in the treatments without debris deposition (Fig. 4). Block effects were not unique to gastropods in the CTE; they occurred for soil microbes (Cantrell et al., 2014), and for phosphorous content of green leaves (Lodge et al., 2014). Soil characteristics and mineral content of green vegetation are important environmental factors that may structure gastropod communities in the LEF (Willig et al., 2013), suggesting that these block effects may be interrelated.

4.1.2. Long-term effects

Long-term trajectories in population- (Fig. 6) and community- (Fig. 7) level attributes of the gastropod fauna were more complex than were the short-term responses to treatments. In addition to arising as a consequence of manipulative treatments, these trajectories were influenced by a variety of spatiotemporal factors in tabonuco forest that were not associated with the CTE: (1) inter-annual variation in environmental characteristics, (2) intra-annual variation in environmental characteristics, (3) the spatial distribution of natural disturbances (e.g., tree falls, landslides) that were unassociated with experimental treatments, and (4) the movement of individuals among plots and blocks of the CTE, as

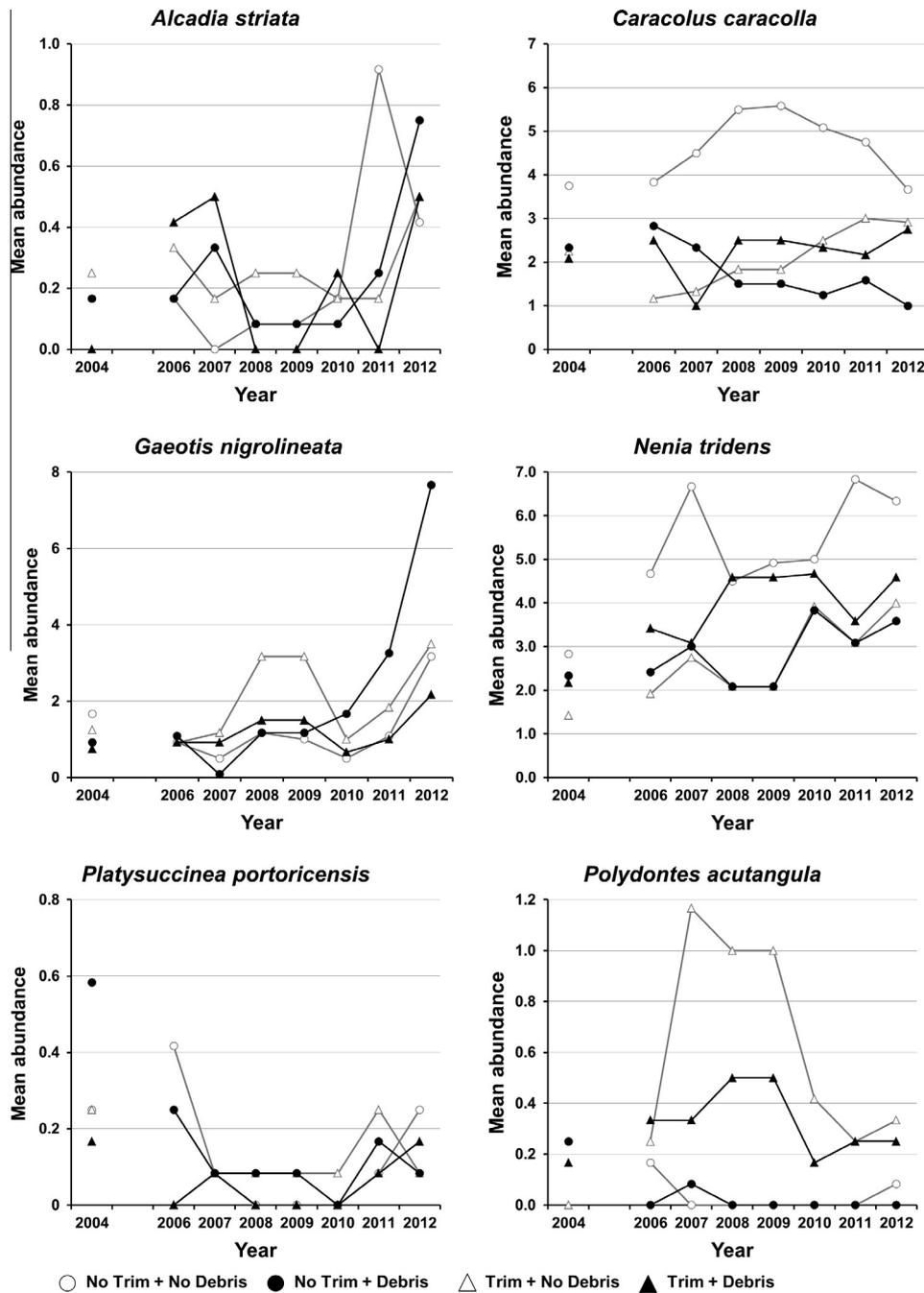


Fig. 6. Mean abundances per subplot (25 m²) prior to experimental manipulation (2004) and for 7 years (2006–2012) following experimental manipulation in the canopy trimming experiment for each combination of canopy trimming and debris deposition for each of six species of gastropod.

well as between plots and blocks in the CTE and adjacent areas of the non-manipulated forest. These sources of variation likely overwhelmed or compromised the identification of treatment-specific responses. In contrast, disturbances that manifest at some larger spatial scale than that of the CTE (e.g., the extensive and intensive disturbance of Hurricane Hugo) likely would overwhelm these sources of local spatial and temporal environmental variation, resulting in dramatic and easily detectable responses to disturbance (e.g., Willig and Camilo, 1991).

In the absence of any manipulative disturbances and the resulting secondary succession, we predicted that temporal variation in species composition would be smallest and non-directional in the reference treatment (No Trim + No Debris). In contrast, we

predicted that temporal variation would be greater in the other treatments due to experimental manipulations. More specifically, each manipulative treatment would be characterized by (1) an initial and large displacement between 2004 and 2006 because of canopy opening or debris addition, and (2) a subsequent trajectory between 2006 and 2012, representing secondary succession, in which species composition would return to its pre-manipulative state. Moreover, similarities between treatments in trajectories of species composition from 2004 to 2012 (i.e., correlations) would reflect the importance of particular treatments in molding temporal variation.

Empirical trajectories failed to corroborate any of these predictions. First, compositional displacements associated with

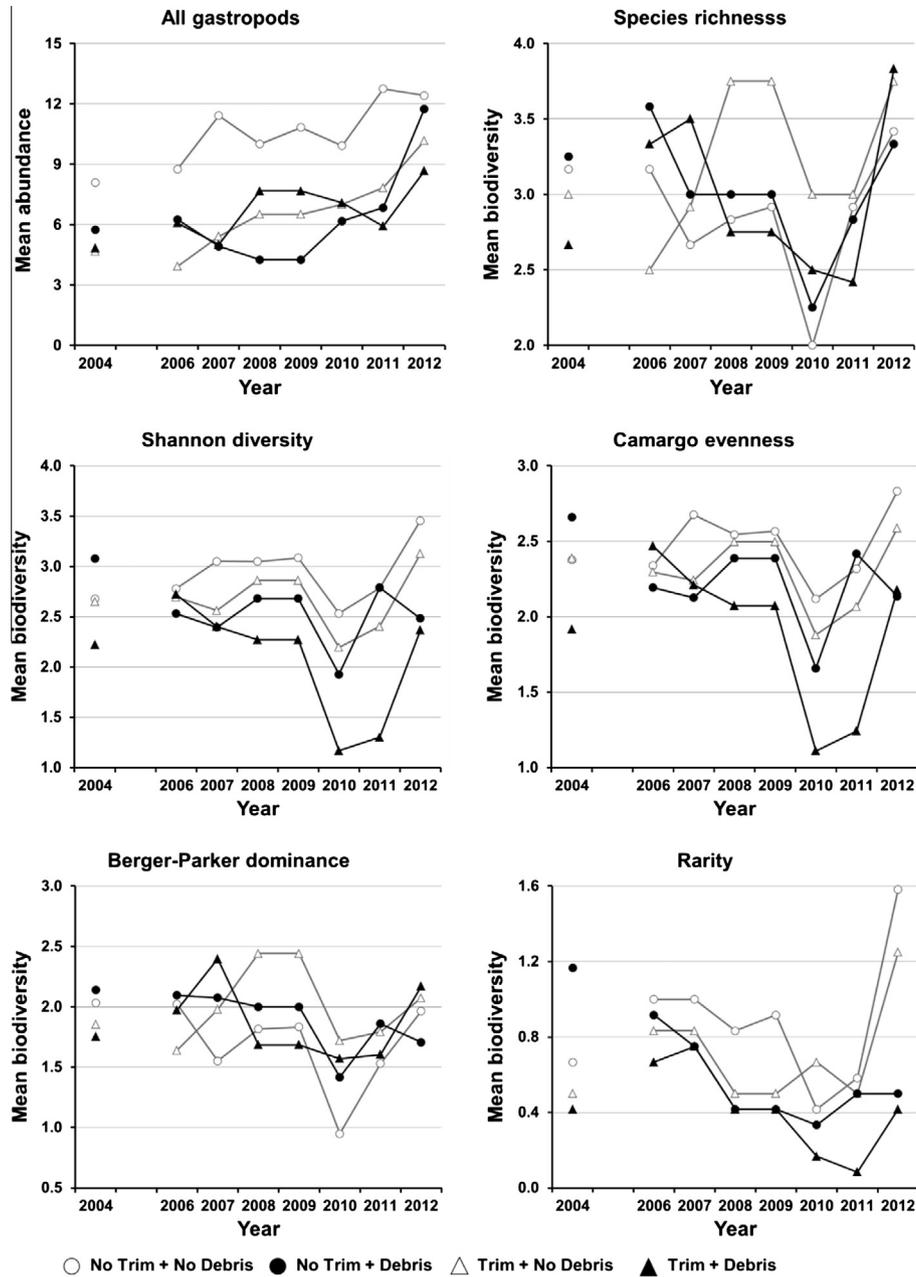


Fig. 7. Mean values per subplot for 5 indices of taxonomic biodiversity as well as for total gastropod abundance prior to (2004) and for 7 years (2006–2012) following experimental manipulation in the canopy trimming experiment for each combination of canopy trimming and debris deposition. Each index of biodiversity was transformed into its numbers equivalent (this adjusts the index for dominance so that large values represent high biodiversity and low dominance).

manipulative treatments were not larger than that observed in the reference treatment (i.e., compare line segments between 04 and 06 in Fig. 8). Second, post-manipulation composition for each treatment combination in 2006 occurred within the range of variation in species composition among groups prior to manipulation (i.e., circles labeled 06 occurred within the compositional spaced defined by black and gray rectangles). Third, species composition during the last year of the study (i.e., 2012, represented by an open circle) was not particularly close to the pre-manipulation state compared to the compositional states during intervening time periods. Finally, the absence of correlation between any pair of treatment combinations, based on dimension 1 or dimension 2 from non-metric multidimensional scaling, suggests that temporal variation in species composition was not driven strongly by

particular treatments (i.e., temporal changes in species composition were not occurring in similar fashions as a consequence of either canopy opening or debris addition). Rather, species composition within each treatment combination varied over time in ways unrelated to temporal variation in the other treatment combinations, including the reference treatment, and did not result in directional trajectories whereby species composition returned to its pre-manipulation state (no evidence of resilience). The implication is that spatiotemporal environmental variability unrelated to the experimental manipulations and unrelated to annual variation in environmental characteristics was driving empirical changes in gastropod composition in tabonuco forest. Alternatively but less likely, the distinctive patterns of post-manipulation changes in species composition in each of the four treatment combinations may

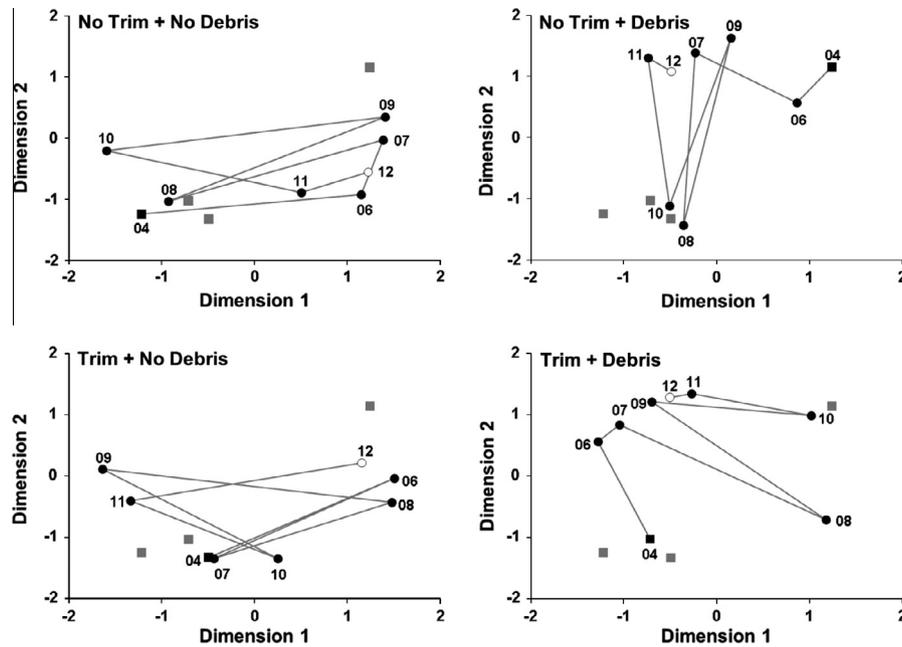


Fig. 8. Temporal trajectories (2004 through 2012) of species composition for each treatment combination from the CTE (No Trim + No Debris, No Trim + Debris, Trim + No Debris, and Trim + Debris) as represented by plots along Dimension 1 and Dimension 2 based on Non-Metric Multidimensional Scaling (see text for details). Black rectangles represent species composition in 2004 (pre-manipulation); circles represent species composition after application of experimental manipulations (2006–2012); open circles distinguish the species composition seven years after the application of manipulations (2012) from earlier post-manipulation time periods (black circles). For a reference, light gray squares within a particular panel represent species composition for non-focal treatment combinations during 2004 (pre-manipulation). Line segments connect consecutive time periods and two digit numbers represent years (i.e., 2004 [04] to 2012 [12]).

be caused by synergistic interactions between debris addition and canopy removal, or may be due to differences in species composition among blocks and among plots prior to the application of experimental manipulations (i.e., successional trajectories are highly contingent on starting conditions). From the perspective of gastropods, the CTE may have more strongly mimicked environmental circumstances associated with large treefall gaps or those arising from less intense hurricanes (e.g., Hurricane Georges rather than Hurricane Hugo), disturbances to which the gastropod fauna is well adapted and from which it can be rescued by recruitment of individuals from nearby and less disturbed areas in the landscape.

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