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Research article

Negative density dependence and environmental heterogeneity effects on tree ferns across succession in a tropical montane forest

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ABSTRACT

Although tree ferns are an important component of temperate and tropical forests, very little is known about their ecology. Their peculiar biology (e.g., dispersal by spores and two-phase life cycle) makes it difficult to extrapolate current knowledge on the ecology of other tree species to tree ferns. In this paper, we studied the effects of negative density dependence (NDD) and environmental heterogeneity on populations of two abundant tree fern species, *Cyathea caracasana* and *Alsophila engelii*, and how these effects change across a successional gradient. Species patterns harbor information on processes such as competition that can be easily revealed using point pattern analysis techniques. However, its detection may be difficult due to the confounded effects of habitat heterogeneity. Here, we mapped three forest plots along a successional gradient in the montane forests of Southern Ecuador. We employed homogeneous and inhomogeneous *K* and pair correlation functions to quantify the change in the spatial pattern of different size classes and a case–control design to study associations between juvenile and adult tree ferns. Using spatial estimates of the biomass of four functional tree types (short- and long-lived pioneer, shade- and partial shade-tolerant) as covariates, we fitted heterogeneous Poisson models to the point pattern of juvenile and adult tree ferns and explored the existence of habitat dependencies on these patterns. Our study revealed NDD effects for *C. caracasana* and strong environmental filtering underlying the pattern of *A. engelii*. We found that adult and juvenile populations of both species responded differently to habitat heterogeneity and in most cases this heterogeneity was associated with the spatial distribution of biomass of the four functional tree types. These findings show the effectiveness of factoring out environmental heterogeneity to avoid confounding factors when studying NDD and demonstrate the usefulness of covariate maps derived from mapped communities.

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Introduction

Determining the processes that promote species coexistence and the maintenance of high diversity is a central issue in ecology, especially in mega diverse tropical forests (Wright, 2002). Previous studies have proposed several processes including gap dynamics, niche segregation, ecological drift and negative density dependent relationships (Wright, 2002; Zimmerman et al., 2008).

Negative density dependence (NDD) reduces the aggregation of conspecifics affecting especially early life stages such as saplings or seedlings when they occur in high densities or near conspecific adults. Resource competition among congeners and the abundance of specialist pathogens and herbivores increase with density resulting in depressed recruitment in the close vicinity of adults (for a recent review see Terborgh, 2012). It is hypothesized that NDD enhances plant diversity by making space available for other plant species (Janzen, 1970; Connell, 1971). However, NDD effects may be difficult to detect due to the confounding effects of habitat heterogeneity (e.g., habitat filtering), which can affect both adult and juvenile density irrespective of plant–plant interactions.

Tree ferns represent a conspicuous fraction of tropical, temperate and cool wet forests (Smale et al., 1997; Bellingham et al., 1999). Surprisingly, few studies have focused on this biological component (Kramer, 1993; Márquez et al., 1997; Arens, 2001; Jones et al., 2007; Bystriakova et al., 2011) compared to flowering species. Unfortunately, our knowledge on NDD and habitat filtering in other trees cannot be directly applied to tree ferns, as these organisms

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Table 1
Main questions, statistical approach, and related figures of this study.

Questions	Statistical approach	Related figures
(1) Is the spatial distribution of the two tree ferns (*Cyathea caracasana* and *Alsophila engelii*) affected by large-scale environmental heterogeneity?	*L*-function of adults and juveniles of the two tree ferns populations, using a null-model of "complete spatial randomness" (CSR)	Fig. 3
(2) Which factors are driving the spatial heterogeneity on juveniles and adults of the two tree ferns populations, and how this factors change across succession?	(a) Fit log-linear models for tree-fern intensity (density) to several maps summarizing the distribution of four functional tree types (guilds) in each forest plot (b) Inhomogeneous-*L* function of adults and juveniles of the two tree ferns, using the weighted-average log-linear models as estimate of the intensity function	Fig. 4 and Fig. S1. Tables 2 and 3
(3) Is NDD affecting the spatial pattern of these two tree ferns and how are the effects of NDD changing across succession?	(a) Differences of *K*-functions and pair-correlation functions under a case–control design using a null model of random labeling. (b) Differences of *K*-functions and pair-correlation functions under a case–control design using a *modified* random labeling null model	Figs. 5 and 6 and Figs. S2 and S3

present two independent life phases (a tiny and relatively simple gametophyte and a well-developed, conspicuous sporophyte) with different biotic and abiotic filters and ecological determinants of their performance (Watkins et al., 2007). To gain insight on how plant diversity is assembled in these forests, we need to address the challenging question of how and where tree ferns recruit.

In this study, we explored the spatial patterns of two abundant tree ferns, *Cyathea caracasana* and *Alsophila engelii*, in three contrasting successional stages in a montane tropical forest in southern Ecuador. Our aim was to determine if negative density dependence exists in the studied populations, as widely reported for tropical trees, and if so, to separate the effects of this process from those of other drivers of coexistence, such as habitat filtering or plant–plant interactions (Law et al., 2009). In order to do this, we used recent techniques of spatial point pattern analysis (Wiegand and Moloney, 2004).

Spatial patterns are known to be responses to some underlying ecological processes (McIntire and Fajardo, 2009), and negative density dependent processes are probably among those with a more evident spatial signal (Kenkel, 1988; Moeur, 1997; Plotkin et al., 2002). When NDD operates, adults appear spaced as a function of the intensity of negative dependence and are less aggregated than juveniles (Janzen, 1970; Stoll and Bergius, 2005). Consequently, the existence of NDD and its effects can be determined by analyzing changes in spatial patterns over time (Sterner et al., 1986; Kenkel, 1988; Moeur, 1997; Getzin et al., 2008; Murrell, 2009) or by comparing the spatial distribution of individuals of different ages when no mortality data are available (Getzin et al., 2008; Zhu et al., 2010; Bagchi et al., 2011). Although spatial point pattern analysis is an efficient tool for revealing NDD effects, spatial patterns may also be the result of first-order effects (i.e., coarse scale habitat heterogeneity) operating simultaneously in the community (Chapin et al., 1989; He and Duncan, 2000; Wright, 2002; Wiegand et al., 2007; Murrell, 2009). For example, heterogeneity can cause higher densities of individuals in favorable sites due to microhabitat differences and plant preferences, or higher mortality and poor growth in less favorable sites (Purves and Law, 2002; Wright, 2002; Getzin et al., 2008; Murrell, 2009). However, a clear separation of these two processes and their effects may not always be feasible (Law et al., 2009). For example, plant aggregation could be due to locally suitable environment, which is the opposite of what we would expect under NDD, leading to an increase in clustering along the ontogeny (Murrell, 2009). Thus, in order to detect NDD effects (if present) or other spatial signals that may be influenced by plant–plant interactions, the effects of spatial heterogeneity must also be considered (Law et al., 2009). The importance of environmental heterogeneity in determining the spatial pattern of trees is being increasingly recognized and some approaches have been proposed (e.g., Wiegand et al., 2007; Getzin et al., 2008). However, few attempts have been made to explicitly test the effects of specific environmental factors (but see Bagchi et al., 2011) or community properties (e.g., spatial distribution of functional diversity, but see Perry et al., 2013) as a source of heterogeneity when studying NND or other spatial signals in plant populations.

With this in mind, we fully mapped three plots representing contrasting succession stages in an evergreen tropical montane forest in southern Ecuador. We conducted parallel analyses in successional stages as plant–plant interactions and ontogenetic necessities shift abruptly along succession in tropical forests (Franklin and Rey, 2007). Some studies suggest different tolerance to light environment among tree ferns (Bittner and Breckle, 1995; Arens and Baracaldo, 2000; Arens, 2001; Jones et al., 2006), and both *C. caracasana* and *A. engelii* are long-lived pioneer species which require a high-light environment for successful establishment and survival (Arens, 2001). Therefore, we used the spatial distribution of functional groups of trees with different affinity for light as a rough proxy of light conditions in this forest to account for environmental heterogeneity while examining the existence of NND effects in the populations of these two species.

We specifically aimed to determine: (i) the effect of environmental heterogeneity on the spatial distribution of two age-classes (adults and juveniles) of these two tree ferns, (ii) the role of NDD as a driver of their spatial pattern and (iii) whether the effects of NDD and environmental heterogeneity change across succession.

The specific questions, analyses and related figures of this study are summarized in Table 1.

Materials and methods

Site description and data collection

Three plots of approximately 0.5 ha were established and fully mapped in the upper San Francisco River in Prov. Zamora-Chinchipe, southern Ecuador (Fig. 1). Plots were located at a distance of less than 1 km from one another at altitudes around 2000 m.a.s.l., on the steep slopes (30°) of an impressive gorge. Climate is classified as tropical and per-humid (Lehnert, 2007). Mean annual precipitation is around 4000 mm/year (Rollenbeck, 2006). Two plots were located in the Chamusquín Biological Station of the Universidad Técnica Particular de Loja (UTPL) and the third in the Biological Reserve San Francisco (RBSF). Each plot represents different stages in the succession of the tropical montane rain forest (Beck et al., 2007). The plot in San Francisco (5200 m^2) is located within an extensive patch of undisturbed tropical montane rainforest (Beck et al., 2007), whereas the two plots in Chamusquín follow the shape of two forest fragments of recently disturbed montane

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