Perspectives in Plant Ecology, Evolution and Systematics 18 (2016) 23–32

Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.com/locate/ppees

Research article

Spatial segregation of subordinate species is not controlled by the dominant species in a tropical coastal plant community

Mário L. Garbin[a,*], Karlo G. Guidoni-Martins[b], Renan K. Hollunder[c], Pierre Mariotte[d], Fabio R. Scarano[e,f], Tatiana T. Carrijo[c]

[a] Universidade Vila Velha, Programa de Pós-Graduação em Ecologia de Ecossistemas, Laboratory of Functional Ecology, Rua Comissário José Dantas de Melo s/n, Boa Vista, 29102-770, Vila Velha, ES, Brazil
[b] Universidade Federal do Espírito Santo, Centro Universitário Norte do Espírito Santo, Rodovia BR 101 Norte, Km 60, Bairro Litorâneo, 29932-540, São Mateus, ES, Brazil
[c] Universidade Federal do Espírito Santo, Centro de Ciências Agrárias, Departamento de Biologia, Laboratory of Botany, Rua Alto Universitário s/n, Guararema, 29500-000, Alegre, ES, Brazil
[d] The University of Sydney, Center for Carbon, Water and Food, Biogeochemistry Group – Room 204, 380 Werombi Rd, Camden, NSW 2570, Australia
[e] Fundação Brasileira para o Desenvolvimento Sustentável, Rua Engenheiro Álvaro Niemeyer 76, São Conrado, 22610-180, Rio de Janeiro, RJ, Brazil
[f] Universidade Federal do Rio de Janeiro, Departamento de Ecologia, IB, CCS, Ilha do Fundão, 21941-970, Rio de Janeiro, RJ, Brazil

ARTICLE INFO

Article history:
Received 15 April 2015
Received in revised form 3 November 2015
Accepted 22 December 2015
Available online 23 December 2015

Keywords:
Community assembly
Plant–plant interactions
Plant functional traits
Spatial pattern
Species coexistence
Subordinate species

ABSTRACT

Subordinate species composition and distribution are regarded as a result of the dominant species structure. However, the spatial organization of subordinate species can also be related to dispersal abilities and interactions (competition and facilitation) within subordinate species. Here, we tested the influence of dominant species on subordinate species and examined traits of subordinate species together with their spatial patterns within a tropical coastal plant community. We hypothesized that the identity of dominant species determines subordinate abundance, and dispersal and persistence trait values variation, within coexisting subordinate species. Moreover, we expected that functionally similar subordinate species aggregate in space, regarding these values. We used the relative abundance of shrubs and trees from 83 vegetation patches in 2 ha of Restinga vegetation in southeastern Brazil. We determined trait value dissimilarities between dominant and subordinate species and within subordinates, and tested for the effect of the dominant species on subordinate abundance and trait values variation. Spatial cross-correlation functions were estimated for the four most abundant subordinate species with spline and Moran's *I* cross-correlograms. Our results showed that dominant and subordinate species exhibit contrasted trait values for dispersal and persistence. However, the composition of subordinate species in patches and the variation in their functional traits were not controlled by the identity of dominant species. Surprisingly, subordinate species segregated in space. Spatial segregation was related to dissimilar trait values within subordinates. However, the identity of dominants and patch size had no control over subordinates' abundance. We suggest that such spatial segregation can result from competitive interactions. Dissimilar functional trait values within subordinate species seem to explain the spatial segregation of these species, principally led by differences in seed production and potential allelopathic interactions (*e.g.* Myrtaceae species). Therefore, independently of the identity of dominant species, subordinate species have a direct effect on the community composition of the Restinga vegetation. Together, our findings considerably increase knowledge on subordinate species in tropical plant communities and provide new insight into the potential role of subordinate species in community assembly.

1. Introduction

Plant communities are generally composed by few dominant species and contain numerous co-existing subordinate species, which results in the observed lognormal species abundance distribution (Grime, 1998; Mariotte, 2014; Ulrich et al., 2010). Dominant species are the most competitive species and account for a high

* Corresponding author.
E-mail addresses: mlgarbin@gmail.com (M.L. Garbin), karlogregorio@gmail.com (K.G. Guidoni-Martins), renanhollunder@gmail.com (R.K. Hollunder), pierre.mariotte@sydney.edu.au (P. Mariotte), fscarano@fbds.org.br (F.R. Scarano), tcarrijo@gmail.com (T.T. Carrijo).

http://dx.doi.org/10.1016/j.ppees.2015.12.002
1433-8319/

proportion of the biomass in the community, while less competitive subordinate species represent its most diverse component. According to the mass ratio hypothesis, dominant species are expected to drive ecosystem processes within the plant community (Grime, 1998). However, recent studies showed also that subordinate species are responsible for important ecosystem processes in grasslands (Mariotte et al., 2013) and maintain diversity in tropical communities (Garbin et al., 2014, 2012). Both species-groups seem functionally important in the plant community but the mechanism generating their relative abundance is still unclear.

Deterministic niche-based processes such as habitat filtering and niche differentiation have been suggested to explain species relative abundance and diversity (*e.g.*, Cornwell and Ackerly, 2010). Habitat filtering selects individuals with suitable functional traits for a given habitat (Díaz et al., 1998), while niche differentiation select species with trait dissimilarities to promote the complementarity of resource use in space and time (Carroll et al., 2011). Both processes occur simultaneously in plant communities, and dispersal, abiotic factors and species interactions can act as filters (Kraft et al., 2015; Violle et al., 2012). Maire et al. (2012) showed that dominant species are mainly affected by habitat filtering whereas subordinate species are stabilized by niche differentiation (*i.e.* associated with dissimilar plant traits). Thus, subordinate species are expected to differ in plant functional traits and to be distributed in a patchy pattern in the plant community (Mariotte, 2014). Differences in trait values have been used to explain species coexistence of dominant and subordinate species in grasslands, while this phenomenon remains poorly studied in tropical forest and shrub communities. In the subtropics, fine-scale spatial aggregation (10 m–50 m) of subordinate species can be explained by functional traits (Perry et al., 2013), especially the traits related to dispersal ability (Perry et al., 2013; Zhang et al., 2013). This interplay between dispersal traits and small-scale spatial aggregation makes the numerous subordinate plant species, growing under or nearby dominant species, an interesting model to understand plant coexistence. Determining the functional dissimilarity between dominant and subordinate species and within subordinate species in tropical plant communities would considerably increase knowledge on the mechanisms involved in community assembly and diversity of these species rich ecosystems.

Since dominant species are more numerous, in most cases competitively superior, and possess the most suitable attributes (or trait values, *sensu* Violle et al., 2007) to persist in the ecosystem (*i.e.* habitat filtering), they play a key role in the structure of the plant community and exert strong controls over the assembly and the identity of subordinate species. For example, the architecture, phenology, genotype number and genotype variability of the foundation species (Gibson et al., 2012; Grime, 1998), as well as changes that these species induce in soil properties (Grman and Suding, 2010), have been shown to differentially affect the success of subordinate species in the community. In several plant communities, dominant species can act as nurse plants creating novel environments that alleviate stressful environmental conditions and provide structural support for many other species (McIntire and Fajardo, 2014). This results in the well-documented clumped patterns of subordinate species around dominant nurse plants (see reviews in Callaway, 1995; Brooker et al., 2008; McIntire and Fajardo, 2014). However, the understanding of how the set of facilitated subordinate species coexists under the canopy of dominant nurses has seldom been evaluated.

Species interactions (competition and facilitation), environmental factors and dispersal directly influence spatial patterns in plant communities (Hubbell, 2001; Tirado and Pugnaire, 2005). Dispersal traits may explain small-scale spatial pattern of plant species (*i.e.* the aggregation of conspecific individuals) because species with similar attributes are expected to follow the same spatial patterns (Perry et al., 2013). Disentangling the relative roles of dispersal ability, local environmental conditions and species interactions in shaping local communities linked by dispersal is a central goal of ecology (Leibold et al., 2004; Lortie et al., 2004). Surprisingly, few studies addressed the role of dispersal traits in explaining the spatial organization of plant communities (Flinn et al., 2010). Highlighting the relationship between patch quality (defined by dominant species identity) and the dispersal traits of subordinate species would help understanding such spatial patterns in tropical communities. The study of spatial patterns, *per se*, offer clues to understand the underlying causes acting over the detected patterns (Legendre and Fortin, 1989; Maestre et al., 2005). Spatial patterns of individual species and co-occurrence patterns of any two species in space can be quantified with simple and cross-correlation functions (Fortin and Dale, 2005). The objective is to determine how much of the observed variation can be attributed to spatial factors and at which scales the variation is expressed (Robertson and Gross, 1994). The spatial pattern is then used to reveal the most important ecological processes responsible for the observed patterns (McIntire and Fajardo, 2009) because these process leave spatial signatures that serve as a basis for generating testable hypotheses about community assembly (Schenk et al., 2003). Despite the various drivers of spatial patterns in plant communities, we can use the spatial pattern itself as an indication of the most important processes in action in a given community.

In our study site, a tropical sandy coastal plain in Brazil ('*restinga*' thereof; see Scarano, 2002), there is a history of investigation in this topic. Restinga vegetation consists of shrub patches, scattered over a matrix of white sand and herbaceous clumps. Each patch is dominated by a single dominant species and this ecosystem provides an excellent model to study the impacts of a single dominant species over subordinates. Dias et al. (2005) showed that architectural differences between dominant species (including one nurse plant) influence the density of understory juvenile species, a pattern that can be explained by differential attractiveness for dispersers. Subordinate species seem to present constant temporal patterns of seed rain throughout the year, while dominants disperse in well-defined and different periods (Braz and de Mattos, 2010). Dominant species, whether nurse plants or not, seem to have important filtering effects over subordinate species composition by attracting different seed dispersers and/or by creating different environmental conditions under their canopy. Therefore, the identity of dominant species might greatly influence the abundance and the identity of coexisting subordinate species, selecting for functionally dissimilar species in terms of dispersal and persistence. Moreover, Rosado and de Mattos (2010) found that differences in abundance between dominant and subordinate species can arise by differences in water stress tolerance. Slow growth species, with a conservative resource use, would attain dominance due to higher tolerance to water deficits. Subordinate species in the site can positively affect the diversity and abundance of climbing plants (Garbin et al., 2012), especially stem twining climbers (Garbin et al., 2014). The understanding of how subordinate species organize in space can thus provide clues about the mechanisms of community assembly in the restinga. However, the degree and scales of aggregation of subordinate species and the role of dispersal or persistence functional traits in explaining such aggregation patterns are unclear.

The objectives of this study were threefold. First, we examined traits related to the dispersal and persistence (*sensu* Weiher et al., 1999) of both dominant and subordinate species in this same restinga site. We hypothesized that both species-groups exert contrasted trait values, regarding dispersal and persistence, which could explain the coexistence of a high number of species in the