



The importance of plant life form on spatial associations along a subtropical coastal dune gradient

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Keywords

Brazil; Competition; Environmental gradient; Facilitation; Plant interactions; Restinga; Sand dune vegetation; Stress gradient hypothesis; Succession

Abbreviations

SGH = Stress gradient hypothesis

Nomenclature

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Abstract

Questions: Does the spatial association between isolated adult trees and understorey plants change along a gradient of sand dunes? Does this association depend on the life form of the understorey plant?

Location: Coastal sand dunes, southeast Brazil.

Methods: We recorded the occurrence of understorey plant species in 100 paired 0.25 m² plots under adult trees and in adjacent treeless sites along an environmental gradient from beach to inland. Occurrence probabilities were modelled as a function of the fixed variables of the presence of a neighbour, distance from the seashore and life form, and a random variable, the block (i.e. the pair of plots). Generalized linear mixed models (GLMM) were fitted in a backward step-wise procedure using Akaike's information criterion (AIC) for model selection.

Results: The occurrence of understorey plants was affected by the presence of an adult tree neighbour, but the effect varied with the life form of the understorey species. Positive spatial association was found between isolated adult neighbour and young trees, whereas a negative association was found for shrubs. Moreover, a neutral association was found for lianas, whereas for herbs the effect of the presence of an adult neighbour ranged from neutral to negative, depended on the subgroup considered. The strength of the negative association with forbs increased with distance from the seashore. However, for the other life forms, the associational pattern with adult trees did not change along the gradient.

Conclusions: For most of the understorey life forms there is no evidence that the spatial association between isolated adult trees and understorey plants changes with the distance from the seashore, as predicted by the stress gradient hypothesis, a common hypothesis in the literature about facilitation in plant communities. Furthermore, the positive spatial association between isolated adult trees and young trees identified along the entire gradient studied indicates a positive feedback that explains the transition from open vegetation to forest in subtropical coastal dune environments.

Introduction

It is broadly accepted that facilitation and competition can occur simultaneously between interacting plants (Holzapfel & Mahall 1999; Maestre et al. 2003), but the conditions under which one type of interaction prevails are not well understood. The stress gradient hypothesis (SGH) is a general conceptual model predicting that the relative frequency of facilitation and competition will vary inversely

across gradients of stress, with facilitation being the dominant interaction under highly stressful conditions (Bertness & Callaway 1994; Brooker & Callaghan 1998). Several empirical studies conducted in different ecosystems have confirmed the predictions of the SGH (Callaway et al. 2002; Gómez-Aparicio et al. 2004; Holzapfel et al. 2006), although some empirical works do not support SGH (Pennings et al. 2003; Maestre & Cortina 2004; Bowker et al. 2010). It is possible that these contradictions are due,

at least in part, to uncontrolled factors that also influence the outcome of plant interactions, such as ontogenetic effects (Armas & Pugnaire 2009), the performance measure used (Goldberg et al. 1999), the nature of the stress factor (Dullinger et al. 2007; Kawai & Tokeshi 2007), the methodology used to quantify biotic interactions (Michalet 2006) and, to a large degree, the traits of both the beneficiary and the benefactor species being investigated (Gómez-Aparicio et al. 2004; Liancourt et al. 2005). Recently, Maestre et al. (2009) argued that SGH should be refined through incorporation of species traits to explain why co-occurring species may not show the same response to a common neighbour under the same environmental conditions. They suggest that species might be classified according to their life histories as 'competitive' or 'stress-tolerant' – following the CSR classification of Grime (1977, 2001).

Although the proposal of Maestre et al. (2009) refines the SGH, the application of their ideas is still challenging in tropical and subtropical systems. The information needed to classify species according to their life histories includes not only morphology but also physiology and morphogenetic responses to stress (Grime 2001), information rarely available for the numerous species common in these regions. Thus, an alternative is the simpler distinction of life forms of interacting species. In fact, some studies have shown that the life form of the interacting plant species largely influences the outcome of interaction (Dullinger et al. 2007; Gómez-Aparicio 2009). Although each life form exhibits a wide range of strategies linked to the tolerance–competitive trade-off (Grime 2001), in a general way, different life forms may reveal general tendencies in their abiotic tolerances and requirements. In this way, despite its simplicity, life-form classification could represent a first step toward refining the SGH in environments where species life-history information is scarce.

A common approach used to infer interactions between plants is spatial association (Callaway 1995), in which interspecific aggregation is interpreted as facilitation and segregation is interpreted as competition. However, aggregation may result from other processes, such as shared microhabitat requirements and dispersal processes (Callaway 1995). Manipulative experiments provide stronger evidence but have intrinsic logistic limitations, which may explain why most experimental studies have been conducted using only pair-wise interactions. Accordingly, despite its limitations, the spatial association approach is a key tool as the first step toward identifying patterns in the entire community, generating hypotheses and guiding further experiments.

In coastal dune vegetation, the natural gradient from the beach to inland areas makes these communities ideal for testing the SGH. Because of the proximity of the ocean and the age of the substrate, there is a gradient of stress

and disturbance from wind exposure, salt spray, sand burial, soil salinity and moisture, that decrease towards inland (Wilson & Sykes 1999; Lortie & Cushman 2007; Lane et al. 2008; Carboni et al. 2011). While several studies have investigated plant interactions along such environmental gradients (see Forey et al. 2009; Maltez-Mouro et al. 2010; Santoro et al. 2011), few of them were conducted in subtropical or tropical coastal dunes (see Franks 2003).

In this study, we addressed two questions: (1) does the spatial association between isolated adult trees and understorey plants change along a gradient of subtropical sand dunes, and (2) does this association depend on the life form of the understorey plant? Assuming that the distance from the seashore is a surrogate for the stress gradient, we predicted that the probability of understorey plants occurring under trees would be comparatively higher near the sea than in the adjacent treeless areas (positive association) as a consequence of facilitation. However, as the distance from the seashore increases, we expected a higher probability of understorey plants occurring in the treeless areas (negative association) as a result of intensified competition. We also predicted that the spatial pattern of association would change in magnitude or type depending on the life form of the understorey species, classified here as tree, shrub, herb or liana.

Methods

Study area and vegetation

The study was conducted along a sand dune gradient near Marujá, a small fishing village located on the southern shore of Ilha do Cardoso State Park, a coastal island in southeast Brazil (25°12' S, 44° 17'W; Fig. 1). The mean annual precipitation in Ilha do Cardoso ranges from 1400 to 2380 mm, with 70% of the rain falling between November and April. The mean annual temperature ranges from 21 to 23 °C, but summers are warmer (mean monthly maximum of 26.0 °C in February) and winters are cooler (mean monthly minimum of 18.3 °C in July).

The sand dune gradient of southeast Brazil is formed by a mosaic of plant communities that occupy sandy plains formed by marine deposits in the late Quaternary and which lie between the sea and the Atlantic forest, that grows in more ancient and fertile soils inland (see details in Lacerda et al. 1993). At the local scale, the dune system at the study area is formed of parallel beach ridges occupying an approximately 400-m strip of land between the ocean and an inland estuary. The first vegetation along the beach-to-inland gradient is a narrow strip of beach community, in which creeping psammophytes grow on the shifting sands of the upper part of the beach. Behind these embryo dunes is the foredune, a slightly higher and older beach ridge dominated by grasses. Just shorewards of the

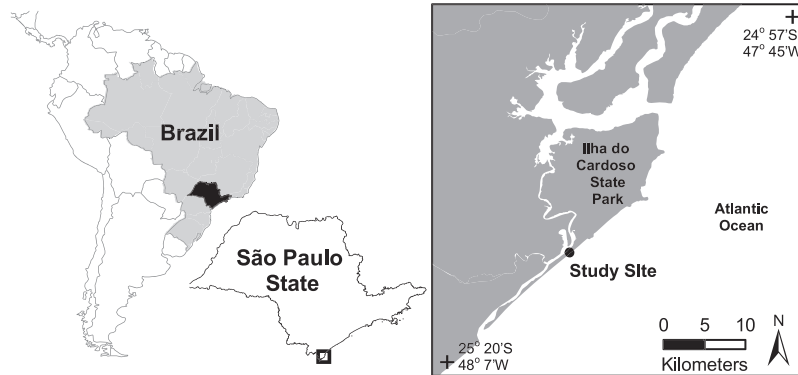


Fig. 1. Location of the study area at Ilha do Cardoso State Park, Cananéia, São Paulo, Brazil.

foredune are the rear dunes, which are several parallel older and slightly higher beach ridges that are not directly affected by the beach-exchange process. Between the ridges of the rear dunes there are depressions flooded by the water table during the summer, the dune slacks. On the ridges of the rear dunes, there is open scrub vegetation with sparse, isolated 1–3 m trees and shrubs, wood thickets of various sizes and a perennial herbaceous cover on the sandy substrate (Photo S1). Vegetation cover and biomass increase with increasing distance from the seashore, and on the inland end of the gradient there is a strip of forest with a 4–6-m high canopy. Communities with similar structures but different species compositions along a beach-to-inland gradient have been described in other regions of the tropical and subtropical coast (Araujo 1992; Araujo & Pereira 2004; Lubke 2004).

Sampling was conducted in the open scrub vegetation of the rear dunes where isolated adult trees occur, allowing us to test their effect on other plants. All sampling was carried out on the portions of the ridges facing the sea and not flooded by the water table.

Sampling design

In September 2008, 100 isolated adult trees of similar height and canopy size were randomly selected along the open scrub vegetation (70–270 m from the seashore) in an area of 30 ha (Appendix 1). We used 50 cm x 50 cm randomly placed plots to sample the understorey vegetation beneath the canopy of the trees and placed a paired plot (1 m away) in the adjacent, open microsite. The small size of the plot was selected to guarantee that all understorey plants recorded beneath an adult tree were under its canopy influence. In the present study, we define understorey plants as the layer of vegetation shorter than the canopy of the trees (specifically < 0.5 m high), but not necessarily under trees, since this short layer may occur in treeless

patches. In our site, this understorey assemblage includes herbs, lianas and young shrubs and trees. To place the plot beneath the tree, we randomly chose a direction from 0 to 359 ° and placed the plot between the tree trunk and the canopy projection limit. Then we used the same direction to place the paired plot 1 m away from the canopy projection, selecting an open microsite without direct canopy influence from any adult woody plant. If this was not possible, we randomly sampled another microsite that met these criteria to place the paired plot. For each block formed by a plot under a tree and its pair in an open microsite, we recorded its distance from the seashore as well as the height, canopy size and neighbour tree identification. In each plot, we identified all of the understorey species and classified them according to one of four life forms: trees, shrubs, lianas or herbs. To avoid positive pattern associations between trees resulting from the high occurrence of young individuals originating from each isolated parent tree, we excluded all conspecifics from analysis. Additionally, to refine the results for herbs (the life form that includes most of the understorey species found), we subdivided these into grasses, forbs, bromeliads and orchids.

Statistical analyses

If there is spatial association between trees and understorey, the proportion of plots occupied by understorey plants under trees and in open microsites will differ. If the distance from seashore affects the association, as predicted by SGH, this difference will vary along the shore–inland gradient. To test these statistical effects for each life form, we used a general linear mixed model (GLMM). A GLMM combines the properties of two statistical frameworks, generalized linear models (which handle non-normal data by using link functions to keep the response linear) and linear mixed models (which incorporate random effects; Bolker

et al. 2009). GLMM was used to describe the probability of the occurrence of understorey plants (assuming a binomial error distribution with the logit link function) as a function of the fixed prediction variables of the presence of a neighbour, distance from the seashore, type of life form and a random variable, the block (each pair of plots).

To evaluate the importance of each fixed effect inside each block, we compared models with and without each effect. The full model included all fixed effects, second- and third-order interactions, and the random effect. The comparison was done hierarchically, thus, progressively simpler models were fitted by dropping first the third-order interactions, then second-order interactions and finally each single effect. In all models, including the model without any fixed term (here called minimal model), the random effect was retained.

In this study, we assumed that distance from the seashore was a good surrogate for abiotic stress. To reinforce this assumption, in Appendix S2 we present additional analyses indicating that potentially confounding variables that vary with distance from the seashore, such as canopy size and the species of the tree neighbour individual, were insufficient to explain the effect of distance from the seashore on the occurrence of understorey plants.

For statistical inferences, we employed model selection using Akaike's information criterion (AIC), a likelihood-based measure of model plausibility that penalizes more complex models, i.e. those with a higher number of parameters (Burnham & Anderson 2002). Model selection is highly recommended in GLMM inference because it allows a true concomitant comparison of multiple models in a single step and avoids the drawbacks of step-wise multiple regression based on multiple *P*-values (Whittingham et al. 2006). Models were ranked using AIC, in which the best model, the one that sacrifices the least information when it is used to approximate the truth, had the lowest AIC value (Hobbs & Hilborn 2006). The differences between the AIC value of the best model and the values of each model ranked below it (Δ AIC) provide information for evaluating which models in a set are as plausible as the best model. Values of Δ AIC between 0 and 2 indicate similar support (Burnham & Anderson 2002). We used the R environment (version 2.11.1, R Development Core Team 2010; R Foundation for Statistical Computing, Vienna, AT) with the lme4 package for all statistical analyses.

Results

The 100 isolated adult trees sampled as neighbours had heights of 1.4 ± 0.4 m (mean \pm SD) and canopy areas (assuming the canopy shape was elliptical) of 3.1 ± 2.0 m². The trees belonged to 11 species (Table 1). The understorey plants sampled under or near the trees included 56

species: 34 herbs, 12 young trees, seven shrubs and three lianas.

The selected model for probability of occurrence of understorey plants included all main effects as well as the interaction between the presence of a neighbour and understorey plant life form and the interaction between the distance from the seashore and the understorey plant life form (Table 2). The model that included these same terms as well as the second-order interaction between neighbour and distance was equally plausible (Table 2), indicating that there is no certainty about the importance of this last term.

The presence of an isolated adult tree had a strong influence on the occurrence of an understorey plant. However, the associational pattern depended on the life form considered, which causes the interaction between neighbour and life form (Fig. 2). For lianas and herbs, the probabilities of occurrence under an isolated adult tree were very similar to those found in treeless microsites along the entire gradient (neutral association); for shrubs, the probability of occurrence was higher in treeless areas than under trees (negative association; Fig. 2). On the other hand, the occurrence of young trees was positively associated with the presence of adult tree neighbours along the entire gradient (Fig. 2). In accordance with the SGH, we expected that the effect of the presence of a neighbour would change along the gradient. However, the model that included the interaction between the presence of a neighbour and distance from the seashore and the model without this term had similar support. In general, the type of spatial association between isolated adult trees and the four life forms of understorey plants did not change along the gradient for any life form; for young trees, it was always positive, whereas it was always negative for shrubs and neutral for lianas and herbs.

Table 1. Species and number of isolated adult trees in a random sample of 100 trees taken along a coastal sand dune gradient at Ilha do Cardoso State Park, Cananéia, SP, SE Brazil.

Species	Family	Number of individuals
<i>Myrsine parvifolia</i> A.DC.	Myrsinaceae	28
<i>Ternstroemia brasiliensis</i> Cambess.	Pentaphylacaceae	26
<i>Clusia criuva</i> Cambess.	Clusiaceae	16
<i>Guapira opposita</i> (Vell.) Reitz	Nyctaginaceae	14
<i>Erythroxylum amplifolium</i> (Mart.) O.E. Schulz	Erythroxylaceae	5
<i>Ilex theezans</i> Mart. ex Reissek	Aquifoliaceae	3
<i>Sophora tomentosa</i> L.	Fabaceae	2
<i>Ocotea pulchella</i> (Nees & Mart.) Mez	Lauraceae	2
<i>Psidium cattleianum</i> Afzel. ex Sabine	Myrtaceae	2
<i>Maytenus robusta</i> Reissek	Celastraceae	1
<i>Myrcia multiflora</i> (Lam.) DC.	Myrtaceae	1

Of the 34 herb species, 19 were forbs, eight were grasses, five were bromeliads and two were orchids. The best-competing model for occurrence of herbs was the full model, which included all of the main effects and interactions

Table 2. Model selection for understorey plant occurrence. Model selection results for the probability of occurrence of understorey plants. The models were GLMM with binomial errors and presence of understorey plant as response variables; presence of a tree neighbour, distance from the seashore, understorey life form and their interactions as fixed predictor variables and block as a random variable. The selected models ($\Delta AIC < 2$) are shaded. AIC = Akaike's information criterion and $\Delta AIC = AIC$ of each model – AIC best model.

Models	Terms removed	AIC	ΔAIC
Full		702.8	6.0
Reduced	Neighbour : Distance : Life form	697.6	0.8
	Neighbour : Distance : Life form + Neighbour : Distance	696.8	0.0
	Neighbour : Distance : Life form + Neighbour : Life form	734.8	38.0
	Neighbour : Distance : Life form + Distance: Life form	735.6	38.8
Minimal	All fixed predictors and interactions	1071	374.2

(Table 3). However, the model that excluded the third-order interaction and the one that excluded the third-order interaction and the interaction between the presence of a neighbour and the distance from the seashore were equally plausible to the best model (Table 3).

The subdivision of herbs into four groups revealed different responses among herbs. The spatial association between isolated adult trees and herbs depended greatly on the subgroup of herbs. Although for bromeliads and orchids the occurrence probabilities were very similar with and without a neighbour along the entire gradient (neutral association), for grasses there was evidence of a negative association (Fig. 3). For forbs, the probability of occurrence was higher in treeless areas than beneath crown trees, and the strength of this negative association increased with distance from the seashore (Fig. 3).

Discussion

This study shows that the spatial association between isolated adult trees and understorey plants clearly depends on the life form of the understorey plant, which is consistent with other recent studies of plant interactions (Dullinger et al. 2007; Gómez-Aparicio 2009). The positive association

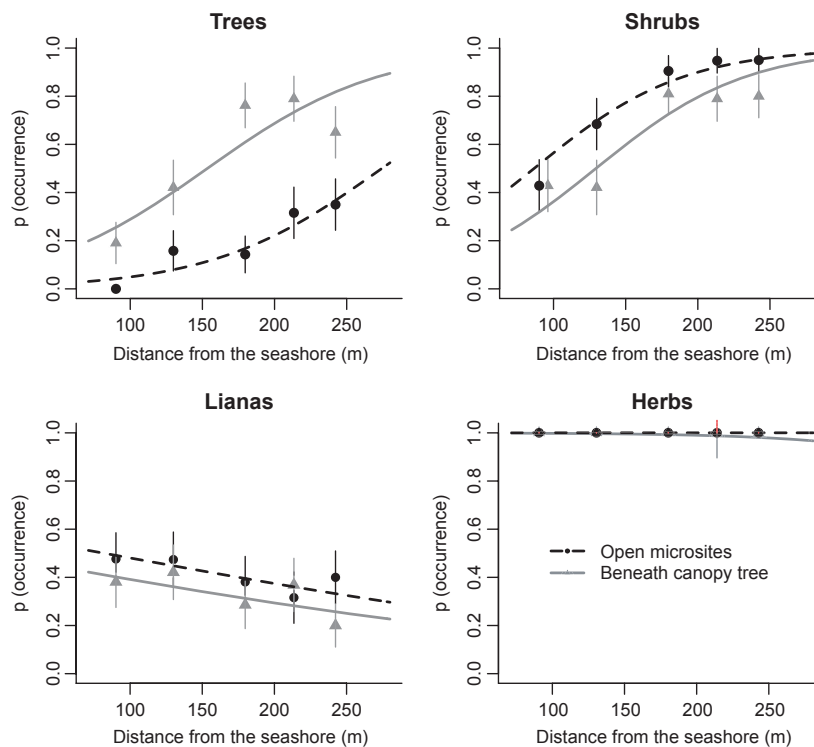


Fig. 2. Observed proportions and predicted probabilities of occurrence of the four life forms of plants under the canopy tree and adjacent open microsites with distance from the seashore. The lines represent the occurrence probabilities predicted by the selected model. (logit(y)–neighbour + distance + life form + neighbour:life form + distance:life form + block). Circles and triangles represent the observed proportion in five classes of distance and their respective standard errors.

Table 3. Model selection results for the probability of occurrence of herbs. The models were GLMM with binomial errors and presence of herb as response variables; presence of a tree neighbour, distance from the seashore, herb subgroup and their interactions as fixed predictor variables and block as random variable. The selected models ($\Delta\text{AIC} < 2$) are shaded. AIC = Akaike's information criterion and $\Delta\text{AIC} = \text{AIC of each model} - \text{AIC best model}$.

Models	Variable removed	AIC	ΔAIC
Full	–	882.1	0.0
Reduced	Neighbour: Distance: Subgroup	883.1	1.0
	Neighbour: Distance: Subgroup + Neighbour: Distance	882.3	0.2
	Neighbour: Distance : Subgroup + Neighbour: Subgroup	900.4	18.3
	Neighbour: Distance: Subgroup + Distance: Subgroup	983.0	100.9
Minimal	All fixed predictors and interactions	1108.0	225.9

expected in a harsh environment such as the dune system was found only when the understorey plant was a young tree. On the other hand, grasses and forbs were negatively associated with isolated adult trees. The variation in the spatial association with the life form of the understorey species may be a result of differences in stress tolerance and

the competitive responses of different life forms, since the trade-off between these traits is of great importance to the net outcome of plant interactions (Liancourt et al. 2005). Although each life form comprises a wide range of strategies linked with the tolerance–competitive trade-off, in a general way, trees have a higher competitive ability and are less stress-tolerant than herbs, which present a wider range of strategies (Grime 2001). High competitive ability and low tolerance to stress enable a species to minimize the costs of negative interactions and to maximize the benefits of habitat amelioration provided by neighbours (Liancourt et al. 2005). Because the most vulnerable phase in the tree life cycle is the early phase (Kitajima & Fenner 2000), the observed positive association between isolated adult trees and young trees may be explained by the well-documented nurse plant effect (Franco & Nobel 1989). Indeed, some studies performed in dune systems have found high performance of the early stages of tree species under woody neighbours (Kellman & Kading 1992; Joy & Yong 2002).

Although the positive association between adult and young trees could be a result of plant facilitation, the same aggregation pattern could be generated by preferential dispersal. Since seed-dispersing animals generally perch in woody vegetation, the number of animal-dispersed seeds

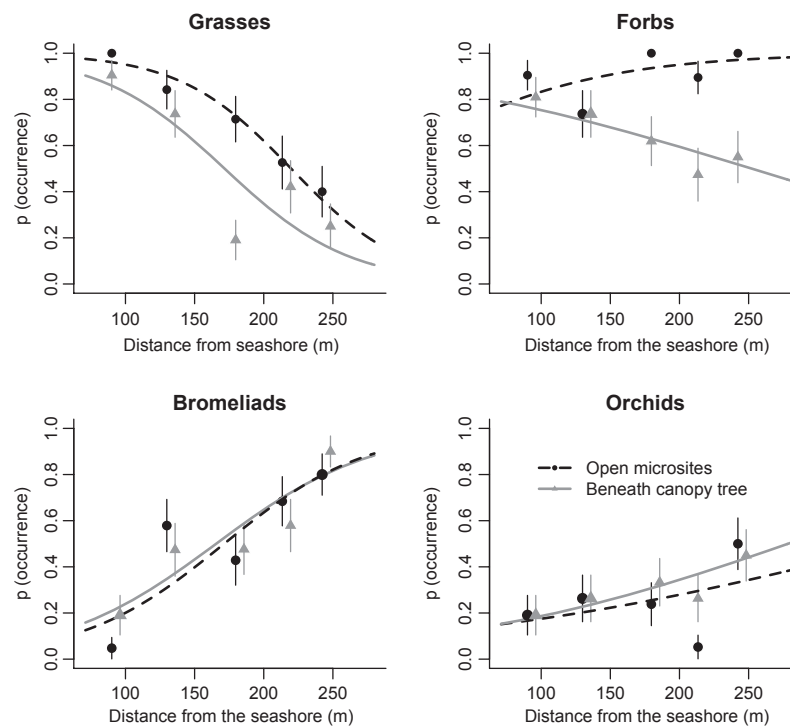


Fig. 3. Observed proportions and predicted probabilities of occurrence of four herb subgroups under the canopy tree and adjacent open microsities with distance from the seashore. The lines represent the occurrence probabilities predicted by the selected model. ($\text{logit}(y) \sim \text{neighbour} + \text{distance} + \text{subgroup} + \text{neighbour:subgroup} + \text{neighbour:distance} + \text{distance:subgroup} + \text{neighbour:distance:subgroup} + \text{block}$). Circles and triangles represent the observed proportion in five classes of distance and their respective standard errors.

below trees is higher than in the open areas (Slocum & Horvitz 2000; Holl 2002). In the present study, the tree understorey group (young trees) was composed of 12 species, all of them dispersed by animals, mainly birds (Campassi 2002). Because ten of the 11 isolated adult tree species are also dispersed mainly by birds and therefore probably provide perches for these frugivorous dispersers, the positive association between adult and young trees could result from preferential dispersal. Further experimentation is needed to understand whether the positive associational pattern observed here between isolated adults and young trees is a result of seed shadow effects, true facilitation or both.

For most life forms considered, the distance from the seashore, a surrogate for abiotic stress, did not change the associational pattern between adult trees and understorey plants, as predicted by the SGH. One exception was observed for forbs; their occurrence was higher further from adult trees than under them as the distance from the seashore increased. This result is in accordance with the SGH because although there is no evidence of a shift in the outcome of interactions, there is evidence that negative interactions between tree neighbours and forbs become more intense as the environmental stress decreases.

Why did the distance from the seashore not affect the spatial association between isolated adult trees and the other life forms? Studies on coastal sand dunes have demonstrated a gradient of stress and disturbance strongly related to distance from the sea (Wilson & Sykes 1999; Lortie & Cushman 2007; Lane et al. 2008; Carboni et al. 2011), which makes the distance from the sea a good proxy for abiotic stress. However, it is possible that the stress gradient range considered in this study was too short and insufficiently heterogeneous for abiotic stress conditions, preventing observations of their effect on associational patterns of most life forms. Indeed, some studies conducted on coastal dunes have found that the shift in plant associational patterns along environmental gradients varied with the spatial scale. Forey et al. (2009) did not find support for the SGH when they studied plant interactions in coastal dunes of France at a local scale, but found support for SGH when the authors extended the observation to a regional scale, where the environmental differences were stronger. Similar results were found by Maltez-Mouro et al. (2010) studying plant co-occurrence patterns on yellow coastal dunes in Portugal. In the literature about plant interactions on coastal dunes, the SGH has been highlighted mainly in temperate ecosystems and there is little information about plant interactions in tropical and subtropical ecosystems. In tropical and subtropical coastal dunes with high precipitation indices, the sea–inland gradient might be buffered by the more favourable general conditions, making the stress gradient less marked than in

temperate regions. Indeed, the only previous study we know that investigated how plant interactions shift along a sea–inland gradient in a subtropical region did not support SGH either (Franks 2003). More studies in tropical and subtropical regions are clearly needed in order to understand how the relation between stress and plant interaction varies among coastal dunes under different geographic climatic regimes.

The positive association observed only between isolated adult trees and young trees along the environmental gradient suggests a positive feedback relationship with potential importance for accelerating the rate of succession in this subtropical dune system. If we assume a chronosequence in dunes along the beach-to-inland gradient, we can see a change in the vegetation physiognomy through succession, with an initial predominance of herbs, changing to a later predominance of woody species (forest), as observed in other dune systems (Lichter 1998; Lubke 2004). The positive feedback created by the presence of initial trees results in patches of woody species that grow in size until they coalesce to create a continuous forest canopy. This rationale also explains the pattern found in intermediate areas of the dune gradient formed by patches of woody species scattered in a matrix of white-sand herbaceous plants (Araujo 1992). This process is very similar to the nucleation process proposed by Yarranton & Morrison (1974) to explain primary succession in temperate dunes. These authors found that nucleation is initiated by a tree species, *Juniperus virginiana* L., which benefits persistent subsequent species. A similar process has been suggested for the tropical dunes of Rio de Janeiro (southeast Brazil), where the formation of vegetation islands and succession are triggered by the colonization of pioneer plants, such as the geophyte palm species *Allagoptera arenaria* (Gomes) Kuntze. and the tree *Clusia hilariana* Schlecht (Zaluar & Scarano 2000; Scarano 2002). The role of pioneer woody species in nucleating the settlement of more woody species in open vegetation have been reported in other studies, but most of them have been conducted in secondary successional habitats, such as abandoned pastures (Vieira et al. 1994; Slocum & Horvitz 2000; Holl 2002). The positive pattern association between trees observed in this study seems to be a key to understanding the transition between herbaceous–woody physiognomies along the successional development of this subtropical dune vegetation.

In conclusion, the associational pattern between isolated adult trees and understorey plants along the coastal dune gradient depends on the life form of the understorey plant. The positive association expected in a harsh environment, such as dune systems, was found only for young trees. However, an experimental approach is needed to determine whether the observed pattern results from higher seed shading under trees, if adult trees truly facilitate the

youngest trees under their canopy or if both processes are present. Regardless of the process behind the positive associations between trees, the potential feedback identified in this study may be a crucial element to understanding the transition between open vegetation, dominated by light-demanding herbs, and communities where trees are the dominant life form. In this way, our study contributes to understanding the dynamics of plant communities in subtropical coastal dunes through the pattern–process approach, which has proven to be an essential method for understanding community organization (Watt 1947; Brown 1995). Moreover, the shift in the associational pattern expected by the SGH prediction also depends on the life form of the understorey plant, adding one more condition for refining the effects of stress on net plant interactions.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Distribution of the experimental blocks in the study area.

Appendix S2. Testing potentially confounding factors along the stress gradient.

Photo S1. Open scrub vegetation at the study site.

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