No place for phylogeny in structuring a sandy coastal plain community

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Abstract

Although inference of assembly processes from phylogenetic patterns has become ubiquitous in community ecology, surprisingly few studies simultaneously test assumptions of such an approach and integrate over spatial scales and plant life stages. Here we investigate the roles of phylogeny, functional traits, and abiotic conditions in the spatial structuring of a sandy coastal plain community using data on 2800 finely mapped adult individuals and on the survival time-series of 500 seedlings. We demonstrate that phylogeny is a poor predictor of functional traits and that convergence in these traits is pervasive. In general, the community is not phylogenetically or functionally structured regardless of spatial scale. Leaf area, however, is strongly overdispersed across all spatial scales, which is generally taken as evidence of competition. We also show that seedling survival is dramatically increased when shaded by an adult, suggesting that seedlings are being facilitated. We also demonstrate species-specific effects on seedling survival that are independent of phylogeny. Overall, we show that phylogeny has very limited influence on the fine-scale assembly of that community, and that its role should always be tested instead of assumed.

1 Introduction

Phylogenies have been increasingly used to address questions about community ecology (Emerson and Gillespie, 2008; Cavender-Bares et al., 2012), and a number of studies have asked whether co-occurring species are more or less phylogenetically related than expected by chance to infer aspects of the assembly process (Webb, 2000; Webb et al., 2002; CavenderBares et al., 2004; Horner-Devine and Bohannan, 2006; Kembel and Hubbell, 2006; Kraft et al., 2008; Swenson et al., 2012). This approach is rooted in the idea that closely related taxa tend to have similar niches (Harvey and Rambaut, 2000; Freckleton et al., 2002; Wiens and Graham, 2005; Losos, 2008), and that the degree of phylogenetic similarity may, in part, explain species interactions and their responses to abiotic factors. There are, nevertheless, limitations and pitfalls when interpreting community phylogenetic patterns (Cavender-Bares et al., 2009; HilleRisLambers et al., 2012). Non-random phylogenetic structure can be the result of historical contingency and biogeographic history (Leibold et al., 2010; Ives and Helmus, 2011). Different ecological processes, such as facilitation and plant-pollinator interactions, can also produce non-random phylogenetic structure (Valiente-Banuet and Verdú, 2007; Sargent and Ackerly, 2008; Valiente-Banuet and Verdú, 2013). Conversely, even strong competition can fail to result in the predicted overdispersed community (Bennett et al., 2013), and may in fact tend to result in clustered communities (Mayfield and Levine, 2010), highlighting the intrinsic difficulty in linking pattern and process. More importantly, the fundamental premise that evolutionary relationships correlate with niche is debatable, because many niche axes can be highly labile or convergent (Losos, 2008; Cavender-Bares et al., 2009).

The spatial scale of the analysis can also have large a effect on estimates of community structure (Cavender-Bares et al., 2006; Swenson et al., 2006), especially because environmental heterogeneity tends to increase as spatial scales get larger (Cavender-Bares et al., 2009), factoring in additional sources of complexity. Despite that, relatively few studies have sampled communities at varying spatial resolutions (but see Swenson et al., 2007; Kraft and Ackerly, 2010) and even fewer have data on spatial scales at which individuals are likely to interact (but see Slingsby and Verboom, 2006; Willis et al., 2010). Similarly, few studies account for instraspecific variability in key plant functional traits (but see Baraloto et al., 2012). Yet, recent theory suggests that taking within species variation into account can significantly improve estimates of phylogenetic signal (Ives et al., 2007; Felsenstein, 2008; Freckleton and Jetz, 2009), and therefore properly test the fundamental assumption of niche conservatism in community phylogenetic analyses. Direct estimation of ecological processes that may be driving community assembly is key mechanistically understand community phylogenetic patterns Webb et al. (2006), Uriarte et al. (2010), Castillo et al. (2010), and Lebrija-Trejos et al. (2014). The seedling stage is likely the most sensitive in a plant's life history, when they are especially susceptible to the effects of competition, predation and pathogens (Maun, 1994; Terborgh, 2012). Thus, the ecological processes operating at that life stage may be largely determining the spatial and phylogenetic patterns observed in the adults (Webb et al., 2006; Paine et al., 2012; Lebrija-Trejos et al., 2014). For example, Janzen-Connell effects should cause high seedling mortality rates when they grow nearby a closely related adult (Metz et al., 2010; Xubing Liu et al., 2012), resulting in a phylogenetic overdispersed community. Yet, the lack of specificity and convergence in host-pathogen relationships and the simultaneous action of other processes such as facilitation can often negate these simple predictions (Mayfield and Levine, 2010; Lebrija-Trejos et al., 2014).

Sandy coastal plain plant communities provide an excellent system to study the role of phylogeny and functional traits on community structuring. First, they are geologically young, on the order of 3 to 7 kya (Martin et al., 1993; Martin, 2003; Dillenburg and Hesp, 2009), reducing the chance that phylogenetic patterns are a product of historical factors. Second, there is little variation in elevation and soil composition, especially at short spatial scales, minimizing the role of unmeasured abiotic factors in determining the observed community structure. Third, the harsh conditions imposed by the sandy coastal environment on the organisms provide good biological justification for choosing functional traits that are correlated with water use efficiency and leaf thermoregulation (Rosado and E. A. d. Mattos, 2010). Furthermore, the abundance of vegetation islands dominated by an adult individual surrounded by bare sand also permits evaluating the effects of phylogeny and abiotic factors in seeding survival.

Here we use a unique dataset on 2800 finely mapped individual plants in a sandy coastal plain plant community in southeastern Brazil to understand the role of phylogeny and four functional traits, specific leaf area (SLA), leaf dry matter content (LDMC), leaf area and plant maximum height, in structuring that community. We also evaluate how phylogeny and vegetation patch characteristics influence rates of seedling mortality. Specifically, we (1) explicitly test the hypothesis that phylogeny is a good predictor of function, (2) estimate how the phylogenetic and functional structure of the community vary across spatial scales, and (3) evaluate how phylogenetic distance and other vegetation patch covariates affect seedling survival.

2 Methods

2.1 Study system and sampling

This study was conducted in Costa do Sol State Park (S 22°55’55”, W 42°12’40”), Rio de

Janeiro, Brazil. The site is representative of a sandy coastal plain community characterized by patchy scrub vegetation and a low canopy, rarely reaching 5m (Araujo, 2000). The soils are quartzitic sands that have low water-retention capacity, high acidity, and low nutrient levels (Scarano, 2002; Rosado and E. A. D. Mattos, 2007; Araujo et al., 2009). The plant community was sampled in 224 quadrats of $50m^2$ inside a contiguous 0.6ha plot. Every individual plant within each quadrat was mapped and their height and crown diameter were measured. In the case of Cactaceae we recorded the diameter of the largest stem. The final sample is composed of 2832 individuals in 42 species across the Eudicot tree of life (see suppl. figure 4), representing 87% of the woody diversity in that community (Araujo et al., 2009).

We chose to track seedling survival under four key woody species in the community: *Byrsonima sericea*, *Clusia fluminensis*, *Erythroxylon ovalifolium* and *Ocotea notata*. For each of these species, we selected ten patches dominated by a single individual and established two $1m^2$ seedling plots, one inside the vegetation patch and another immediately outside of the patches' canopy. Therefore, seedlings were censused in 80 plots of $1m^2$ each. All individual seedlings within each plot were marked two weeks after the plots were established (t0, Jun 2011), and then censused at four points in time during a year: Sep 2011 (t1), Dec 2011 (t2), Mar 2012 (t3), and Jun 2012 (t4). The seedlings were identified based on morphology using a seedling catalog available at the herbarium of the Botanical Gardens in Rio (RB).

2.2 Phylogenetic reconstruction

We constructed an initial phylogeny for the 42 species in the community using Phylomatic (Webb and Donoghue, 2005). Topological resolution was then refined by hand using the recent literature on the focal clades, e.g. (Xi et al., 2012). Divergence time estimates taken from (Bell et al., 2010) were set to internal nodes using Mesquite (W. P. Maddison and D. R. Maddison, 2016).

Because the phylogeny spans several major orders of the flowering plants, the tree topology is fully resolved with the exception of two young clades of Myrtaceae (suppl. figure 4).

2.3 Functional trait data

The four functional traits, specific leaf area (SLA), leaf dry matter content (LDMC), leaf area and maximum plant height were measured for 210 individuals belonging to the 42 species. In addition, an aggregate functional dissimilarity was defined as the value of the first eigenvector (PC1) from a PCA analysis of all other traits. SLA is the ratio between the leaf area and amount of dry matter (in $dm^2\ g^{-1}$), and captures a trade-off between cheaply constructed leaves (high SLA) and more robust leaves (more mass per unit area) with low SLA values. SLA is know to be negatively correlated with leaf life span and positively correlated with net photosynthesis (Reich et al., 2003). SLA is also strongly negatively correlated with drought tolerance (Wright et al., 2004), making it a trait of special interest in water limited environments like sandy coastal plains. LDMC measures the amount of dry matter per gram of wet matter. Although Cornelissen et al. (2003) propose this trait to be measured in mgg^{-1} mg/g, we are reporting LDMC values in gg^{-1} (proportion) because it provides the intuitive notion of the inverse of water content in the leaf. LDMC has been shown to negatively correlate with environment productivity, and is better than SLA in detecting soil fertility gradients independent of shading conditions (Hodgson et al., 2011). Leaf Area is reported in cm^2 and represents a trade-off between increasing photosynthetic area and the ability to dissipate heat and hold water (Cornelissen et al., 2003; Swenson, 2009). Maximum height has been used in ecology as a proxy of adult light niche (King et al., 2006). For the leaf traits, we measured three fully exposed and mature leaves from each individual, totaling 630 leaves sampled. Leaf wet and dry weight were measured in a precision scale (0.001g) and the prepared according to the protocol outlined by Cornelissen et al. (2003). We left the leaves hydrating overnight in the dark at 4°C using distilled water prior to weighing wet mass. Dry mass was estimated after drying the leaves at 60°C for at least 3 days. Leaf area was estimated by scanning the leaves with a desk scanner and computing their area using ImageJ v10.2 (Abràmoff et al., 2004).

We estimated the phylogenetic signal of each trait separately as well as the signal of the total functional dissimilarity using the K statistic (Blomberg et al., 2003) as implemented in the Phytools R package (Revell, 2012). A K value of 1 indicates that the trait dissimilarity is proportional to the time since divergence as predicted by a Brownian motion model of evolution. K values smaller than 1.0 indicate trait convergence or high lability, whereas values greater than one are interpreted as trait conservatism, that is, traits are less divergent than expected by Brownian motion (Blomberg et al., 2003). Recent theory suggests that taking within species trait variation into account can vastly improve estimates of phylogenetic signal (Ives et al., 2007; Felsenstein, 2008). This is implemented in Phytools (Revell, 2012) by incorporating the standard error of a trait for each species as an extra argument to the phylosig function. Therefore, K for leaf area, dry mass fraction and SLA were estimated both using only the mean trait value and using the intra-specific variation. Statistical significance of the phylogenetic signal estimates are computed by comparing the observed K to their null distributions calculated by randomizing the species values 999 times.

2.4 Phylogenetic and functional community structure

We assessed the phylogenetic and functional structure of the community with two widely used indices, Mean Phylogenetic Distance (MPD) and Mean Nearest Taxon Distance (MNTD) (Webb et al., 2002). MPD is the average sum of distances (phylogenetic or functional) between species in a given plot whereas MNTD measures the average distance between each species and its closest relative in a plot. Both indices can be weighted by species abundances (Kembel et al., 2010). These indices were computed for each site and compared to a null distribution generated by shuffling the species labels in the phylogenetic and functional distance matrices 999 times. We defined significant clustering or overdispersion as observations that fell in the lower or upper 2.5% of the null distribution, respectively. A standardized effect size (SESmntd and SESmpd) of the observed metric versus the null distribution was calculated by dividing the difference between the observed metric and the mean of the null distribution by the standard deviation of the null distribution (Webb et al. 2002). Negative SES values indicate clustering whereas positive values indicate overdispersion. All of the analyses were carried using the R package Picante (Kembel et al., 2010).

2.5 Seedling survival

The survival functions for the whole seedling data associated with different conditions (e.g. dominant adult identity) were first estimated and visualized using the Kaplan-Meier estimator implemented in the R package Survival (Therneau, 2015). To model how seedling survival is affected by different variables, we used a Cox proportional hazards model (CPH) (Therneau and Grambsch, 2000), also implemented in the Survival package (Therneau, 2015). Because we wanted to understand the effects of the dominant adult species on seedling survival, we measured the phylogenetic distance between that adult and each of the seedlings. We used AICc to compare models with different combinations of the following covariates: phylogenetic dissimilarity from the dominant adult, plot position (outside versus inside the patch), dominant species identity, and patch area.

3 Results

3.1 Functional trait phylogenetic signal

Leaf area and maximum height were the only functional traits to show detectable phylogenetic signal as inferred from K (Table 1). LDMC and SLA had a non-significant K, meaning that their evolution is statistically independent from the community phylogeny. In all cases, K was estimated to be well below one, showing widespread phylogenetic convergence of the functional traits in question (Figure 1, Table 1). Accounting for intraspecific variation instead of using mean trait values for each species influenced the estimate of K for leaf area, but had no significant impact on the phylogenetic signal inference for SLA and Leaf Dry Mass Fraction (Table 1).

3.2 Community phylogenetic and functional structure

SESmpd (Mean Phylogenetic Distance) and SESmntd (Mean Nearest Taxon Distance) are in broad agreement regarding the direction of the community structure, although the magnitude of the clustering/overdispersion was variable between these two indices. There is no evidence for phylogenetic clustering at any spatial scale when using the MPD index (Figure 2, Table 2). Only 5.6% of the sites at the 2.5m scale were significantly more clustered than expected by the null model (Table 2). MNTD estimates reveal only marginal phylogenetic clustering (suppl. figure 5 and table 5), with 14% of the sites significantly clustered at the coarser spatial scale, though that signal weakens at finer spatial scales (suppl. table 5).

On the other hand, the functional trait leaf area is strongly overdispersed in the community regardless the metric used and the spatial scale. At the coarser scale, MPD reveals that 62.5% of the sites are significantly overdispersed (Table 2, Figure 2) whereas MNTD indicates that 37.5% are so (suppl. table 5). Leaf area overdispersion weakens at finer spatial scales for both MPD and MNTD estimates (Table 2, suppl. table 5). The remaining functional traits do not present an overall pattern and are rarely significantly structured, with the exception of SLA, which is marginally overdispersed in the MPD estimates (Figure 2, Table 2). The first eigenvector form the functional PCA analysis, PC1, seems to be mostly reflecting leaf area dissimilarity (Figure 2).

3.3 Seedling survival

We censused 504 individual seedlings belonging to 26 different species. The most abundant species were *Anthurium maricense* (195), *Erythroxylon ovalifolium* (59) and *Stigmaphyllon paralias* (26). A total of 385 seedlings (76%) survived to the end of the first year. Comparisons of the different CPH models using AICc indicate that plot position, whether the seedlings were growing inside or outside of the vegetation patch, and dominant species identity are the covariates that better explain seedling survival (Table 3). On the other hand, the CPH model using only the phylogenetic distance from seedling to dominant species had the worst fit to the data (Table 3).

The CPH model estimates coefficients that multiply the risk of death of individuals that fall in a given category when compared to a baseline. The best CPH model (cph1; Table 3) estimated that seedlings growing inside a vegetation patch are 2.8 times more likely to survive than the ones growing out in the open (Table 4, Figure 3). The identity of the dominant species in the patch also influences the probability of survival: Growing by any of the dominant species other than *Byrsonima* (taken as baseline) decreased the risk of seedling death (Table 4). In other words, survival rates were the lowest in seedlings growing by *Byrsonima sericea*, as shown in figure 3.

4 Discussion

4.1 Does phylogeny predicts function?

The idea that evolutionary relatedness reflects niche is at the core of community phylogenetics (Webb et al., 2002; Emerson and Gillespie, 2008). Our results demonstrate that the functional traits SLA, LDMC, Leaf area and Maximum height have either very weak or no phylogenetic signal at all, that is, phylogeny does not correlate with function. Conversely, a number of studies both in the tropics and in the temperate zone have found these leaf traits to be phylogenetically conserved at coarser taxonomic scales (Cavender-Bares et al., 2006; Kraft et al., 2008; Cornwell and Ackerly, 2009; Kraft and Ackerly, 2010; Baraloto et al., 2012). The lack of phylogenetic signal in these leaf traits may be an artifact of strong habitat filtering at larger geographic scales (Emerson and Gillespie, 2008; Vamosi et al., 2009). Most species inhabiting the sandy coastal plains come from adjacent forests

(Scarano et al., 2009) and they likely represent a non-random sample of leaf functional traits. This hierarchical habitat-filtering process (Silvertown et al., 2006) may therefore drastically change the composition of the regional species pool and, and in turn, bias estimates of phylogenetic signal.

4.2 Community phylogenetic and functional structure

The lack of phylogenetic structure at all spatial scales comes without surprise given the overall absence of match between the functional traits and phylogeny (Figure 1). On the other hand, co-occurring species tended to have leaf sizes more dissimilar than expected regardless of spatial scale or the metric used (Table 2, Figure 2, suppl. table 5). Overdispersion in leaf traits such as leaf area and SLA has been identified in a variety of systems, including the Californian chaparral (Cornwell and Ackerly, 2009), Amazonian forest (Kraft et al., 2008), within Floridian Oaks (Cavender-Bares et al., 2004; Cavender-Bares et al., 2006), among others (review in Vamosi et al., 2009). In all of the cases mentioned above, trait overdispersion was interpreted as the product of interspecific competition. Consequently, the widespread pattern of leaf area overdispersion found in this study would generally be seen as the result of niche partitioning because individuals are strongly competing for light (Webb et al., 2002; Sterck et al., 2011; Lasky et al., 2014). Although possible, there are reasons to take that interpretation with a grain of salt. As stated before, experimental studies have show that even strong competition can fail to produce an overdispersed trait pattern, and in fact result in trait clustering (Mayfield and Levine, 2010; Burns and Strauss, 2012; Bennett et al., 2013). Intense competition for light also seems unlikely in an open community where excess light is usually the villain rather than a rare resource (Scarano et al., 2009; Rosado and E. A. d. Mattos, 2010). Finally, the fact that the frequency of plots with significantly overdispersed leaf area decreased at finer spatial scales also contradicts that interpretation, since competition should be stronger (or captured more frequently) at smaller scales spatial (Slingsby and Verboom, 2006; Cavender-Bares et al., 2006).

4.3 Seedling survival

Contrary to what has been found in several other studies, the phylogenetic distance to the dominant adult species had no effect on seedling survival (Webb et al., 2006; Metz et al., 2010; Paine et al., 2012; Lebrija-Trejos et al., 2014). These studies were carried out in wet forests, where the influence of competition, predation and disease probably outweighs the effects of abiotic factors. Susceptibility to pathogens has been shown to be phylogenetically conserved (Gilbert and Webb, 2007; Xubing Liu et al., 2012), providing an explanation for the observed phylogenetic effects.

The results from the CPH model show instead that growing inside a vegetation patch has a large positive effect on seedling survival (Table 4, Figure 3) regardless of the phylogenetic distances or patch size. Therefore, this finding provides strong evidence that the adult individuals are acting as nurse plants, facilitating the establishment and survival of seedlings growing in their shade (Brooker et al., 2008; Callaway, 1995). Facilitation is known to be specially important for seedling establishment and survival in harsh abiotic conditions (Valiente-Banuet and Ezcurra, 1991; Callaway et al., 2002; Valiente-Banuet and Verdú, 2013), and nurse plants have been hypothesized to play a key role in the demographic dynamics of the sandy coastal plain communities in southeastern Brazil (Scarano, 2001; Scarano, 2002).

We observed in the field that patches of *Byrsonima* filtered out less light and accumulated more leaf litter beneath. Lower levels of shade inside the patch may increase temperatures and leaf litter can often negatively affect seedlings establishment and growth (Molofsky and Augspurger, 1992; Santos and Válio, 2002). Regardless of the mechanisms behind the species effects, these results show that species differences not captured by phylogenetic relatedness can have a large effect on seedling survival.

This study adds to a growing body of work that fail to find the signature of phylogeny in niche and functional traits (Losos et al., 2003; Swenson, 2009; Uriarte et al., 2010), spatial pattern of species in the communities (Peres-Neto, 2004; Silvertown et al., 2006; Slingsby and Verboom, 2006; Xiaojuan Liu et al., 2013) and in important ecological processes (Cahill et al., 2008; Mayfield and Levine, 2010; Bennett et al., 2013). It is increasingly evident that the "phylogeny pendulum might have swung too far" (Losos, 2008), and the putative influence of deep evolutionary history on current ecological dynamics must be tested instead of assumed a priori. As literature accumulates and new probabilistic methods are developed and improved (Ives and Zhu, 2006; Ives and Helmus, 2011), it should become evident when, where and at what scales phylogenies can provide insights into ecological questions and which statistical approaches would be the most appropriate.

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6 Main Text Figures and Tables

Table 1: Phylogenetic signal of four functional traits as estimated by Bloomberg's K using a) only the mean value for the traits and b) accounting for intraspecific variation.

	SLA	LDMC	Leaf Area	Maximum Height	Function PC1
K – sp. mean	0.2249	0.1612	0.28	0.3031*	0.1958
K – itrasp. variation	0.2387	0.1753	0.4309*	—	—

Table 2: Percentage of plots phylogenetically or functionally structured as measured with SESmpd (Mean Phylogenetic Distance). Three spatial scales were evaluated, 10x10m (n = 56), 5x5m (n = 219) and 2.5x2.5m(n = 545).

		Phylogeny	SLA	LDMC	Leaf Area	Max Height	PC1
10m	Clustered	5.30%	—	—	—	—	—
	Overdispersed	—	10.70%	—	62.50%	1.7	39.20%
	Median SESmpd	-0.742	1.328	-0.4	2.244	-0.178	1.737
5m	Clustered	4.10%	—	0.90%	—	—	—
	Overdispersed	1.30%	11.80%	1.30%	35.60%	0.90%	19.10%
	Median SESmpd	-0.495	0.976	-0.311	1.459	-0.342	1.2
2.5m	Clustered	5.60%	—	—	—	—	—
	Overdispersed	2.90%	13.20%	1.40%	19%	1.20%	13%
	Median SESmpd	-0.064	0.329	-0.258	1.069	-0.4	0.759

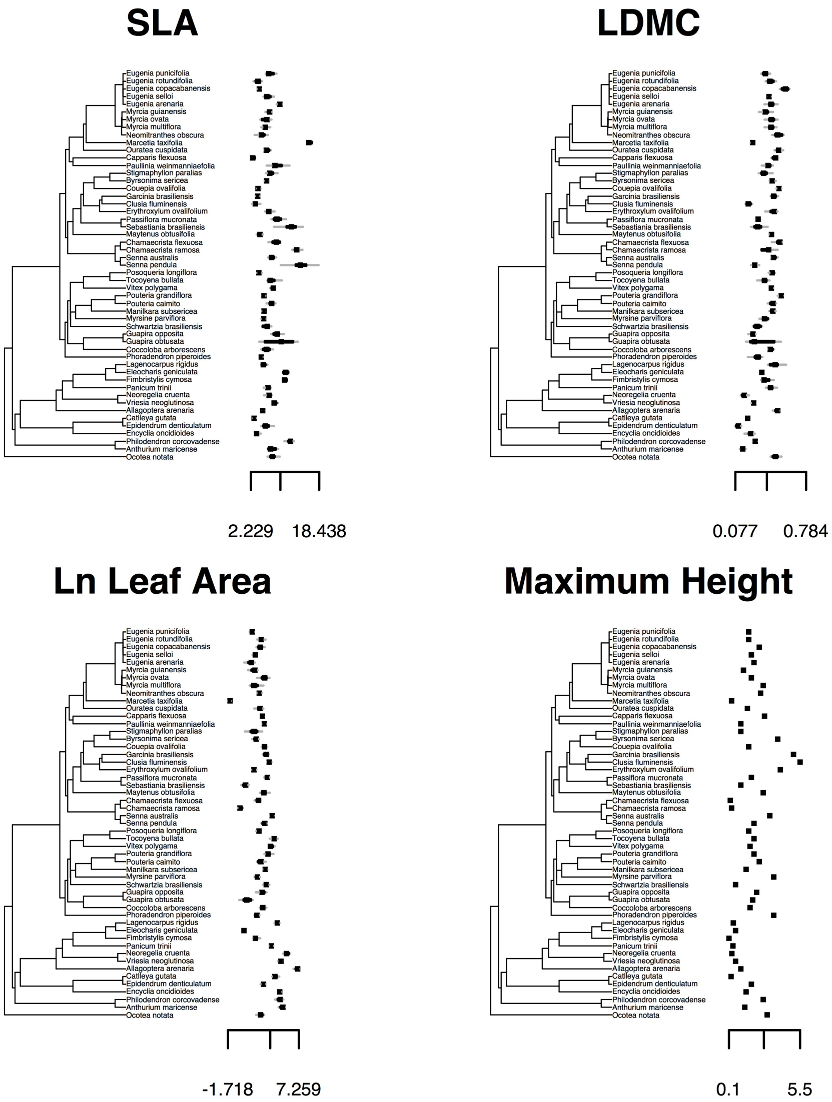
Table 3: Comparison of different proportional hazards models of seedling survival. DoF stands for degrees of freedom and the best model as selected using AICc is embolden.

Model	Covariates	DoF	LogLik	AICc
cph0	Patch Area + Plot Position + Dominant Sp. + Phylo.	6	-389.3555	790.8874
cph1	**Plot Position + Dominant Sp.**	**4**	**-390.2573**	**788.5982**
cph2	Dominant Sp.	3	-397.8576	801.7654
cph3	Patch Position	1	-396.3922	794.7927

cph4	Phylo.	1	-404.8456	811.6995

Table 4: Estimates of the effects of plot position and dominant species on seedling survival from the best proportional hazards model (cph1). Coefficients larger than one implicate increased risk while smaller than one represent decreased risk. The states Plot Position = inside and Dominant Sp = Byrsonima were taken as baseline, i.e. exp(coef) = 1.

	exp(coef)	CI 2.5%	CI 97.5%	z-score	p-value
Plot Position: Outside	2.825	1.7181	4.6451	4.093	4.26E-05
Dominant Sp.: Clusia	0.4333	0.2216	0.8475	-2.443	0.014546
Dominant Sp.: Erythroxylon	0.2846	0.1404	0.5766	-3.488	0.000487
Dominant Sp.: Ocotea	0.5135	0.2661	0.9909	-1.987	0.046909



SLA

LDMC

Ln Leaf Area

Maximum Height

Figure 1: Phylogenetic distribution of the estimates of four functional traits for each species on in the community. Mean values are represented by squares and quartiles are shown as whiskers. LDMC is the ratio between dry and wet leaf mass

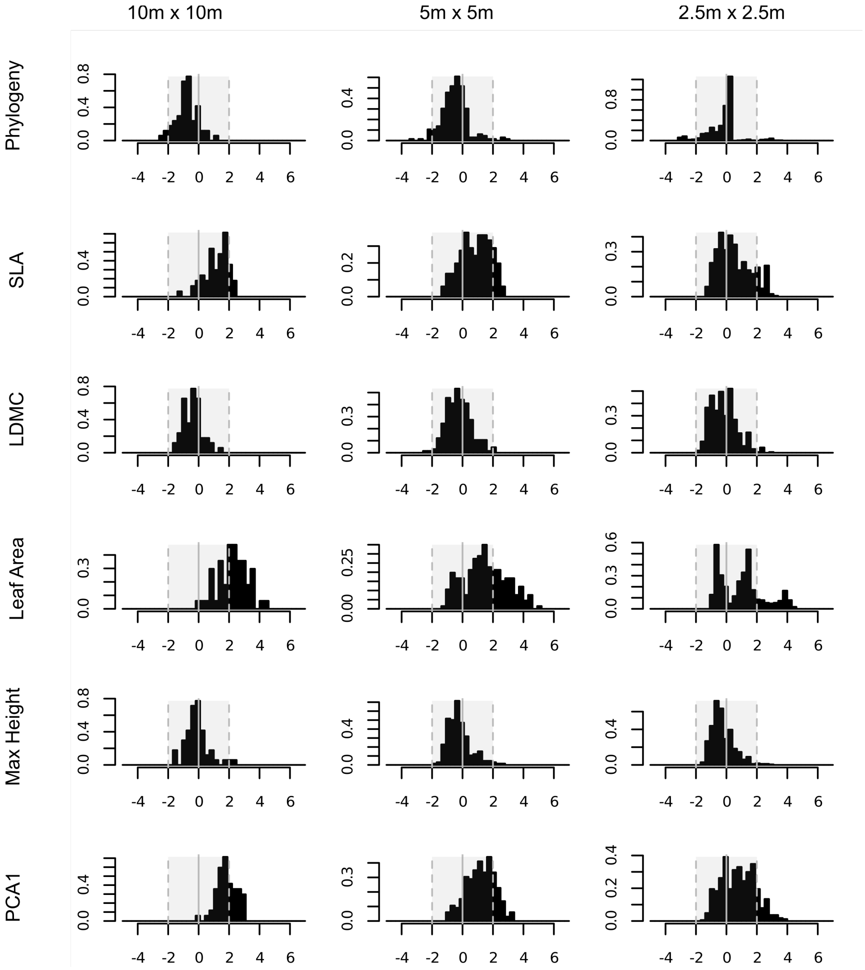


Figure 2: Community phylogenetic and functional structure across three spatial scales. Histograms show the frequency of plots with different SESmpd values. Negative SESmpd estimates represent clustering and positive values mean overdispersion. The shaded grey area marks 2 standard deviations about the mean of the null distributions.

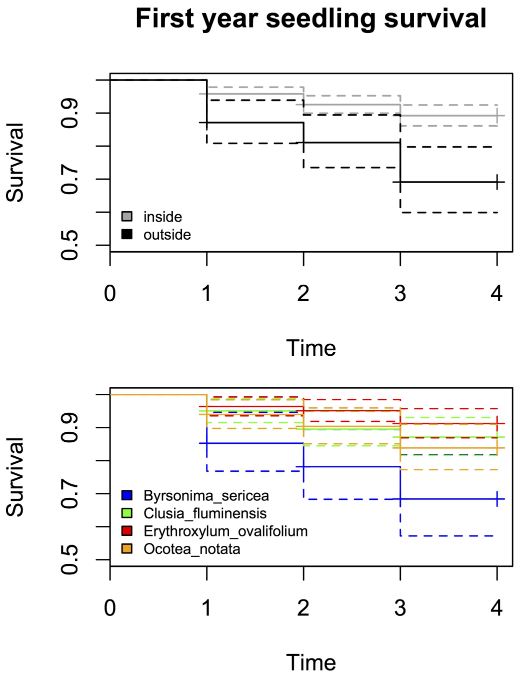


Figure 3: Kaplan-Meier estimates of first year seedling survival a) between plots inside and outside vegetation patches (plot position) and b) among the four different dominant plants.

7 Supplement

Figure 4: Phylogenetic tree for the 42 species in the open scrub Massambaba community. Time (y-axis) given in million years.

Table 5: Percentage of plots phylogenetically or functionally structured as measured with SESmntd (Mean Nearest Taxon Distance). Three spatial scales were evaluated, 10x10m (n = 56), 5x5m (n = 219) and 2.5x2.5m(n = 545)

	Phylogeny	SLA	LDMC	Leaf Area	Max Height	PC1

10m	Clustered	14.20%	—-	—-	—-	—-	—-
	Overdispersed	—	3%	—	37.50%	—	5%
	Median SESmntd	-1.42	-0.245	-0.61	1.471	-0.633	0.992
5m	Clustered	12.30%	—	0.40%	—	—	—
	Overdispersed	—	2.70%	1.80%	31%	0.90%	8.60%
	Median SESmntd	-0.943	0.16	-0.346	1.142	-0.386	0.812
2.5m	Clustered	8.90%	—	0.18%	—	—	—
	Overdispersed	1.20%	12.80%	2%	26.40%	1.10%	10.40%
	Median SESmntd	-0.039	0.195	-0.235	0.9905	-0.351	0.607

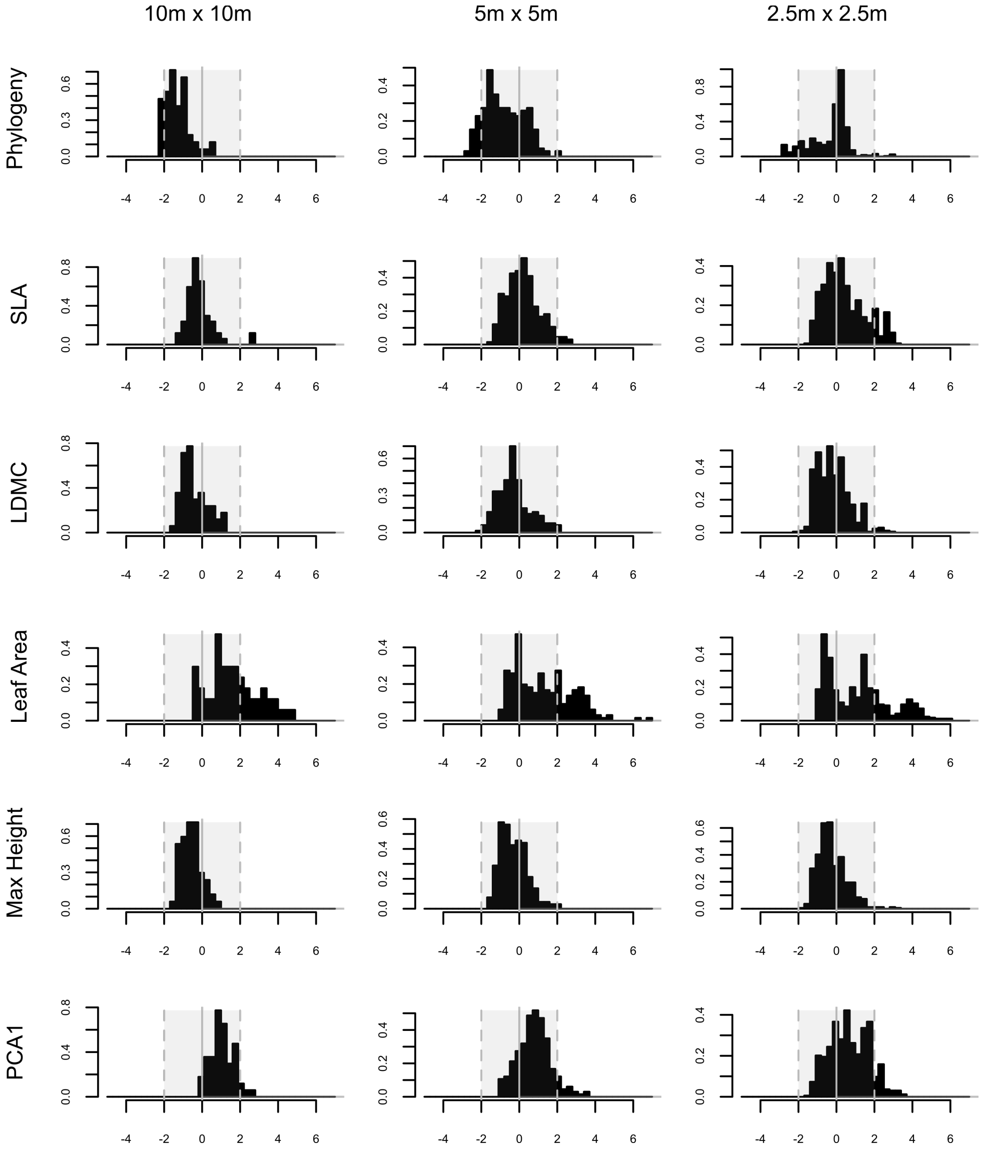


Figure 5: Community phylogenetic and functional structure (SESmntd) across three spatial scales. Negative values represent clustering and positive values mean overdispersion. The shaded grey area marks 2 standard deviations about the null distributions means