Two bromeliad species with contrasting functional traits partition the understory space in a South American xerophytic forest: correlative evidence of environmental control and limited dispersal

Ignacio M. Barberis · Patricia S. Torres · William B. Batista · Gustavo Magra · Luciano Galetti · Juan Pablo Lewis

Abstract We examined the spatial distribution of two bromeliad species with contrasting functional traits in the understory of a xerophytic South American Chaco forest. *Aechmea distichantha* is a facultative terrestrial species with well-developed phytotelma and short rhizomes, whereas *Bromelia serra* is a strictly terrestrial species with soil-exploring roots and long rhizomes. Both bromeliads develop colonies on relatively elevated patches in *Schinopsis balansae* forests. We evaluated the roles of environmental controls, limited dispersal, and interspecific competition as drivers of the different distribution of these bromeliads. We mapped the overstory, understory and topography of 16 forest plots with bromeliads (400 m² each, subdivided in 100 4-m² subplots). We sampled soil characteristics on sectors dominated by each bromeliad species. We used structural equation modeling to assess direct and indirect associations of each bromeliad species cover with environmental conditions, abundance of conspecifics in the vicinity, and local abundance of the other species. *A. distichantha* cover increased on elevated subplots with high tree/shrub basal area, whereas *B. serra* cover showed the opposite pattern. In addition, *A. distichantha* cover was negatively associated with *B. serra* cover, but not vice versa, and cover of both species increased with the abundance of nearby conspecifics, suggesting that limited vegetative dispersal partly accounted for their distribution. Sectors dominated by *A. distichantha* had lower soil bulk density and higher organic matter content than those dominated by *B. serra*. According to our model, influences of competition and limited vegetative dispersal reinforce the association between distribution of these bromeliads and environmental heterogeneity of the forest understory.

Keywords Bromeliads · Competition · Heterogeneity · Niche · Understory

J. P. Lewis passed away on 5 December 2012.

I. M. Barberis (✉) · P. S. Torres · G. Magra ·
L. Galetti · J. P. Lewis
Facultad de Ciencias Agrarias, Universidad Nacional de
Rosario, C.C. 14, S2125ZAA Zavalla, Argentina
e-mail: ibarberi@fcagr.unr.edu.ar;
ignaciobarberis@yahoo.com

I. M. Barberis · J. P. Lewis
CONICET, Buenos Aires, Argentina

P. S. Torres
CIUNR, Buenos Aires, Argentina

W. B. Batista
IFEVA, CONICET and Facultad de Agronomía,
Universidad de Buenos Aires, Av. San Martín 4453,
C1417DSQ Buenos Aires, Argentina

Introduction

Spatial distribution of plant species in forest understories is often patchy (Beatty 1984; Karst et al. 2005; Royo and Carson 2006; Jones et al. 2008). Such a pattern may be controlled, at least partly, by

differential adaptations and tolerances of plant species to the components of an environmental mosaic (Givnish 1999; Royo and Carson 2006; Aiba et al. 2012; Kern et al. 2012). Both canopy trees and fine-scale soil heterogeneity produce spatial heterogeneity in light, water, and nutrient availability, and may influence local regimes of disturbances, such as mechanical damage, fire, flooding, and animal activity, that affect understory plants (Fine et al. 2004; Wyatt and Silman 2004; Jones et al. 2006; Burton et al. 2011). For example, pulses of waterlogging and drought may change over space as a result of runoff and infiltration patterns associated with microrelief and with rainfall interception and water uptake by trees (Beatty 1984; Tuomisto et al. 2003; Gilbert and Lechowicz 2004; Tuomisto 2006; Zuquim et al. 2009). The distribution of canopy trees also results in spatial patterns of light incidence and nutrient input via litter falling onto the understory (Thomsen et al. 2005; Barbier et al. 2008; Burton et al. 2011). The resulting environmental heterogeneity may segregate plant species with different life-history traits into different micro-environments within the forest understory (Skillman et al. 1999; Grubb et al. 2008; Swenson 2009). In addition, the patchy distribution of plant species in forest understories may be reinforced by limited seed production and dispersal, by spatially-limited vegetative dispersal of understory plants, and by competitive interactions among understory species (Hubbell 2001; Royo and Carson 2006; Wang et al. 2012).

Forests dominated by *S. balansae* Engl. occupy extended plains in the eastern South American Chaco, a humid temperate-to-warm region with mean annual temperature around 20 °C and annual rainfall about 1,000 mm (Lewis 1991). These forests occur on locally undulated allomorphic soils with low hydraulic conductivity frequently subjected to patchy waterlogging and drought (Espino et al. 1983). The marked soil microrelief is the result of abiotic factors like pseudo-karstic processes and wind deflation in past times that produced depressions and wind-borne and hydraulic accumulation processes that produced convex microrelief, as well as biotic factors like vegetation- soil and animal-soil interactions (e.g. the formation and collapse of huge ant nests of *Atta wollewonderii*) (Lewis 1991). The canopy of these forests exhibits a marked spatial heterogeneity associated with soil microrelief, as relatively elevated patches that cover

about 10 % of the area in the study site and ranged in area from 5 to 1,000 m^2, have higher tree and shrub densities than level and concave patches (Lewis 1991; Barberis et al. 1998; Barberis et al. 2002). This heterogeneity is likely to affect resource input to the understory; under the denser canopy associated with relatively elevated patches, light incidence and rainfall are expected to be lower, and litter fall is expected to be more abundant, than under the relatively open canopy associated with level and concave patches (Carnevale and Lewis 2001; Cavallero et al. 2009; Montero et al. 2010). A conspicuous feature of *S. balansae*-dominated forests is the occurrence of dense understory colonies of two bromeliad species, *Aechmea distichantha* Lem. and *Bromelia serra* Griseb. (Lewis 1991; Barberis et al. 2002). These bromeliads are largely restricted to relatively elevated patches, but apparently differ in their fine-scale patterns of local cover, and tend to be spatially segregated within each patch (c.f. Barberis et al. 1998; Barberis and Lewis 2005).

Aechmea distichantha and *Bromelia serra* differ markedly in a number of ecophysiological characteristics. *A. distichantha* plants may live as terrestrial or epiphytic, have a well-developed phytotelma, or tank formed by foliar bases with absorptive trichomes, and roots limited mostly to a mechanical function (i.e. a Type III bromeliad sensu Benzing 2000). The tank, which may accumulate up to 2.5 l of water, is colonized by a diverse assemblage of arthropods that feed on captured litterfall (Cavallero et al. 2009; Montero et al. 2010). In contrast, *B. serra* plants are exclusively terrestrial with weakly developed phytotelma and relatively unspecialized trichomes on leaf bases. *B. serra* individuals have roots adapted for water and nutrient absorption from the soil, and occasionally grow apogeotropic roots able to uptake resources from leaf bases (i.e. a Type II bromeliad sensu Benzing 2000). As a result of their traits, these bromeliads are likely to differ in their patterns of resource acquisition (Smith and Downs 1979). *A. distichantha* plants would absorb most water and nutrients via specialized trichomes from their tanks, thus depending mainly from local rainfall and litterfall for acquisition of these resources, whereas *B. serra* plants would uptake these resources mainly from the soil and therefore depend on patterns of soil spatial heterogeneity and dynamics. In addition, these bromeliad species also differ in their strategies of clonal

growth (Smith and Downs 1979). *A. distichantha* plants produce short rhizomes adapted for a conservative strategy of consolidation of acquired space, whereas *B. serra* plants grow long rhizomes which would allow them to develop a relatively opportunistic strategy of colonization of new sites. Some studies have analyzed the frequency of occurrence, life form, geographical distribution, and habitat specificity of different bromeliad types growing in the overstory and understory of several ecoregions of Bolivia (Acebey et al. 2006, 2010). However, to our knowledge no study has yet evaluated to what extent the contrasting adaptations of different bromeliad types correlate with differences in their spatial distribution at a local scale in the understory of Neotropical forests.

The spatial distribution of *A. distichantha* and *B. serra* in the understory of *S. balansae*-dominated forests could be associated with (1) the spatial heterogeneity of resource input (light, water, and nutrients), (2) the ways these species capture resources, (3) the growth habits whereby these species colonize the forest floor, and (4) the interactions between individuals of both bromeliad species (e.g. competition). As these two bromeliads belong to different ecophysiological groups, we hypothesize that environmental heterogeneity associated with local topography and patterns of woody plant cover, proximity to bromeliad colonized areas, and competition between these species may affect their distributions differently (Fig. 1). These factors have been observed to directly or indirectly affect the spatial distribution of bromeliad species (Freitas et al. 1998; Benzing 2000; Cogliatti-Carvalho and Rocha 2001; Sampaio et al. 2002, 2004, 2005; Scarano et al. 2002; Ticktin 2003; Medina et al. 2006). In this paper, we report on a study aimed at assessing direct and indirect influences on the spatial distribution of *A. distichantha* and *B. serra* in the understory of a *S. balansae*-dominated forest in Argentina. We constructed detailed maps of the overstory and understory of forest patches located at relatively higher elevation where these species occur, and used them to examine the correlations between the cover of these bromeliad species and descriptors of local topography and forest cover (Fig. 1). We tested hypotheses about these correlations using structural equation modeling (Pugesek et al. 2003; Grace et al. 2010; Lam and Maguire 2012). Finally, we assessed whether there were differences in soil characteristics between sectors dominated by each bromeliad species.
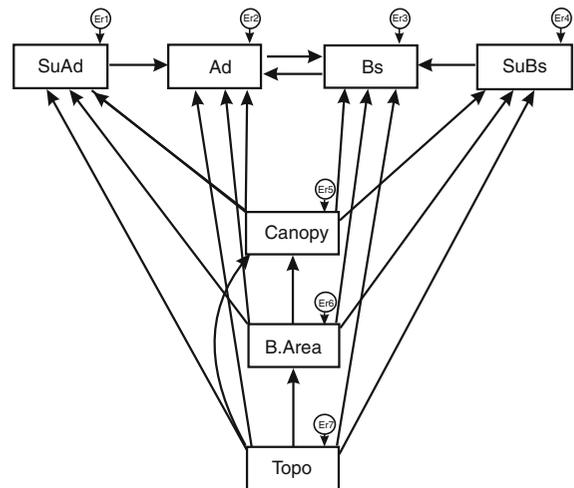
Fig. 1 Proposed structural equation model to explain the plant cover of each bromeliad species. *Er* is the error for each measured variable. *Ad A. distichantha* cover (%), *Bs B. serra* cover (%), *SuAd* surrounding *A. distichantha* cover (%), *SuBs* surrounding *B. serra* cover (%), *Canopy* cover of woody plants above 1.0 m, B. Area = summed basal area of woody plants (dm^2), Topo = relative elevation (cm)

Methods

Study area

The study was conducted in a 400-ha stand of *S. balansae* forest type (*'quebrachal'*; Lewis et al. 1997) located at Las Gamas, Santa Fe, Argentina (Estación Experimental Tito Livio Coppa, 29°28′S, 60°28′W, 58 m a.s.l.). In this forest, most woody species have small deciduous leaves and spiny structures (Lewis et al. 1997). The climate is humid temperate to warm, with a mean annual temperature of about 20 °C, and a mean annual precipitation of about 1,000 mm. Rainfall is concentrated in summer (December–March), and a dry season of variable length occurs in winter (June–August). The forest is located on a mosaic of soils with low hydraulic conductivity and high sodium content (Espino et al. 1983); soil surface has a noticeable microrelief comprising elevation differences of up to 50 cm over distances of a few meters (Barberis et al. 1998). Relatively elevated patches range in area from 5 to 1,000 m^2 and cover about 10 % of the area in the study site (Barberis et al. 1998). On these relatively elevated patches, both *A. distichantha* and *B. serra* occur as terrestrial understory plants (Lewis 1991; Barberis et al. 2002). Individuals of these two species exhibit plastic phenotype changes

when growing under different light conditions (Cavallero et al. 2009, 2011). Although these species may propagate both sexually and asexually (Smith and Downs 1979; Bianchi et al. 2000; Scrok and Varassin 2011; Klekailo et al. 2012), asexual reproduction appears to be predominant in this and other forests (Benzing 2000; Barberis IM, pers. obs.). Peccaries or feral pigs may dislodge and eat the rhizomes of bromeliad species (Ticktin 2003), but this kind of disturbance is not common in the study area (Barberis IM, pers. obs.).

Data acquisition

Within a 70 ha field located in the study area, we selected 16 relatively elevated patches based on their size (larger than 400 m^2) and on the presence of terrestrial bromeliads in the understory. These independent patches were separated from each other by distances ranging from 40 to 700 m. In each selected patch, we established a 20×20-m plot with 100 2×2 m subplots (1,600 subplots in total). Within each subplot, we visually estimated the proportion of surface covered by each bromeliad species (A. distichantha and B. serra). In addition, we measured the soil elevation at the four corners of each subplot with an automatic compensation optic level (NI 050, Carl Zeiss, Jena, Germany), and we calculated the average soil elevation of each subplot. We also recorded the diameter at 20 cm height of all shrubs with stems >1 cm and the diameter at breast height of all trees >5 cm, and used these data to calculate the summed basal area of woody plants within each subplot; tree basal area accounted for almost 85 % of the summed basal area. Finally, we estimated the overall cover of woody plants above 1.0 m in each subplot using a visual scale from 1 (open canopy), 2 (large gaps), 3 (small gaps), 4 (complete cover by trees) to 5 (complete cover by large trees and evergreen shrubs).

From each plot, we selected four sectors at least 3 m apart with high bromeliad cover (>50 %) for each bromeliad species. From each sector, we took three small soil samples (6 cm in diameter and 5 cm in depth) for the soil chemical variables (i.e. pH, organic matter, phosphorus, and conductivity). For each plot, we got a composite sample for each bromeliad species by mixing its twelve small soil samples (i.e. three small samples/sectors × four sectors). These soil samples were air-dried and sieved through a 2-mm

sieve. We measured pH, organic matter (Walkley and Black method), extractable phosphorus (Bray and Kurtz 1), and conductivity (Page 1982). From each sector, we also took one large soil sample (17 cm in diameter and 10 cm in depth) for estimating bulk density through the cylinder method (Klute 1986). Finally, we randomly selected five of the 16 plots, and used the composite samples for each bromeliad species to determine soil texture by the pipette method (Miller and Miller 1987).

Data analysis

We first summarized our data by computing the frequency distributions of estimated cover of A. distichantha and B. serra, as well as those of relative elevation, summed basal area of woody species and cover of woody species among all 1,600 subplots. We compared the mean cover between bromeliad species by means of a paired-observation Z test.

We fitted a structural equation model to our data to analyze apparent direct and indirect influences of environmental heterogeneity, limited dispersal, and interactions between bromeliad species on the estimated cover of A. distichantha and B. serra (Pugesek et al. 2003). In the model, these apparent influences were estimated as path coefficients (i.e. standardized partial regression coefficients) and represented by arrows of a path diagram connecting the included variables (Fig. 1). Direct influences are estimated by the standardized coefficients associated with each single-headed arrow linking two variables in a path diagram, whereas when one or more intermediary variables exist between two other variables indirect influences are estimated as the product of the intermediate standardized coefficients (Pugesek et al. 2003). Environmental heterogeneity entered in our structural equation model as the apparent influences of topography (i.e. relative elevation) on the cover of our target bromeliads in the 4 m^2 subplots; these influences could be either "direct" (i.e. through associated substrate properties) or mediated by patterns of woody species abundance (woody basal area and woody cover) which are known to control the light environment, air moisture and litterfall in the understory (Carnevale and Lewis 2001; Cogliatti-Carvalho and Rocha 2001; Barberis et al. 2002; Scarano et al. 2002; Medina et al. 2006). We assumed that biotic influences like pests, pathogens or herbivores affecting the

distribution of other plant groups, have negligible influence on bromeliads (Benzing 2000; Grubb et al. 2008). Limited dispersal entered in our model as the estimated influence of the mean cover of each bromeliad in the surrounding subplots on its cover in each target subplot. Interactions between our target bromeliads entered in the model as the estimated apparent direct influences of each species' cover on the cover of the other one within subplots.

The structural equation model was fitted to reflect the nesting structure of the data (i.e. 100 subplots nested within each plot), by adjusting the standard errors and scaling the model Chi square statistic (Lam and Maguire 2012). Data were log transformed (i.e. log x + 1) to conform to normality. As the proposed model was non-recursive (i.e. there was a path from *A. distichantha* to *B. serra* and back), we used a stability index to check for the instability that may emerge due to the existence of feedback loops. We assessed model goodness of fit with a χ^2 test comparing the variance–covariance structure implied by the model with the variance–covariance structure of the data (Pugesek et al. 2003). Finally, we further evaluated the proposed model using two other fit measures, which balance objective-simplicity and goodness of fit, the parsimony ratio and the Root Mean Square Error of Approximation (RMSEA). The parsimony ratio expresses the number of degrees of freedom of the model being evaluated as a fraction of the number of degrees of freedom of the independence model. The RMSEA measures the degree of misspecification per model degree of freedom, adjusted for sample size; it should be close to 0 for correct models (Lam and Maguire 2012). For each bromeliad species cover, we used the path coefficients to partition the estimated overall influence of each variable into direct and indirect components. Because the subplots were regularly distributed within each of the 16 plots, we evaluated the spatial independence of errors in the estimated cover values of *A. distichantha* and *B. serra* by means of Mantel tests of the correlations between spatial distances and differences between residuals within each of the 16 grids (Quinn and Keough 2002). The *p* values from the Mantel tests conducted for each bromeliad species were adjusted by the Dunn-Sidak method to control for multiple testing (*p adj* = 1 − $(1 − p)^{16}$, Quinn and Keough 2002). The structural equation modelling was carried out with Linear Structural Relations software (LISREL 8.8; Jöreskog

and Sörbom 2006), and the Mantel tests were carried out with PC-Ord (Version 6.0; McCune and Mefford 2011).

The proposed model converged to an admissible solution, but the resulting fit was poor (scaled-χ^2 = 6.00, *df* = 2, *p* = 0.05), and the RMSEA was 0.035 with 95 % confidence interval between 0.00037 and 0.069. The statistical package (LISREL) suggested setting a covariance path between errors of SuAd and SuBs. We accepted this suggestion because these variables were measured using same method (Schumacker and Lomax 2010). As the direct effects of SuAd on Ad and of SuBs on Bs were similar in the first model (0.92 and 0.86, respectively), we set them equal in order to gain one degree of freedom.

Differences in soil bulk density between sectors dominated by each bromeliad species were analysed using a completely randomized block design, whereas differences in the other soil variables were analysed with a Student's paired *t* test (Quinn and Keough 2002). The tests were carried out with the R statistical package (The R Foundation for Statistical Computing, ver. R 2.9.0).

Results

Either or both of the bromeliads were recorded in most subplots. The two species appeared together in 61.4 % of our subplots. However, *B. serra* was more frequent than *A. distichantha* as it appeared as the only bromeliad in an additional 35.1 % of the subplots, whereas *A. distichantha* did so in only 2.6 % of the subplots. Mean bromeliad cover of both species was low but showed a wide variation (Fig. 2a). Overall mean estimated cover was not significantly different between *A. distichantha* and *B. serra* (7.30 ± 10.91 % SD and 7.68 % ± 7.38 % SD, respectively; *p* = 0.259). However, local cover of *A. distichantha* in the subplots where this species was present was substantially shifted to higher values than those attained locally by *B. serra* (Fig. 2b). There was also a high variation in relative elevation between subplots (range about 70 cm wide). Subplots also varied widely in summed woody basal area (mean = 118 cm^2; range = 0–2,827 cm^2), and in cover of woody plants (median = 3; range = 1–5).

The estimated correlation coefficients between variables included in our structural equation model
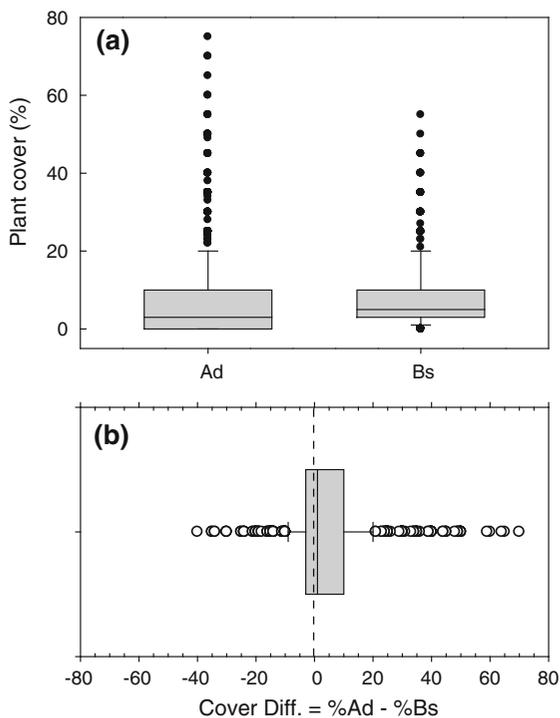
Fig. 2 *Boxplots* of (**a**) plant cover of *A. distichantha* (Ad) and *B. serra* (Bs) for all 1,600 subplots, and (**b**) paired-differences in plant cover on each subplot between *A. distichantha* (Ad) and *B. serra* (Bs) on subplots where both species were present (i.e. Cover difference = Ad cover–Bs cover; N = 1,024). The *boxplot* includes the 25th percentile, the median, and the 75th percentile. Whiskers (*error bars*) above and below the *box* indicate the 90 and 10th percentiles

were not high, but differed significantly from zero in 16 out of 21 cases (Table 1). The modified structural equation model fitted our data well (Fig. 3; scaled-$\chi^2 = 1.472$, $df = 2$, $p = 0.479$); the parsimony ratio was low (0.095), but the model was stable (Stability index = 0.820) and showed adequate RMSEA (0.026 with 95 % CI between 0 and 0.045). In addition, the error covariance for SuAd and SuBs was also significant at a 5 % level of significance. The model explained 41 % of the variance of *A. distichantha* cover data, and 33 % of the variance of *B. serra* cover data. According to the Mantel tests, correlations between distance and differences between the path-analysis residuals were not significant in any of the 16 grids for *A. distichantha* and for *B. serra* ("Appendix").

According to the estimated path coefficients, basal area per 4 m^2 subplot increased significantly with subplot relative elevation, and cover of woody plants

increased significantly with basal area (Fig. 3). Our two target bromeliads, in turn, exhibited contrasting patterns of apparent influences of the environmental conditions in the understory. *A. distichantha* cover exhibited significant positive direct associations with subplot elevation and with woody-plant basal area (Fig. 3). In contrast, cover of *B. serra* exhibited significant negative direct associations with subplot basal area and cover of woody plants (Fig. 3). In addition, the path coefficients were consistent with the notion that the characteristics of the understory environment also affect the cover of the bromeliad species indirectly, via the availability of ramets from the neighborhood of each subplot. For both species, cover was significantly and positively associated with the mean cover of conspecifics in the neighborhood (Fig. 3); these were the strongest direct associations identified by our model, accounting for 77.4 % of the direct apparent effects on *A. distichantha* cover and 81.1 % on *B. serra* cover. However, the mean cover of *A. distichantha* surrounding each subplot decreased with elevation and increased significantly with both its basal area and cover of woody plants, while the mean cover of surrounding *B. serra* decreased significantly with elevation and woody cover of the target subplot (Fig. 3). Finally, estimated path coefficients indicate that local cover of *B. serra* had a significant negative apparent influence on the cover of *A. distichantha* but not vice versa. Overall, the estimated indirect associations reinforce the contrast between the apparent direct influences of the characteristics of the understory environment on the cover of the two bromeliads (Table 2).

Sectors dominated by *A. distichantha* had lower bulk density and greater organic matter content than sectors dominated by *B. serra* (Fig. 4). However, there were no significant differences between bromeliad species with regard to conductivity, pH or phosphorus (Fig. 4). There were differences in soil texture between sectors dominated by each bromeliad species, where sectors dominated by *A. distichantha* had lower clay and slightly higher silt content than sectors dominated by *B. serra* (Fig. 4).

Discussion

Stands of the *S. balansae* forest type are composed of relatively elevated patches, sustaining high density of

Table 1 Correlation coefficients between the variables included in the structural equation model

	ln Topo	ln B. area	ln Canopy	ln SuBs	ln SuAd	ln Bs
ln B. area	**0.096**					
ln Canopy	**0.074**	**0.120**				
ln SuBs	**−0.062**	0.002	**−0.265**			
ln SuAd	−0.020	**0.088**	**0.193**	−0.016		
ln Bs	−0.026	**−0.064**	**−0.193**	**0.558**	−0.043	
ln Ad	**0.129**	**0.114**	**0.151**	−0.054	**0.642**	**−0.099**

Bold numbers denote significant correlation values ($p < 0.05$). *Ad A. distichantha* cover, *Bs B. serra* cover, *SuAd* surrounding *A. distichantha* cover, *SuBs* surrounding *B. serra* cover, canopy = cover of woody plants above 1.0 m, B. area = summed basal area of woody plants, Topo = relative elevation
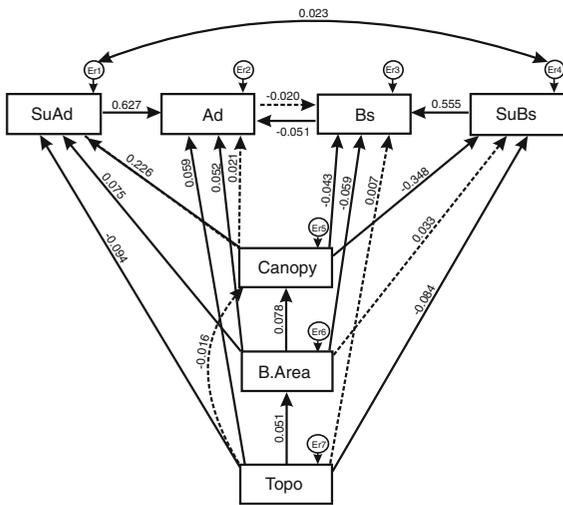
Fig. 3 Structural equation model results. Standardized path coefficients are shown in the figure. All variables were log-transformed. Paths that were not significant ($p \geq 0.10$) are indicated by *dotted arrows*. *Double-headed arrow* denotes covariance path between errors. *Er* error variable. *Ad A. distichantha* cover, *Bs B. serra* cover, *SuAd* surrounding *A. distichantha* cover, *SuBs* surrounding *B. serra* cover, canopy = cover of woody plants above 1.0 m, B. Area = summed basal area of woody plants, Topo = Relative elevation

Table 2 The direct and indirect effects of explanatory variables on plant cover of each bromeliad species

Dependent variables	Explanatory variables	Direct (d)	Effects Indirect (i)	Total (e = d + i)
ln Ad	ln Topo	**0.059**	−0.054	0.005
	ln B. area	**0.052**	**0.063**	**0.115**
	ln Canopy	0.021	**0.154**	**0.175**
	ln SuBs	0.000	−0.028	−0.028
	ln SuAd	**0.627**	0.001	**0.628**
	ln Bs	**−0.051**	0.000	**−0.051**
ln Bs	ln Topo	0.007	**−0.046**	−0.039
	ln B. area	**−0.059**	−0.002	**−0.061**
	ln Canopy	**−0.043**	**−0.197**	**−0.240**
	ln SuBs	**0.555**	0.001	**0.556**
	ln SuAd	0.000	−0.013	−0.013
	ln Ad	−0.020	0.000	−0.020

Direct effects are the standardized path coefficients linking two variables. Indirect effects are the product of intermediate standardized path coefficients. Bold numbers denote significant values ($p < 0.05$). *Ad A. distichantha* cover, *Bs B. serra* cover, *SuAd* surrounding *A. distichantha* cover, *SuBs* surrounding *B. serra* cover, canopy = overall = cover of woody plants above 1.0 m, B. area = Summed basal area of woody plants, Topo = relative elevation

trees and shrubs, and relatively depressed patches, sustaining mostly scattered trees (Lewis 1991; Lewis et al. 1997; Barberis et al. 2002). The present analysis shows that a similar pattern occurs at a finer spatial scale within these relatively elevated patches, as both woody overstory and the summed basal area of woody species were found to be positively correlated with local elevation. Environmental conditions in the understory are likely to vary with elevation. In relatively elevated areas, soil moisture is expected to remain low as a consequence of runoff, rainfall interception by the woody canopy, and tree water consumption (Barbier et al. 2008; Godefroid and Koedam 2010). In addition, because of a denser woody canopy, elevated areas tend to be shadier and cooler inducing decreased atmospheric demand for understory plants.

A regional study that analyzed bromeliad distribution in different ecoregions of Bolivia, showed that *A. distichantha* and *Bromelia serra* were recorded in
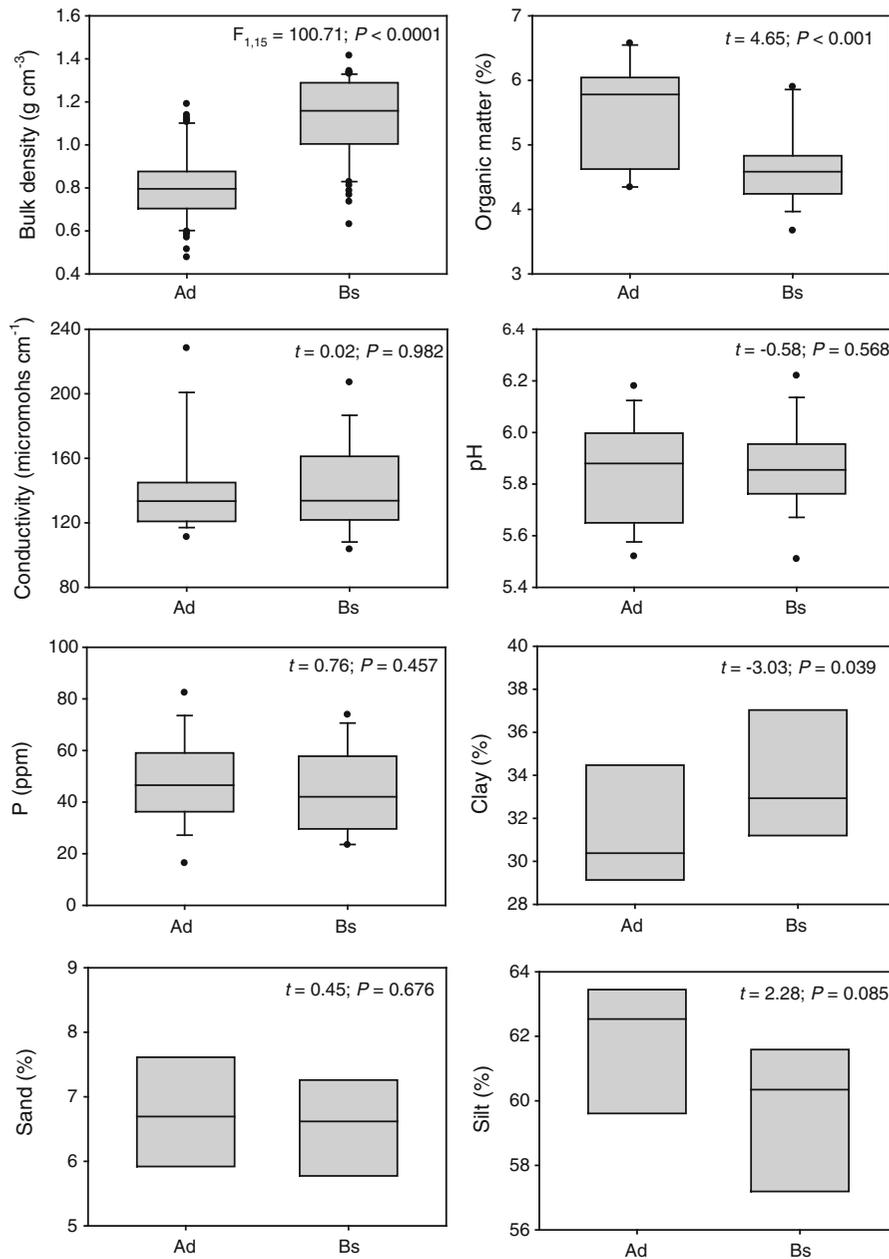
Fig. 4 *Boxplots* of different edaphic variables for sectors dominated by *A. distichantha* (Ad) and *B. serra* (Bs). F and paired-t statistic values and the associated probability are shown

many sites but with low cover (Acebey et al. 2006, 2010). However, they mentioned that these bromeliads may attain very high local cover (i.e. 60 %) in some sites (Acebey et al. 2006, 2010). In our study, which was carried out a local scale in the understory of *S. balansae* forests, the two bromeliad species showed contrasting patterns of spatial distribution. We found

A. distichantha plants selectively distributed to a moderate number of subplots where they often attain high cover; these subplots tended to be elevated, have high woody basal area, low bulk density and high organic matter. In contrast, *B. serra* plants were more widely scattered and tended to have decreased cover in subplots with high basal area and cover of woody

plants, a pattern reflecting indirect influences of local elevation. Partial segregation of *A. distichantha* and *B. serra* in the understory space may be explained, at least in part, in terms of environmental heterogeneity and of expected differences between these two bromeliads in the patterns of resource uptake and vegetative dispersal.

Aechmea distichantha plants acquire most water and nutrients from their phytotelmata (tanks) rather than absorbing them from the soil. This would allow this species to become more abundant in the understory areas where the relatively elevated soil tends to remain dry and trees provide abundant litterfall to the phytotelma (cf. Barberis et al. 2002). Where the woody canopy is dense, and thus light in the understory is limiting but atmospheric demand is low, *A. distichantha* plants develop long, narrow, thin leaves which might have increased light interception efficiency (Cavallero et al. 2011). In contrast, where the woody cover is sparse and thus light is less limiting but evaporation in the understory is more intense, they develop wide leaves forming a tank able to store increased amounts of water (Cavallero et al. 2009, 2011). According to our results, cover of this species would be limited by the competition with *B. serra* (presumably for space) in areas where the two species come into contact. It is likely that this pattern may emerge from differences in competitive ability between Type II and Type III bromeliads, but this topic is in need of further research. In addition, our path analysis indicated that the patchy distribution of *A. distichantha* plants in the forest understory is strongly reinforced by their very limited spread through short rhizomes (Smith and Downs 1979). As a result of this pattern of vegetative reproduction, *A. distichantha* ramets would rarely establish away from areas already colonized but rather tend to form solid colonies in situ.

Bromelia serra plants depend mostly on the soil for water and nutrient supply. This would explain the decreased cover of this species in the most elevated areas with high woody basal area, as the soil there is loose and very dry, presumably limiting the establishment or the survival of *B. serra* ramets. The scarcity of soil resources for these plants in elevated areas might be extreme where the density of shrubs is high, as

association patterns observed in the *S. balansae* forest suggested that bromeliads compete more intensely with shrubs than with trees (Barberis et al. 2002). As areas with low woody basal area and canopy cover tend to be locally depressed and frequently flooded, increased cover of *B. serra* within them would depend on the extensive root system and long rhizomes anchoring these plants firmly to the soil (Barberis, pers. obs.). *B. serra* plants propagate by long rhizomes which grow horizontally below the soil surface forming large ramet systems (Smith and Downs 1979). According to our path analysis, this vegetative dispersal, though not as spatially limited as for *A. distichantha*, partly accounts for the spatial distribution of *B. serra* reinforcing the patterns of association of this species with environmental conditions.

Our study shows how these two bromeliads partition the understory space within relatively elevated patches of the *S. balansae* forest. The observed patterns of partial segregation of these two species to different environmental scenarios in the forest understory are consistent with the notion that niche differences and local environmental heterogeneity are major controls of their distributions (Jones et al. 2006; Aiba et al. 2012; Kern et al. 2012). Within the boundaries established by the spatially varying environmental conditions, direct competition for space and limited dispersal account for the fine-scale distribution of these two bromeliad species over the forest understory (Hubbell 2001; Karst et al. 2005; Jones et al. 2006; Burton et al. 2011).

Appendix

See Table 3.

Table 3 Standardized mantel correlation coefficients and associated Dunn-Sidak adjusted *p* values for the correlation between a matrix of residual differences and a matrix of spatial distances for *Aechmea distichantha* (Ad) and *Bromelia serra* (Bs) on each relatively elevated area

Grid	Ad		Bs	
	r	p adj	r	p adj
1	−0.028	0.873	−0.026	0.898
2	−0.001	0.999	−0.044	0.264
3	0.033	0.609	−0.036	0.415
4	0.001	0.999	−0.014	0.989
5	0.040	0.396	0.035	0.763
6	0.048	0.322	0.023	0.954
7	0.050	0.311	−0.006	0.999
8	−0.002	0.999	−0.023	0.948
9	−0.042	0.529	0.007	0.999
10	−0.031	0.653	−0.004	0.999
11	−0.031	0.713	0.002	0.999
12	−0.021	0.868	−0.017	0.979
13	0.018	0.954	−0.004	0.999
14	0.002	0.999	−0.039	0.462
15	−0.024	0.924	−0.010	0.998
16	−0.001	0.999	0.043	0.396

References

Acebey A, Kessler M, Maass B, Krömer T (2006) Aráceas y bromeliáceas de Bolivia. In: Moraes M, Øllgaard B, Kvist LP, Borchsenius F, Balslev H (eds) Botánica económica de los Andes Centrales. Universidad Mayor de San Andrés, La Paz, pp 434–448

Acebey A, Krömer T, Maass B, Kessler M (2010) Ecoregional distribution of potentially useful species of Araceae and Bromeliaceae as non-timber forest products in Bolivia. Biodivers Conserv 19:2553–2564

Aiba M, Takafumi H, Hiura T (2012) Interspecific differences in determinants of plant species distribution and the relationships with functional traits. J Ecol 100:950–957

Barberis IM, Lewis JP (2005) Heterogeneity of terrestrial bromeliad colonies and regeneration of *Acacia praecox* (Fabaceae) in a humid-subtropical-Chaco forest, Argentina. Rev Biol Trop 53:377–385

Barberis IM, Pire EF, Lewis JP (1998) Spatial heterogeneity and woody species distribution in a *Schinopsis balansae* (Anacardiaceae) forest of the Southern Chaco, Argentina. Rev Biol Trop 46:515–524

Barberis IM, Batista WB, Pire EF, Lewis JP, León RJC (2002) Woody population distribution and environmental heterogeneity in a Chaco forest, Argentina. J Veg Sci 13:607–614

Barbier S, Gosselin F, Balandier P (2008) Influence of tree species on understory vegetation diversity and mechanisms involved—a critical review for temperate and boreal forests. For Ecol Manag 254:1–15

Beatty SW (1984) Influence of microtopography and canopy species on spatial patterns of forest understory plants. Ecology 65:1406–1419

Benzing DH (2000) Bromeliaceae. Profile of an Adaptive Radiation. Cambridge University Press, Cambridge

Bianchi MB, Gibbs PE, Prado DE, Vesprini JL (2000) Studies on the breeding systems of understorey species of a Chaco woodland in NE Argentina. Flora 195:339–348

Burton JI, Mladenoff DJ, Clayton MK, Forrester JA (2011) The roles of environmental filtering and colonization in the fine-scale spatial patterning of ground-layer plant communities in north temperate deciduous forests. J Ecol 99:764–776

Carnevale NJ, Lewis JP (2001) Litterfall and organic matter decomposition in a seasonal forest of the eastern Chaco (Argentina). Rev Biol Trop 49:203–212

Cavallero L, López D, Barberis IM (2009) Morphological variation of *Aechmea distichantha* (Bromeliaceae) in a Chaco forest: habitat and size-related effects. Plant Biol 11:379–391

Cavallero L, Galetti L, López D, McCargo J, Barberis IM (2011) Morphological variation of the leaves of *Aechmea distichantha* Lem. plants from contrasting habitats of a Chaco forest: a trade-off between leaf area and mechanical support. Rev Bras Biociências 9:455–464

Cogliatti-Carvalho L, Rocha CFD (2001) Spatial distribution and preferential substrate of *Neoregelia johannis* (Carriére) L.B. Smith (Bromeliaceae) in a disturbed area of Atlantic Rainforest at Ilha Grande, RJ, Brazil. Rev Bras Bot 24:389–394

Espino LM, Seveso MA, Sabatier MA (1983) Mapa de suelos de la provincia de Santa Fe vol II. MAGSF and INTA EERA Rafaela

Fine PVA, Mesones I, Coley PD (2004) Herbivores promote habitat specialization by trees in Amazonian forests. Science 305:663–665

Freitas CA, Scarano FR, Wendt T (1998) Habitat choice in two facultative epiphytes of the genus *Nidularium* (Bromeliaceae). Selbyana 19:236–239

Gilbert B, Lechowicz MJ (2004) Neutrality, niches, and dispersal in a temperate forest understory. Proc Nat Acad Sci 101:7651–7656

Givnish TJ (1999) On the causes of gradients in tropical tree diversity. J Ecol 87:193–210

Godefroid S, Koedam N (2010) Tree-induced soil compaction in forest ecosystems: myth or reality? Eur J For Res 129:209–217

Grace JB, Anderson TM, Olff H, Scheiner SM (2010) On the specification of structural equation models for ecological systems. Ecol Monogr 80:67–87

Grubb PJ, Jackson RV, Barberis IM, Bee JN, Coomes DA, Dominy NJ, De La Fuente MAS, Lucas PW, Metcalfe DJ, Svenning JC, Turner IM, Vargas O (2008) Monocot leaves are eaten less than dicot leaves in tropical lowland rain forests: correlations with toughness and leaf presentation. Ann Bot 101:1379–1389

Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton

Jones M, Tuomisto H, Clark DB, Olivas P (2006) Effects of mesoscale environmental heterogeneity and dispersal limitation on floristic variation in rain forest ferns. J Ecol 94:181–195

Jones M, Tuomisto H, Borcard D, Legendre P, Clark D, Olivas P (2008) Explaining variation in tropical plant community composition: influence of environmental and spatial data quality. Oecologia 155:593–604

Jöreskog KG, Sörbom D (2006) LISREL 8.8 for Windows. Scientific Software International Inc., Lincolnwood

Karst J, Gilbert B, Lechowicz MJ (2005) Fern community assembly: the roles of chance and the environment at local and intermediate scales. Ecology 86:2473–2486

Kern CC, Montgomery RA, Reich PB, Strong TF (2012) Canopy gap size influences niche partitioning of the ground-layer plant community in a northern temperate forest. J Plant Ecol 6:101–112

Klekailo GN, Tuesca D, Barberis IM (2012) Efectos de la temperatura, el ambiente lumínico y la escarificación sobre la germinación de semillas de *Bromelia serra* Griseb. (Bromeliaceae). Rev Bras Sementes 34:605–612

Klute A (1986) Methods of soil analysis, part 1. Physical and Mineralogical Methods. American Society of Agronomy, Madison

Lam TY, Maguire DA (2012) Structural equation modeling: theory and applications in forest management. Int J For Res 2012. doi:10.1155/2012/263953

Lewis JP (1991) Three levels of floristic variation in the forests of Chaco. J Veg Sci 2:125–130

Lewis JP, Pire EF, Barberis IM (1997) Structure, physiognomy and floristic composition of a *Schinopsis balansae* (Anacardiaceae) forest in the Southern Chaco, Argentina. Rev Biol Trop 45:1013c–1020c

McCune B, Mefford MJ (2011) PC-ORD. Multivariate analysis of ecological data. Version 6.0. MjM Software, Gleneden Beach

Medina BMO, Ribeiro KT, Scarano FR (2006) Plant–plant and plant–topography interactions on a rock outcrop at high altitude in Southeastern Brazil. Biotropica 38:27–34

Miller W, Miller D (1987) A micro-pipette method for soil mechanical analysis. Commun Soil Sci Plant Anal 18:1–15

Montero G, Feruglio C, Barberis IM (2010) The phytotelmata and foliage macrofauna assemblages of a bromeliad species in different habitats and seasons. Insect Conserv Divers 3:92–102

Page AL (1982) Methods of soil analysis, part 2. Chemical and microbiological properties. American Society of Agronomy, Madison

Pugesek BH, Tomer A, von Eye A (2003) Structural equation modeling. Applications in ecological and evolutionary biology. Cambridge University Press, Cambridge

Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge

Royo AA, Carson WP (2006) On the formation of dense understorey layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. Can J For Res 36:1345–1362

Sampaio MC, Perissé LE, Oliveira GA, Rios RI (2002) The contrasting clonal architecture of two bromeliads from sandy coastal plains in Brazil. Flora 197:443–451

Sampaio MC, Araújo TF, Scarano FR, Stuefer JF (2004) Directional growth of a clonal bromeliad species in response to spatial habitat heterogeneity. Evol Ecol 18:429–442

Sampaio MC, Picó FX, Scarano FR (2005) Ramet demography of a nurse bromeliad in a Brazilian restingas. Am J Bot 92:674–681

Scarano FR, Duarte HM, Rôças G, Barreto SMB, Amado EF, Reinert F, Wendt T, Mantovani A, Lima HRP, Barros CF (2002) Acclimation or stress symptom? An integrated study of intraspecific variation in the clonal plant *Aechmea bromeliifolia*, a widespread CAM tank-bromeliad. Bot J Linn Soc 140:391–401

Schumacker RE, Lomax RG (2010) A beginner's guide to structural equation modeling. Taylor and Francis Group, New York

Scrok GJ, Varassin IG (2011) Reproductive biology and pollination of *Aechmea distichantha* Lem. (Bromeliaceae). Acta Bot Bras 25:571–576

Skillman JB, García M, Winter K (1999) Whole-plant consequences of crassulacean acid metabolism for a tropical forest understory plant. Ecology 80:1584–1593

Smith LB, Downs RJ (1979) Bromelioideae (Bromeliaceae). Flora Neotropica Monogr 14(3):1493–2142

Swenson NG (2009) Herbaceous monocot plant form and function along a tropical rain-forest light gradient: a reversal of dicot strategy. J Trop Ecol 25:103–106

Thomsen RP, Svenning JC, Balslev H (2005) Overstorey control of understorey species composition in a near-natural temperate broadleaved forest in Denmark. Plant Ecol 181:113–126

Ticktin T (2003) Relationships between El Niño Southern Oscillation and demographic patterns in a substitute food for collared peccaries in Panama. Biotropica 35:189–197

Tuomisto H (2006) Edaphic niche differentiation among *Polybotrya* ferns in western Amazonia: implications for coexistence and speciation. Ecography 29:273–284

Tuomisto H, Ruokolainen K, Yli-Halla M (2003) Dispersal, environment, and floristic variation of Western Amazonian forests. Science 299:241–244

Wang YJ, Shi XP, Peng Y, Zhong ZC, Tao JP (2012) Effects of fine-scale pattern of dwarf bamboo on understory species diversity in *Abies faxoniana* forest, southwest, China. Sains Malays 41:649–657

Wyatt JL, Silman M (2004) Distance-dependence in two Amazonian palms: effects of spatial and temporal variation in seed predator communities. Oecologia 140:26–35

Zuquim G, Costa F, Prado J, Braga-Neto R (2009) Distribution of pteridophyte communities along environmental gradients in Central Amazonia, Brazil. Biodivers Conserv 18:151–166