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Scale-dependent effects of pines on the herbaceous layer diversity in a semi-arid mediterranean ecosystem

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Abstract: In arid and semi-arid ecosystems, the presence of woody neighbours affects the existence of several herbaceous species by modifying critical aspects of the environment (e.g., soil humidity, nutrient content or light availability) beneath their canopies. Herbaceous species growing in the understory of *Pinus pinaster* may be distinct from those in open areas due to litter fall, light interception and changes in nutrient availability. We suggest that the overall effect of woody neighbours on herbaceous layer diversity may vary with the scale focus of analysis. To examine this hypothesis, we collected data on the abundance of herbaceous species in open pineland forests of the central Iberian Peninsula (Spain) using sample quadrats of 0.5 m × 0.5 m distributed beneath, at the edge, and outside the canopy of pines in a landscape composed of dunes and plains. The results of CCA ordination revealed significant spatial segregation of herbaceous species reflecting the occurrence of pines and dunes in the landscape. Nested ANOVA disclosed markedly lower species richness beneath the pines, particularly in the dune sites. Species richness partitioning showed higher pine-induced heterogeneity than expected from the sample-based randomized model, leading to significantly increased species richness at the patch level. Hence, the outcome of pine-induced effects on the herbaceous plant diversity is scale-dependent, negative if we focus on separate communities, but positive if the scale focus is extended to whole patches comprising the sum of communities beneath, at the edge, and outside pine tree canopies. These results emphasize the necessity of using various scale perspectives to clarify the different ways in which pines and other woody nurse species affect structure of herbaceous communities in semi-arid Mediterranean ecosystems.

Abbreviation: CCA—Canonical Correspondence Analysis.

Introduction

Ecologists consider species interactions as major processes controlling species composition and richness in communities (Cornell and Lawton 1992, Cornell 1999, Huston 1994, 1999). These processes have been analyzed for pairwise interactions (Callaway et al. 1991, Pugnaire et al. 1996, Moro et al. 1997, Callaway and Walker 1997, López-Pintor et al. 2003, Maestre et al. 2005, Callaway 2007). More recently, some ecologists have recognized the scale as a decisive factor in woody species contributing to structuring of herb-rich plant communities (Cavieres and Badano 2009, López et al. 2009). Interestingly, woody species negatively affect the diversity of herbaceous layer if the number of herbaceous species of their understories is lower than that in open habitats. Conversely, woody species may exert positive effects on the herbaceous layer diversity in cases there are more species found below the woody canopy than outside, owing to fertility islands (Pugnaire et al. 1996, Moro et al.

1997, Callaway and Pugnaire 1999, Twexbury and Lloyd 2001, Pugnaire and Lázaro 2000, Ha-Lin Zhao et al. 2007). A net positive balance of woody-herbaceous plant interactions is more likely under stress conditions where positive impacts of nurse individuals affecting higher soil humidity or nutrient availability exceed the negative impacts (e.g., light interception, allelopathic substances, etc.). Net negative balance, in turn, is more likely under more mesic conditions whereby some highly competitive species become dominant (Bertness and Hacker 1994, Bertness and Callaway 1994, Greenlee and Callaway 1996, Brooker and Callaghan 1998, Pugnaire and Luque 2001). However, it is difficult to determine whether woody species determine net positive or negative impacts on herbaceous plant communities since a number of factors (e.g. species physiology, life histories and environmental stress) may have a decisive role driving plants interaction (Tewksbury and Lloyd 2001, Maestre et al 2005, Liancourt et al. 2005, Kawaii and Tokeshi 2007). We suggest that the scale is relevant for better understanding of how

woody species affect the structure and functioning of the associated herbaceous plant communities (Cavieres and Badano 2009), even in cases where negative interactions are apparent. In our opinion, conclusions on the role of woody species structuring herbaceous communities in semi-natural open forest ecosystems would be misinterpreted or incomplete with the use of a single community-focused approach.

Pines constitute a major component of tree flora in the Mediterranean region of the Iberian Peninsula (Costa-Tenorio et al. 1997, Salvador et al. 2000), and have an important impact on the surrounding vegetation (Pausas et al. 2004, González-Alday et al. 2009). In particular, *Pinus pinaster* stands usually support few herbaceous plants in the understory, as reported by González-Alday et al. (2009). Pines may, however, favour the establishment of some exclusive species, leading to local spatial segregation of the herb-rich communities due to soil and micro-climatic variability (Barbier et al. 2008). Accordingly, simultaneous limitation and segregation of herbaceous species in the tree understory may result in a net significant increase in species richness within a single patch (comprising the sum of herbaceous plant species beneath, at the edge, and outside the influence of pines). Whether pines facilitate herbaceous species richness, even if the number of understory herbaceous species is lower than that in open habitats, remains to be established. Even since the initial suggestions (Gutiérrez et al. 1993), this subject has seldom been addressed (see current reports by Cavieres and Badano 2009, and López et al. 2009).

To clarify this issue, we analyzed response of herbaceous species composition and richness to pine trees at two different scales: (1) At the community focus we studied the influence of trees comparing separate communities beneath, at the edge, and outside the influence of pine canopies. (2) At the patch focus we studied the contribution of heterogeneity among communities (pine influence) to whole patch species richness (comprising communities beneath, at the edge and outside the influence of pines).

Materials and methods

Study area

The study area was the Tierra de Pinares Segoviana, a region of North Central Spain (Province of Segovia; 41°22′/41°20′ N – 4°21′/4°13′ W). This area is characterized by a semiarid continental mediterranean-type climate, with an average annual temperature of 11°C and average annual precipitation of 480 mm occurring mainly between November and May (Calonge 1987). The area is located in the Northern Plateau of the Iberian Peninsula at altitude of 850 m, built of Miocene sedimentary basal clays. The region is located over an extensive area where this sedimentary substrate is covered by a thick sandy layer originating from partially dismantled granites of the Sistema Central mountains (Álvarez et al. 1987, Calonge 1987). The poor, sandy, acidic and poorly-structured soils enhance the aridity of these semiarid continental Mediterranean conditions. During the

Quaternary, dominant winds led to partial redistribution of this sandy cover creating dunelands, at several sites surrounded by sandy plains (Termino et al. 1997) (Fig. 1). Currently, fixed dunes have unstructured soils with extremely low organic matter and nutrient content (Álvarez et al. 1993, Termino et al. 1997). However, the surrounding plains in turn contain slightly more humid soil coming from the underground sources. The higher humidity supports soils better supply with water, fosters humification and improves soil structure.

Harsh environmental conditions are well suited to growing *Pinus pinaster* Aiton in form of more or less naturally open forests, stabilized by a traditional sustainable method of exploitation (Calonge 1987). Domestic livestock are traditionally absent, and thus well conserved herbaceous communities are found to occur profusely within this open pineland ecosystem.

Sampling design and data recording

Four homologous 1 ha Patches, ≈2.5 km apart, were selected in the semi-natural open pinelands (two in dune sites and the others in plain sites). Within each patch, we randomly selected 10 small isolated pine groups (4–5 pines), and sampled the herbaceous communities beneath them, at the edge of the group, and in habitats outside the canopy influence. Data on the abundance of herbaceous species (percentage cover of species on the ground) using 10 square quadrats of 0.5 m × 0.5 m. per patch, and position with respect to pine groups, were collected from a total of 120 sampling units. Based on this nested sampling design, we analyzed the influ-

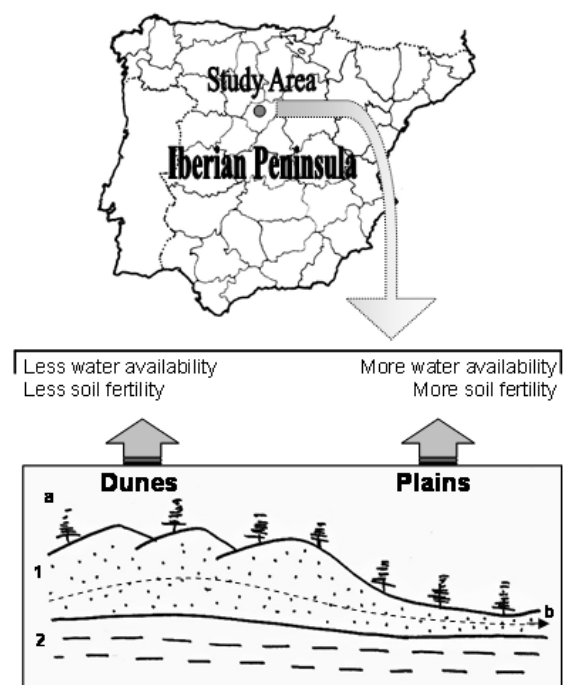


Figure 1. Geographical localization of the study area and short descriptive characterization of the landscape heterogeneity (a-pines, b-water table, 1-sand (Quaternary), 2-clay (Miocene)).

ence of pines on the herbaceous layer considering the *a priori* most important source of landscape variability in the area, soils showing different patterns in dune and plain habitats.

Data analysis

Interactions between pine groups and herbaceous vegetation were assessed in terms of both species composition and richness using a community-focused approach. Canonical Correspondence Analysis was conducted using the species cover \times sampling units matrix, and the environmental variables \times sampling units matrix. Environmental variables were coded as nominal variables (outside/edge/beneath canopy positions on the one hand, and dunes/plains on the other) and plotted next to non-constrained samples scores (SAMP) to clarify the environment-species data relationships. Null model permutations (for the Monte-Carlo test) in CCA were restricted according to data nested structure (Lepš and Šmilauer 2003). CCA was carried out with the computer package CANOCO 4.5 for Windows (ter Braak and Šmilauer 2002).

The effects of pines on herbaceous species richness at the community level (community focus) were analysed using nested ANOVA. Species richness was log-transformed and normality and homogeneity of variance examined with the Shapiro-Wilk test and Levene's test, respectively.

Pine influence on herbaceous layer diversity at the patch level (patch focus) was analyzed using the Additive Partitioning of Species Richness technique with a randomized model for hypothesis testing (Crist et al. 2003). This technique is based on the additive concept of species diversity, and permits simultaneous representation of the contribution of several sources of heterogeneity nested at different spatial scales (Lande 1996, Wagner et al. 2000, Gering et al. 2003). The randomized model (expected model) introduces a pure area-diversity curve (rarefaction curve) where environmental effects are presumably eliminated. Hence, the observed effects of pines can be compared to random distribution of samples (sampled-based randomization; 999 iterations) at this level, and analyzed with the other landscape determinants of species richness, including stress conditions and/or herbaceous species interactions (within a community), distance (within homogeneous landscape conditions) and geomorphological and edaphic heterogeneity (dunes and plains). The alpha levels in this model included sample units (120), community (12), patch (4), homogeneous landscape (2 homologous patches) and heterogeneous landscape (gamma). The beta (heterogeneity) levels were as follows: Beta1 – between samples within communities, Beta2 – between communities within a patch (pine influence), Beta3 – between patches within homogeneous landscape conditions (distance), and Beta4 – between heterogeneous paired patches within the whole landscape (dunes and plains). The observed Alpha2 level (patch level) was separately plotted next to the corresponding Beta2 expected (null model) and Beta2 observed levels. Alpha2-Beta2 (expected) depicts the species richness model in the absence of pine influence whereas Alpha2-Beta2 (observed) shows the species richness model un-

der pine effects. To accept or reject the null hypothesis (H_0 : no differences between expected and observed models), the p -value was computed as the proportion of randomized datasets providing a diversity value greater than the observed value. Thus, a very small p -value (e.g., $p < 0.05$) is indicative of a significantly larger (or higher) observed diversity value. In contrast, a markedly high p -value (e.g., $p > 0.95$) indicates that a large proportion of randomized datasets generates greater diversity (Veech and Crist 2009a). Partitioning of species richness was conducted using PARTITION 3.0 (Veech and Crist 2009b).

Results

Spatial segregation of herbaceous species

The CCA model revealed a first ordination axis (canonical eigenvalue = 0.548; 11.8% of total inertia, $F = 15.517$, $p = 0.001$), which was explained by the effects of pines (*Under*, t -value (regression coefficient) = 20.3771, $p < 0.01$, Fig. 2). *Bromus rigidus* Roth, *Bromus tectorum* L., *Vicia sativa* L., *Lactuca serriola* L. and *Cerastium diffusum* Pers., species (among others) are representatives of below-pine canopy microhabitats. In contrast, *Spergularia purpurea* (Pers.) G. Don f., *Malcolmia triloba* (L.) Spreng., *Corrigiola telephiifolia* Pourret, *Jasione montana* L. or *Mibora minima* (L.) Desv. are more abundant in open sites. Other notable species widely distributed in all habitats include *Alyssum minutum* Schlecht. ex DC., *Vulpia bromoides* (L.) Gray, *Sedum amplexicaule* DC., *Senecio gallicus* Vill. in Chaix, and *Leucanthemopsis pulverulenta* (Lag.) Heywood.

The second ordination axis (canonical eigenvalue = 0.246, 5.3% of total variance, $F_{(\text{all-canonical-axes})} = 9.329$, $p = 0.001$) was significantly explained by dunes (Dunes, t -value (regression coefficient) = 14.7868, $p < 0.01$, Fig. 2). *Linaria*

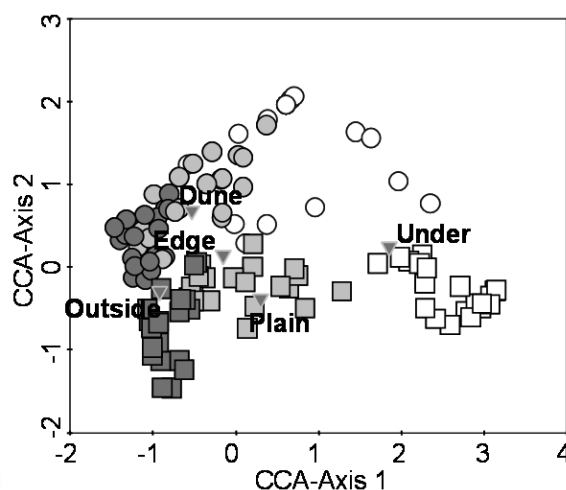


Figure 2. Ordination diagram elaborated with Canonical Correspondence Analysis showing samples outside, at the edge, and beneath pine canopies on one hand (dark grey – outside canopy; light grey – edge canopy; white – beneath canopy), and samples on dunes and plains on the other (circles – dunes; squares – plains).

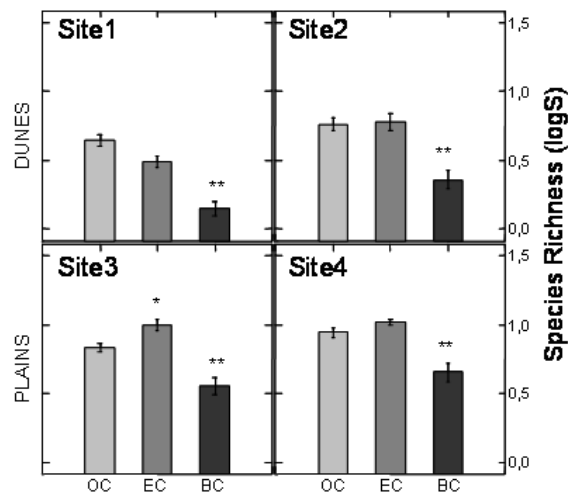


Figure 3. Means \pm s.d. of species richness (log transformed) at each position regarding pine influence (OC-outside canopy; ED-edge canopy; BC-beneath canopy) at individual sites (separate for dunes and plains). Differences are referred to outside canopy category (OC): * significant differences at $p < 0.05$, ** significant differences at $p < 0.01$.

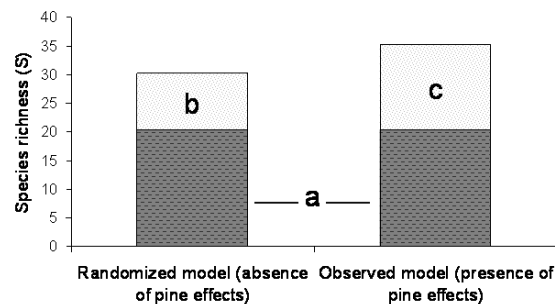


Figure 4. Patch level richness models in the absence (null randomized model) and presence (observed model) of pine effects. For both models, we used Alpha2 (community level) observed in an attempt to replicate the results of real scenarios. a – Alpha2 (observed), b – Beta2 (expected), c – Beta2 (observed). b-c are significantly different at $p = 0.001$.

spartea (L.) Chaz., *Hispidella hispanica* Barnadez ex Lam., *Hordeum murinum* L. and *Micropyrum tenellum* (L.) Link are representative species of dune soils, whereas *Malcolmia triloba* (L.) Spreng., *Trifolium arvense* L., *Lupinus luteus* L. and *Valerianella carinata* Loisel. are more abundant in the plains.

Effects of pines on herbaceous species richness at the community level

Nested ANOVA showed significant effects of pine factors on sample unit species richness (log-transformed) ($F_{(8,108)} = 23.45$; $p < 0.001$). In contrast, neither dune plains nor site factors affected sample unit species richness to a significant extent ($F_{(1,2)} = 7.798$, $p = 0.107$; $F_{(2,8)} = 0.682$; $p = 0.532$, respectively). The log-transformed dependent variable (logS) met normality (Shapiro-Wilk statistic=0.984, $p=0.152$) but not homogeneity of variance (Levene's statis-

tic=2.590; $p < 0.006$). Accordingly, we selected Dunnet's T3 *post hoc* test to distinguish the significant differences associated with pine influence at each site of study. Marked differences in species richness between outside/edge canopy and beneath canopy communities were evident among all four sites of study ($p < 0.01$). Species richness beneath pine canopies was always lower than that outside or at the edge (Fig. 3). Significant differences (at $p < 0.05$) between samples at the edge of and outside pine canopies were only observed in one of the four sites of study (plain).

Effects of pines on herbaceous species richness at the patch level

On average, almost 5 more species occur with the observed Beta2 (15 species) vs. expected Beta2 (10 species) model, which, in conjunction with the number of species of Alpha2 (observed), suggests that species richness in a patch (Alpha3) is notably lower in the absence (randomized model) than the presence of pine effects (observed model) (Fig. 4). The difference between observed herbaceous heterogeneity (Beta2 observed) and that produced by randomization of samples (Beta2 expected) was significant at a p -value of 0.001, i.e., only 0.001% of random combinations of samples exceed the observed species richness values at this level. The observed heterogeneity within a patch (between communities; Beta2) constituted 42% of species richness at the patch level (Alpha3 observed=35 species) and 25.8% of γ (total number, 58 species).

Discussion

The *Pinus pinaster* understory was less species-rich than communities at the edge or outside canopies. Only about half of the herbaceous species inhabit the understory of pines as compared to the edge/open areas. Nested ANOVA model revealed that edge-canopy communities in plain sites are even richer in species than the corresponding communities outside the influence of pine canopies. Thus, slight shading conditions free of high leaf-litter accumulation in not extremely poor sandy soils (such as soils in plains) may facilitate the coexistence of a higher number of herbaceous plants within a 50 cm \times 50 cm quadrat. No significant differences in species richness at the edge and outside pine canopies were observed at the other plain site. Semiarid mediterranean-type climatic conditions often promote positive effects of woody nurse individuals on beneficiary plants (Moro et al. 1997, Pugnaire et al. 2001, López-Pintor et al. 2003). In these cases, facilitation processes are associated with specific ameliorated physical conditions of nurse microhabitats, including moderate temperatures, higher water availability, and more suitable soil properties (Callaway and Pugnaire 1999, Callaway et al. 2000). Positive balance of pine-herbaceous plants interactions at the edge of canopy microhabitats may be explained through slight shading conditions that reduce evaporation stress. The overall effect of nurse woody species on the herbaceous layer usually depends on complex simultaneous combinations of negative and positive interactions

(Callaway 1995). Allelopathy, leaf litter accumulation and root competition underneath pines are important determinants that shift interactions to net negative effects underneath pines (Moir 1966, Callaway and Walker 1997, Birket et al. 2001, Koukoura and Kyriazopoulos 2007, Calvo et al. 2008). Initial attempts to analyze the effects of pine trees on the herbaceous layer led to an assumption that low soil nutrient content, in conjunction with high solar radiation interception, are potentially major determinants for generalized suppression of vegetation in temperate areas (Moir 1966, Gillian and Roberts 2003). A lower number of herbaceous plant species is also reported under increasing density of pines in semi-natural semiarid mediterranean pinelands (Gonzalez-Alday et al. 2009). However, herbaceous plants are not completely absent from pine understories. Certain species can exist and even show a strong preference for, this microhabitat as evident from the significant differences between species composition in the presence and absence of pines. Nurse woody plants facilitate segregation of herbaceous species in semiarid ecosystems of the central Iberian Peninsula through environmental modifications in particular, in solar radiation interception, and distinct soil nutrient and humidity contents (Gutierrez et al. 1993, López-Pintor et al. 2006). In arid and semiarid ecosystems, nurse plants (usually shrubs) understories reportedly support higher numbers of plants (Holzapfel et al. 2006), and occasionally, few but different plants as compared to open habitats (Weedom and Facelli 2008). Herbaceous species with preferences for nurse species understories often exhibit marked functional differences to those inhabiting open sites. The former are usually more shade-tolerant, competitive mesic species whereas the latter are more drought-adapted, shade-intolerant, and less competitive (López-Pintor et al. 2003). Herbaceous species with a preference for pine understories displayed a marked ruderal character in our study. For instance, *Bromus tectorum*, *Bromus rigidus*, *Lactuca serriola* and *Cerastium diffusum* are well-known herbs abundant on highly disturbed and poor (sandy-acidic) soils. Thus, spatial segregation of herbaceous species due to pines in this ecosystem is attributed to factors other than ameliorated environmental conditions under several shrub and tree species in semiarid sites. This suggestion is in direct agreement with findings from temperate pine forest ecosystems, where soils under pine trees are usually poorer in nutrients than those from the understory of other tree species and open sites (Moir 1966).

Pines indirectly affect the pool of species at the patch level through spatial segregation of herbaceous plants. Our results show that heterogeneity generated by pines (observed model) is significantly higher than that expected from the null model, implying that if we eliminate the effects of pines, a lower number of species is generated within a similar sampling area (patch level). A number of authors have already documented this potential effect of nurse species on species diversity (Gutiérrez et al. 1993, Tewksbury and Lloyd 2001), but have not explicitly tested this theory. Recently, Cavieres and Badano (2009) established how the presence of shrub cushions in high altitudinal areas of the Andes induces a sig-

nificantly higher number of herbaceous species at the entire community level (patch level in our study). Similar findings were obtained by López et al. (2009) in a study of shrub-herbaceous species interactions in semiarid Andean subtropics. However, both groups found a higher number of herbaceous species underneath the nurse plants as compared to open area communities. Thus, our data contribute to this novel diversity facilitation hypothesis showing that even when nurse species support a lower number of herbaceous species in their understories, they can generate significantly higher species richness at the patch level simply by inducing environmental changes that facilitate new species. We propose that one of the primary causes explaining our results could be the environmental stress. Facilitation of species richness beneficiaries would increase under more stressful conditions, as noted by Hacker and Gaines (1997). Abiotic stress may significantly limit the number of species in communities outside the influence of nurses, in turn, meaning that new species inhabiting pines understories provide a major contribution to the species pool at the patch level. New evidence to support this theory may be obtained by testing our hypothesis in gradients of environmental stress where nurses determine generalized suppression of the herbaceous species of open areas along the entire environmental gradient.

In conclusion, facilitation of community diversity by nurse species may occur even when they promote direct generalized suppression of most species inhabiting open habitats, particularly in cases where these nurse plants influence the establishment of a diversity of species, and environmental stress limits species pools in open areas. Accordingly, it would be beneficial to employ several-scale approach to determine the outcomes of nurse species-herbaceous community interactions under high-stress conditions, such as found in mediterranean semiarid environments.

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