On the interaction between tree canopy position and environmental effects on soil attributes and plant communities

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Abstract

Questions: Understanding how trees affect their understorey plants and soils is crucial to understand savanna ecosystems. Most studies focus on the differences between canopy and open microsites, but how do different positions within large tree canopies influence soils and plants? Are these potential differences likely to change depending on environmental conditions (i.e. annual rainfall and grazing)?

Location: One hundred sites across a rainfall gradient (220–1400 mm) in NSW, Australia.

Methods: We measured the cover, richness and community composition of understorey plants and 12 soil attributes related to infiltration, erodibility and fertility across three positions within the canopy of large eucalypts (trunk, mid-canopy and edge) and in open areas. We also estimated the percentage similarity in plant communities across microsites, and the percentage species within the landscape occurring solely in one of the four microsites assayed. We tested the interactions between the effect of environmental conditions (rainfall and grazing) and canopy position on all these soil and vegetation attributes.

Results: Soil attributes explained ~50% of the effect of trees on understorey plants, and soil attributes improved with proximity to the trunk and increasing rainfall. The effect of canopy position × rainfall interactions depended on the response variable considered. These interactions did not affect soil attributes, the percentage of facilitation-obligate species or species richness, and weakly affected plant composition. However, we found a strong reduction in similarity among plant communities within edge and mid-canopy compared with open sites towards drier environments, and canopy position × rainfall interactions also significantly affected plant cover. We attribute these weak interactions between canopy position and environmental conditions to richness or the frequency of facilitation to the high turnover of facilitated species across microsites and across different environmental conditions.

Conclusions: Our study can be used to better understand community dynamics in ecosystems with scattered trees by showing the differential effects of trees on their understorey. Our results also contribute to the body of research on the relationships between plant–plant interactions and the environment by illustrating the importance of gradient length and the number of different microsites considered.

Introduction

Trees occupy more than 30% of Earth's land surface and are an important component of dryland ecosystems, such as savannas and woodlands (Weltzin & Coughenour 1990; House et al. 2003; Hirota et al. 2011). Trees have substantial effects on plant communities and soil attributes beneath their canopies by creating markedly different environmental conditions compared with open areas (Jones et al. 1994, 1997; Tewksbury & Lloyd 2001; Oliver et al. 2006; Agra & Ne'eman 2009; Bennett et al. 2009). For example, trees have higher levels of soil water infiltration (Eldridge & Freudenberger 2005) and soil nutrient pools than open areas (Ludwig et al. 2004; Smith et al. 2012). Average radiation and temperature levels are usually lower and less spatially and temporally variable beneath woody canopies than in the open (Segoli et al. 2012). This means that sub-canopy areas are generally cooler and moister than areas away from the canopy (Belsky 1984; Weltzin & Coughenour 1990; Shumway 2000). However, apart from these facilitatory effects on understorey species, trees can also have negative, competitive effects by competing for light, nutrients and soil moisture (Scholes & Archer 1997), intercepting rainfall (Kropfl et al. 2002) or preventing seed germination by creating a dense layer of litter (Facelli & Pickett 1991; Travers & Eldridge 2012). The balance between these facilitative and competitive effects determines the structure and composition of the understorey plant communities (Tewksbury & Lloyd 2001; Cuesta et al. 2010; Dohn et al. 2013).

Interactions between trees and understorey species across environmental gradients have been the subject of considerable interest and study over the past decade (reviewed in Dohn et al. 2013). Recent studies, however, have often produced conflicting results, with a range of positive, negative or neutral relationships found between the strength or frequency of facilitation by trees and precipitation (Callaway et al. 1991; Mordelet & Menaut 1995; Tewksbury & Lloyd 2001; Soliveres et al. 2011; Dohn et al. 2013). Although differences in the functional traits of trees, such as height or N-fixing ability, have recently been shown to partly account for these ambiguous results (Blaser et al. 2013), other factors are likely important. First, the influence of grazing on tree effects has rarely been assessed, even though livestock grazing is the most widespread land use in open savannas (House et al. 2003) and it is likely to co-determine plant–plant interactions together with the abiotic environment (reviewed in Soliveres et al. 2012a). Second, trees are not homogeneous entities; rather, they have contrasting micro-environmental conditions across different positions within their canopies and, therefore, their facilitative or competitive effects are likely to vary accordingly (Weltzin & Coughenour

1990; Hagos & Smit 2005; Schaefer et al. 2012; Smith et al. 2012; Moustakas et al. 2013). Sub-canopy shading, litter amount, soil carbon and seed rain, but not competition for water, have been shown to decline in a linear fashion with increasing distance from the trunk (Travers & Eldridge 2012). The abundance of animal-dispersed and shade-tolerant plant species might, therefore, be highest close to the trunk (e.g. Dean et al. 1999; Hastwell & Facelli 2003). In contrast, the opposite response might be expected for species that require fertile soils or high levels of light, which are more likely to grow close to the edge of the canopy. These contrasting environmental conditions can create different niches for colonization by different understorey plants (Weltzin & Coughenour 1990; Ludwig et al. 2004), potentially leading to increased plant richness at the landscape scale.

Conditions are not uniform across canopy positions (e.g. along trunk-to-edge gradients) and, thus, different canopy positions can vary in their interactions with the environment to define soil and understorey plant attributes (Moustakas et al. 2013). Microsites close to the trunk are preferentially used by herbivores for resting (Dean et al. 1999; Eldridge & Rath 2002), and thus the facilitative effects of these microsites might be more sensitive to grazing pressure than those close to the canopy edge. Mid-canopy positions, however, intercept more water than other canopy positions and are likely to depend more on abiotic conditions than other microsites (Weltzin & Coughenour 1990). Examining the interplay between the effects of different tree canopy positions and contrasting environmental conditions is critical in order to improve our understanding of how trees influence soil properties and plant community composition at the landscape scale.

Here we report on a study of understorey plant community composition changes across three contrasting canopy positions (close to the trunk, mid-canopy, canopy edge) compared with open areas, and how these changes vary across a large rainfall gradient (220–1400 mm rainfall). We also measured soil attributes as the effects of trees on soil properties are often acknowledged as a main driver of their effect on understorey plants (e.g. Ludwig et al. 2004; Riginos et al. 2009; Sitters et al. 2013). Within our large rainfall gradient, we also controlled for differing grazing pressures across the 100 study sites by including dung counts in the analyses. To reduce the confounding effects derived from mixing different biogeographic regions, land management or tree species-specific features (Blaser et al. 2013; Dohn et al. 2013), our gradient was restricted to one region (south-eastern Australia) and we used structurally similar trees (large umbrella-shaped eucalypts). Our initial hypotheses were: (1) soil attributes and understorey plant community composition would differ among the different canopy positions. The largest

effects of canopies on plant richness were predicted at mid-canopy and edge positions, as they can be considered ecotones between open and extremely shaded conditions. The largest effects of canopies on soils and plant cover were expected close to the trunk, where litter deposition is highest. (2) A number of species within the community would show species-specific preferences to different canopy positions (Weltzin & Coughenour 1990), which would increase landscape plant diversity. (3) Positive effects of trees would decrease with increasing rainfall (Dohn et al. 2013) but would be only weakly affected by grazing (Soliveres et al. 2012a). (4) Relationships among tree canopy position and environmental conditions (grazing and rainfall) would vary, with microsites closer to the trunk being more sensitive to changes in grazing than those in the mid-canopy, which would be more sensitive to changes in abiotic conditions.

Methods

The regional rainfall gradient

The study was undertaken in New South Wales (NSW), Australia, along a 1250 km west–east trending transect. The climate is temperate, with slightly more rainfall during the summer months in the north and during winter in the south. Average rainfall varies from west (~220 mm) to east (~1400 mm), but average temperatures are relatively constant at between 17 and 19 °C across the gradient. Soil textures range from sandy loams to loamy sands in the drier end of the gradient, to clay loams in central NSW, and to loams close to the coast. The main forms of erosion range from deep gully erosion in higher rainfall areas, to extensive wind erosion and water sheeting on areas of low slopes in lower rainfall areas. Across the gradient, soils in non-vegetated areas were generally covered with biological soil crusts of varying composition, from dense mats of mosses and cyanobacteria in areas receiving >800 mm·yr^{-1}, to crusts dominated by lichens in areas receiving <500 mm·yr^{-1} (Eldridge 2001). Sites were selected under a number of land uses, including national parks and conservation reserves, travelling stock reserves and some private lands. This provided sites with a range in grazing pressures (mainly sheep, feral goats and kangaroos) from low to moderate levels.

To account for a higher variability in environmental conditions across the rainfall gradient, we selected a large number of sites but limited within-site level replication. Accordingly, we selected 100 sites along the rainfall gradient from Broken Hill in the west (220 mm rainfall) to an area south of Sydney in the east (about 1400 mm rainfall; Appendix S1). Data on annual rainfall were extracted from regional databases (Australian Bureau of Meteorology 2001) and the FAO's Climate Information Tool (http://

www.fao.org/nr/water/aquastat/dbase/index.stm), which covers the global land surface at a 10 'spatial resolution for the period 1961–1990 (FAO 2012). These data are freely available and, as climate stations in western NSW are uncommon, have higher resolution than Australian Bureau of Meteorology data. Tree cover in the sites ranged from isolated trees in grasslands and mallee eucalypts on dunefields in the drier part of the gradient, to dense woodland and open forest in higher rainfall areas. All of our sites supported large eucalypts.

Individual tree gradients

In Sept–Oct 2012, we selected two large eucalypts at each site (median canopy diameter 12.4 m; range: 5–32 m; $n = 200$). Trees were preferably isolated, i.e. more than two canopy diameters from an adjacent tree. We sampled 12 different eucalypt species across the 100 sites. At sites <350 mm·yr^{-1} rainfall, we sampled beneath mainly *Eucalyptus dumosa* and *E. socialis* ('mallee' trees that have a coppicing habit; Noble et al. 1990) and occasionally *E. camaldulensis*. In areas between 350–700 mm·yr^{-1} rainfall, we sampled beneath *E. intertexta* and *E. populnea*. In areas of annual rainfall >700 mm, we sampled beneath *E. albans*, *E. microtheca*, *E. rosii*, *E. viminalis*, *E. crebra* and *E. tereticornis*. The canopy size of all selected trees was calculated by measuring the widest diameter and a second diameter perpendicular to it. We positioned three transects under one tree and two under a second tree to obtain a total of five transects per site. Transects were positioned from the trunk to the open area in a pre-determined direction (Tree 1: N, E, S; Tree 2: W, N). At subsequent sites the transect positions changed in a clockwise manner around the trees (e.g. Site 2: Tree 1: E, S, W; Tree 2: N, E) and so on. In this way we ensured that any potential effects due to transect placement would be averaged across the entire gradient. Along each transect, we arranged four 0.25-m^2 quadrats: (1) adjacent to the trunk, (2) at the mid–canopy, (3) at the canopy edge and (4) in the open. Where possible, the open quadrat was located one canopy radius from the edge of the tree. In dense woodlands, however, we placed this in the nearest open patch. With the canopy diameter data we calculated the distance to the trunk of each sampling quadrat, allowing us to account for both tree size and canopy position with a single variable. For example, in a tree with a canopy radius of 15 m, the distance to the trunk would be 7.5 m for the mid-canopy microsite, 15 m for the edge microsite and 30 m for the open site. Thus, hereafter *canopy position* refers to the position within the canopy of the tree, regardless of the size of such canopy, and distance to the trunk is a continuous variable integrating canopy position and tree size.

Assessment of understorey plant communities

Previous studies have tended to focus on how trees affect grass biomass production (Blaser et al. 2013; Dohn et al. 2013). Rather, we focused on several other important attributes of the understorey plant communities: plant species richness, total plant cover and plant community composition. Within each quadrat ($n = 2000$) we recorded the cover and number of all vascular plant species. These were used as a direct measurement of plant species richness and total plant cover (we used the average of the five quadrats per microsite within each site for cover, and the number of different species found within the five quadrats for each microsite for richness). To summarize plant community composition we used a 3-D non-metric multi-dimensional scaling (MDS) ordination constructed using plant cover by each species (sum of cover by species within the five quadrats per microsite and site). The stress value for the MDS ordination was 0.13, suggesting that the relationship between points was adequately represented in these three dimensions (see Appendix S2 for details).

We calculated percentage similarity in plant community composition between open quadrats and each of the three microsites for each site using the Sørensen similarity index (Clarke & Gorley 2001). This provided a measure of the differences among the niches provided by each microsite. As a complementary analysis, we also quantified the percentage of obligate species (species only occurring at a given tree canopy position but not in the other microsites studied; i.e. exclusive to this particular microsite in this site) for each microsite (see Soliveres et al. 2012a for a related approach).

Assessment of the different microenvironments

We quantified overall grazing pressure at all sites by counting dung (scat) of different herbivores (i.e. sheep or goat, kangaroo, horse, cow, European rabbit) within the 20 0.25-m^2 quadrats at each site. In each site, grazing pressure was expressed as the average number of scat per quadrat for all grazing animals and for each of the four microsites. Cow and horse scat were excluded from the analysis as they were found at only four of the 100 sites.

To assess tree effects on understorey plants that might be mediated by soils, we conducted detailed measurements of soil surface morphology using 12 simple attributes measured in each sampling quadrat (Tongway 1995; Tongway & Hindley 2004; see Appendix S3). The 12 attributes are derived from the Soil Survey Analysis methodology (Tongway & Hindley 2004). These were soil texture, soil hardness, soil surface roughness, surface resistance, physical crust brokenness, physical crust stability, amount of erosion, cover of material deposited on the surface, lit-

ter cover, litter depth, litter origin and degree of litter incorporation into the surface. All these variables were measured within the same 0.5×0.5 m quadrats used for the vegetation survey, using well-accepted methodologies and categorical classifications (see details in Appendix S3). Features of physical soil crusts (hardness, roughness and brokenness) are particularly good surrogates of soil water infiltration and nutrient retention. Litter origin and cover of deposited materials indicate the movement of nutrients and sediments with run-off, and litter depth, and its degree of incorporation into the soil is a useful surrogate for rates of nutrient cycling and the depth of the most active organic soil layer (full rationale in Appendix S3; Tongway & Hindley 2004). Indices developed from these 12 surface attributes have been shown to be strongly related to a range of laboratory-based soil properties, such as water infiltrability, organic matter content, nutrient cycling and resistance to erosion (Tongway 1995; Bartley et al. 2006; Maestre & Puche 2009). Other variables are included within Tongway's (1995) methodology that were not considered in this study, either because we were only focusing on microclimatic amelioration of trees on understorey plants (cover of biological soil crust) or because it was already measured as a response variable in this study (plant cover).

To reduce the number of environmental variables and further simplify our analyses, we performed a PCA ordination with the 12 soil attributes. From this ordination, we retained the first two components (hereafter PCA1 and PCA2), which explained 56.2% of the variability in our environmental data. These components were mainly related to litter cover (-0.38), soil hardness (0.37) and surface resistance (0.38; values for PCA1) and soil erosion (-0.66), and soil texture (0.26; values for PCA2; see Appendix S4 for details). The MDS ordination and similarity analyses for plants, and the PCA including soil were undertaken using the PRIMER v6 statistical package for Windows (PRIMER-E Ltd., Plymouth Marine Laboratory, Plymouth, UK). MDS and similarity analyses were performed using Bray-Curtis distance measure, Type II sum of squares and 999 permutations after square-root transformation of the data. PCA were performed under normalized data to give the same weight to each of the 13 variables, regardless of their different units.

Data analyses

We used structural equation modelling (SEM; Grace 2006) to analyse the effects on, and relationships among, rainfall, distance to the tree trunk, grazing and the interactions between these factors, on our plant (MDS axes, plant cover, plant richness) and soil (PCA1 and PCA2 axes) variables. SEM tests the plausibility that our data fit

an *a priori* causal model based on previous scientific evidence including the expected relationships among the studied variables. Our *a priori* structure assumed a direct effect of canopy position on understorey vegetation (via microclimatic amelioration and increased seed deposition; Dean et al. 1999; Tewksbury & Lloyd 2001; Moustakas et al. 2013) and an indirect effect mediated through soil properties (Ludwig et al. 2004; Riginos et al. 2009). Grazing pressure and rainfall were assumed to affect both soils and understorey vegetation directly and through interactions with canopy position. Lastly, the *a priori* model structure also included a direct effect from soil properties to plant richness and composition (Appendix S5; rationale follows from the Introduction). The set of assumptions forming the *a priori* model is compared with the observed variance–covariance matrix to render an overall goodness-of-fit metric (here we used the most commonly used and widely accepted metric, the χ^2; high *P*-values indicates a good fit between our model and the data). Apart from this overall goodness-of-fit metric, SEM test for the strength and sign of each causal relationship between two variables in the model. The latter are summarized as standardized path coefficients, which range from 0 and 1, and are equivalent to a partial correlation coefficient. The statistical significance of these path coefficients was evaluated by bootstrapping, as this technique is the most robust to departures from normality in the data.

Before the SEM analyses, we converted the canopy positions into one continuous variable, Distance to Trunk (which accounted for both the size of the canopy and the position in relation to the canopy). From our measurements of plant community composition, we analysed plant cover and richness separately to aid interpretation of the effect of the different factors on plant communities. Prior to analyses, we examined the bivariate relationships among all potential variables and transformed them, where appropriate (usually $\log_{10}$ transformation), in order to linearize the relationships. SEM analyses were performed using AMOS (SPSS Inc., Chicago, IL, US).

Differences in the percentage of similarity among the different canopy positions compared with open areas, and their relationship with rainfall and grazing, were analysed using linear models with microsite (trunk, mid-canopy, edge, open), rainfall (square-root transformed) and the grazing pressure index (dung counts) as model predictors. For grazing pressure we considered three different models: (1) dung within each tree microsite as the microsite-specific level of grazing, (2) a ratio between dung counts at each microsite vs dung in the open, and (3) dung in the open microsite as the standard level of grazing characterizing each site. All models returned very similar results (Appendix S6) and thus only those comparing grazing

within each tree canopy position vs open microsites are discussed here. The interactions among the three factors (rainfall, grazing and microsite) were also considered in the linear models. We used the identity link function, assuming normal distribution of errors. An identical analysis was performed using the number of exclusive species for each microsite, i.e. species solely restricted to a particular microsite (facilitation-obligates). Linear models were performed using the MASS library for R 2.10.1 (Venables & Ripley 2002; R Foundation for Statistical Computing, Vienna, AT).

Results

Canopy position and environmental effects on soil and plant attributes

We detected strong positive effects of distance to the trunk on the soil PCA1 (path coefficient [PC] = 0.75; Figs 1 and 2). This was associated with increased surface resistance and soil hardness, and reduced litter cover and incorporation towards open areas (Appendix S4). Distance to the trunk did not affect plant cover directly, although the indirect effects through its interaction with rainfall and its effect on soil properties was negative (Table within Fig. 2). Distance to the trunk was directly associated with an increase in plant richness (PC = 0.16; Fig. 2). Rainfall had a moderately strong and negative effect on PCA1 (−0.30, increasing crust stability and soil hardness) and PCA2 (−0.16; reduced erosion; Figs 1 and 2). Higher annual rainfall increased plant richness (PC = 0.28) and also affected the first dimension of the MDS ordination (PC = 0.84). Despite the lack of a direct effect of rainfall on plant cover (Fig. 2), we found a significant, although weak (PC = 0.11), rainfall × distance to the trunk interaction on cover.

Interestingly, while the first dimension of the MDS ordination (our measure of plant composition) was significantly affected by rainfall (Fig. 1), distance to the trunk had a significant direct effect on the third MDS axis (PC = 0.11) and an indirect negative effect on the second MDS axis, which were very weakly affected by rainfall (see Table within Fig. 1). The latter suggests that both canopy position and rainfall affected mainly different aspects of plant composition, and that their specific effects (independent from each other) were much stronger than the interactions between these two factors (rainfall, distance to the trunk), or their simultaneous effects on a the same composition aspects. Species positively related to MDS1 (Appendix S2) were characteristic of more mesic environments, such as the shrub *Myrsine variabilis*, the tree *Synoum glandulosum* and the tussock grass *Themeda australis*; whereas those species negatively related to MDS1 were more typically from arid environments, such as the native forbs

$\chi^2 = 10.1$; $P = 0.12$, DF = 5
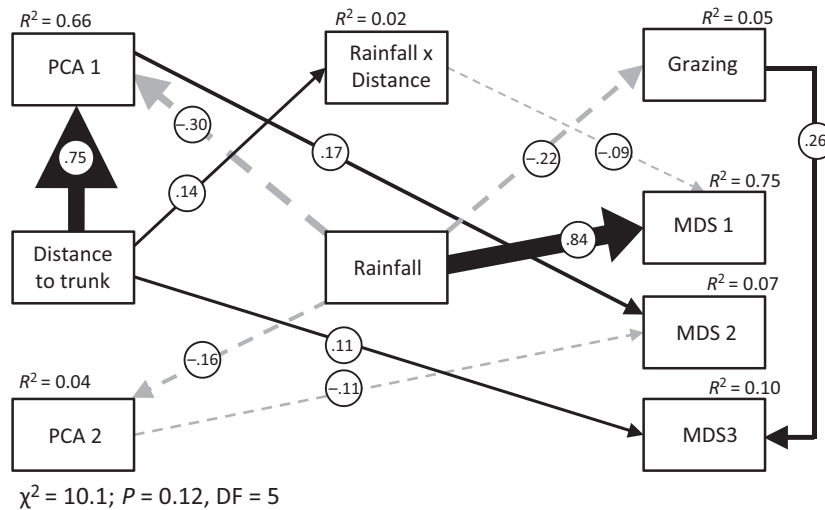
Total effects	MDS1	MDS2	MDS3
Rainfall	0.86	0.03	−0.09
Distance	0.02	−0.21	0.11
Rainfall*Distance	−0.08	0.05	−0.05

Fig. 1. SEM depicting the effects of average annual rainfall (Rainfall), index of grazing pressure (Grazing), distance to the trunk of the tree (Distance to trunk) and the interaction between rainfall and distance to trunk (Rainfall × Distance) on plant community composition (the first three dimensions of the MDS biplot) and abiotic variables (the first two components of the PCA biplot). Numbers associated with arrows indicate standardized path coefficients, analogous to regression weights, and indicative of the effect size of the relationship. Arrow width is proportional to the strength of path coefficients. Continuous black and dashed grey arrows indicate positive and negative relationships, respectively. The proportion of variance explained (R^2) appears above every response variable in the model. Goodness-of-fit statistics for the model are shown in the lower left corner. Only significant pathways are shown. Total effects of direct and indirect effects of Rainfall, Canopy and the Rainfall × Canopy interaction on the first three MDS dimensions are shown in the table.

Sclerolaena diacantha, *Rhagodia spinescens* and the sub-shrub *Enchylaena tomentosa*. Changes in MDS3, however, seemed mostly driven by dispersal mechanisms, with those species dispersed by birds (e.g. *Einadia nutans*, *Geijera parviflora*) found closer to the trunk than wind-dispersed ones (e.g. *Austrostipa scabra*, *Sclerolaena patenticuspis*; Appendix S2).

Grazing had no noticeable effect on soil attributes (Fig. 1), although it did have a positive effect on richness (PC = 0.21) and an equal, but opposite, effect on cover (−0.20; Fig. 2). These grazing effects also translated into significant effects on composition (i.e. MDS3; Fig. 1). Soil properties (the PCA components) affected plant communities differentially. PCA1 (positively affected by distance to the trunk and negatively influenced by rainfall) had a positive effect on the second dimension of the MDS ordination but no effect on plant cover or richness. The second PCA component, which generally decreased under higher rainfall, also affected the second dimension of the MDS ordination and increased plant richness.

Microsite-specific niche differences and the effect on landscape plant diversity

Percentage of similarity between plant communities in the open and those beneath tree canopies decreased towards the trunk (edge [~40% similarity] >mid-canopy >trunk [~10%]; Fig. 3a). Apart from the overall similarity, all tree canopy positions had a similar percentage of niche-specific or facilitation-obligate species, with no significant differences among them (mean of 9–11% of the total species within each site for each one of the different positions; Linear model: $t = -1.10$; $P = 0.26$; Fig. 3b, Appendix S6). These percentages varied widely across the gradient, from 0 to ~50% in the edge and close to the trunk, and from 0 to ~30% in the mid-canopy. However, this variation was neither related to rainfall nor to grazing pressure, i.e. there was no microsite × rainfall, microsite × grazing or microsite × rainfall × grazing interaction ($P > 0.10$ in all cases; Appendix S6).

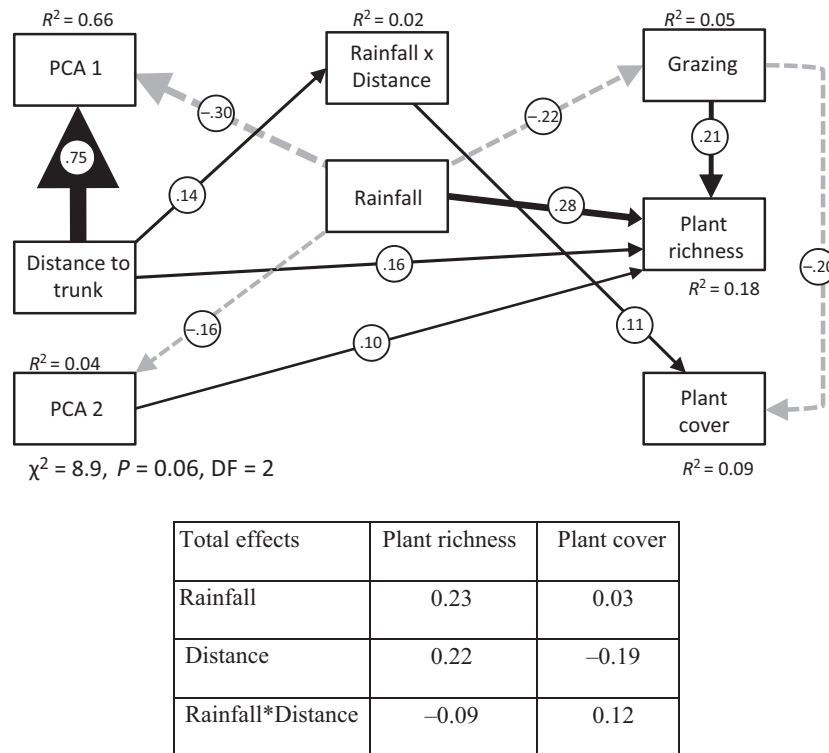| Total effects	Plant richness	Plant cover
Rainfall	0.23	0.03
Distance	0.22	−0.19
Rainfall*Distance	−0.09	0.12

Fig. 2. SEM depicting the effects of average annual rainfall (Rainfall), index of grazing (Grazing), distance to the trunk of the tree (Distance to trunk) and the interaction between rainfall and distance to trunk (Rainfall × Distance) on plant richness, plant cover and on abiotic variables (the first two components of the PCA biplot). Numbers associated with arrows indicate standardized path coefficients, analogous to regression weights, and indicative of the effect size of the relationship. Arrow width is proportional to the strength of path coefficients. Continuous black and dashed grey arrows indicate positive and negative relationships, respectively. The proportion of variance explained (R^2) appears above every response variable in the model. Goodness-of-fit statistics for each model are shown in the lower left corner. Only significant pathways are shown. Total direct and indirect effects of Rainfall, Canopy and the Rainfall × Canopy interaction on plant richness and cover are shown in the table.

Interactions among environmental variables and canopy position on soils and plants

Overall, our analyses suggest a variable effect of interactions between canopy position and environmental conditions depending on the response variable and the environmental factor considered. The rainfall × canopy position interaction term did not affect soils or plant richness, but had significant effects on plant cover and composition (Figs 1 and 2). The grazing × canopy position interaction term, however, did not affect any of the variables examined, and was therefore removed from the models. Lastly, the percentage of species preferring a given canopy position did not change predictably with grazing or rainfall ($P > 0.10$ in all cases; Fig 3b, Appendix S6). However, there was a significant rainfall × canopy position effect, which translated into a decrease in plant similarity between plant communities beneath different canopy positions and those in open areas under the driest conditions (rainfall × microsite: $t = -2.51$, $P < 0.05$). This interaction showed that the similarity between the plant communities growing beneath the edge and the middle of the tree canopy vs open interspaces decreased significantly towards drier environments. In the driest environments sampled the percentage of similarity between open communities and those beneath the tree were consistently low, regardless of the tree microsite considered (Fig. 3a).

Discussion

The effect of trees on understorey plants and soils has received considerable attention over the past few decades (reviewed in Scholes & Archer 1997; Dohn et al. 2013) due to the importance and extent of trees across many of Earth's biomes. Few studies, however, have considered tree canopies as heterogeneous entities with variable understorey plants and soils (e.g. Weltzin & Coughenour 1990; Hagos & Smit 2005; Schaefer et al. 2012; Smith et al. 2012; Moustakas et al. 2013). Here, we complement these previous studies by focusing on the effects of trees on plant species richness and community composition rather than on biomass production (see also Tewksbury & Lloyd 2001;
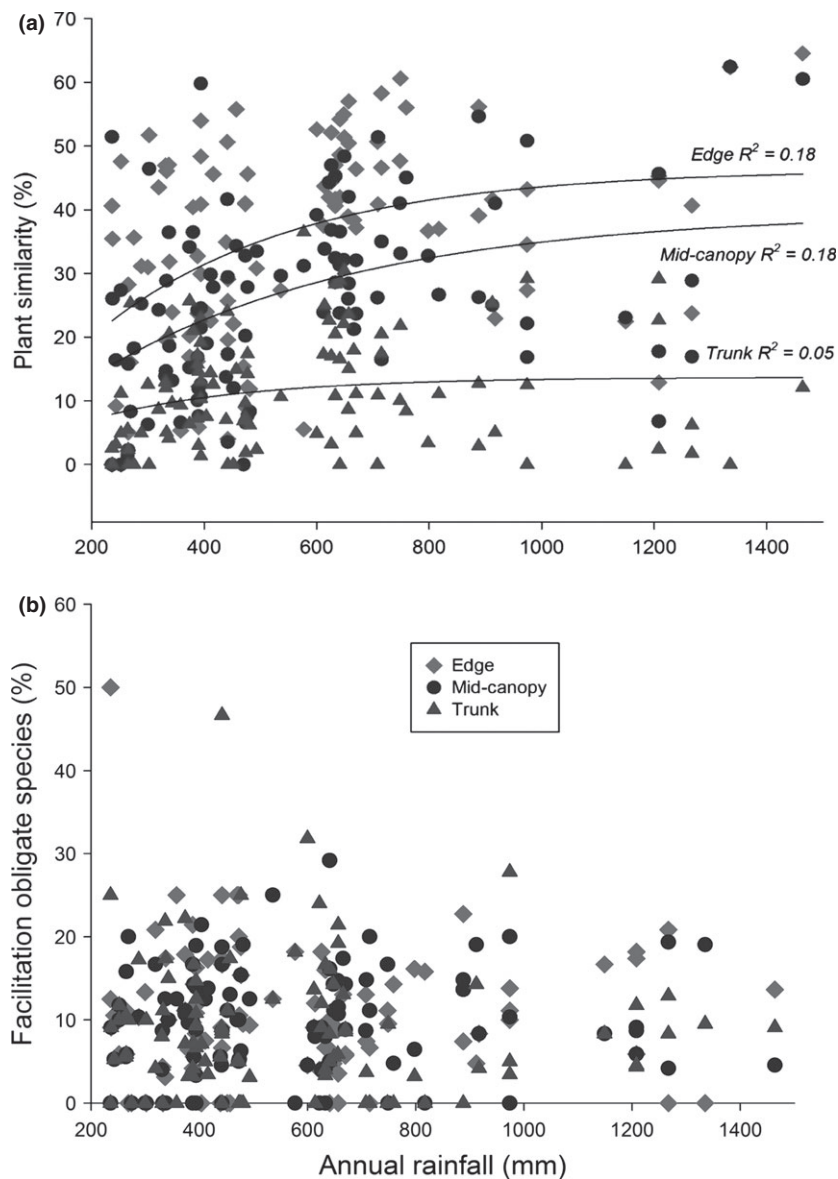
Fig. 3. Plant similarity (**a**) and percentage of species exclusive for a given microsite (**b**) in relation to annual rainfall. Similarity is calculated as the similarity in plant community composition for trunk, mid-canopy, canopy edge microsites in relation to plant community composition in the open. Facilitation-obligate species are those only growing in a given microsite (edge, mid-canopy or trunk) within a given site, and they are calculated as the percentage of species regarding the total richness registered at each site. Significant relationships are shown.

Ludwig et al. 2004), and by considering the differential effects that different canopy positions have on richness and composition across widely contrasting environments (see also Moustakas et al. 2013). Only recently have researchers considered plant–plant interactions using microsites with a finer resolution than the commonly used nurse–open classification. For example, Pescador et al. (2014) used distance to the nurse as a continuous variable, demonstrating that facilitation was more important 'in the halo' (i.e. at intermediate positions between open interspaces and nurses' canopy) for most of the 17 target species

considered. Similarly, Amat et al. (2014) showed that different shrub sub-canopy locations differed in their facilitatory effects on the target shrub *Pistacia lentiscus*. In the latter study, the effect was mainly driven by indirect interactions with other species growing beneath the canopy. Our study adds to the increasing body of evidence that sub-canopy sites vary in their effects on plants and soils, and suggests that acknowledging this wide range of potentially different microsites found beneath the canopies of trees can help us to improve our understanding of plant–plant interactions across environmental gradients.

Microsite-specific niche differences and the effect on landscape plant diversity

Consistent with previous studies, we found a significant influence of tree canopies on the composition of understorey plant species, and an increase in soil fertility and litter cover from open areas to the tree trunk (e.g. Tewksbury & Lloyd 2001; Ludwig et al. 2004; Travers & Eldridge 2012). Apart from the effects found on plant composition (MDS ordination; Fig. 1), the effects on understorey plant composition are supported by the fact that similarity among open and tree canopy positions decreased sharply towards the trunk (Fig. 3). These changes in composition between microsites translated into a higher plant diversity at the site scale, as ~30% of the species (10% per microsite) were present only at a given canopy position. The latter result accords with the notion of species-specific preferences for a given canopy position (Weltzin & Coughenour 1990), which will likely depend on the light, nutrient and water requirements of particular species and how they are provided at different positions across the canopy. Conversely, we did not find any significant microsite effect when analysing either percentage of similarity or obligate (i.e. found exclusively at a given microsite) species. Thus, part of our first hypothesis was rejected by our results because all canopy positions, not just edge or mid-canopy positions, had a similar positive effect on plant diversity by favouring a similar fraction of the species occurring within a given site.

Increases in soil fertility, shading and hydraulic lift are among the most important mechanisms underpinning the positive effects of trees on biomass production and plant diversity (Weltzin & Coughenour 1990; Ludwig et al. 2004; Dohn et al. 2013). However, their relative importance remains largely unknown, and studies isolating these different mechanisms are extremely rare (Moustakas et al. 2013). Our SEM approach allowed us to assess the relative importance of gradients in changing soil properties as drivers of tree effects on understorey plant composition. We found that about 50% of the effects of trees on plant composition were indirectly mediated by soil properties (distance to trunk →PCA1 →MDS2; Fig. 1; Ludwig et al. 2004). Interestingly, an additional 50% of the effect of trees on the understorey plant community was not accounted for in our measurements of microclimatic amelioration (distance to trunk → MDS3). This suggests the existence of other important drivers of tree effects that were not considered in our study. Among them, there may be an effect of dispersal agent, i.e. whether the understorey species are animal-dispersed (Dean et al. 1999; Pausas et al. 2006; Soliveres et al. 2012b) or an abiotic effect relating to the tendency of large *Eucalyptus* trees to pump water from deeper soil layers to the surface (hydraulic lift;

Burgess et al. 1998). Regardless of the exact mechanisms underlying our results, they highlight the fact that, for some tree species at least, an important fraction of their effects on understorey plants might not be related directly to soil amelioration, and that other factors should also be considered.

Interactions among environmental conditions and canopy position on soils and plants

Although grazing affected plant cover, richness and composition, it did not influence tree effects on either soils or their understorey plant community. The large eucalypt trees studied here provided neither shelter nor an associational resistance to grazers compared with spiny shrubs or woody species that have canopies that reach the soil surface (Rebollo et al. 2002; Smit et al. 2007). However, we were expecting some interactions between grazers and tree effects, as microsites closer to the trunk are used most heavily by grazers for camping and resting (Dean et al. 1999; Eldridge & Rath 2002), and this might influence understorey communities through surface disturbance, seed deposition or defecation. We found no support for the latter expectation, probably because the levels of grazing considered here varied relatively little, from low to moderate, and were therefore insufficient to modulate changes in the effects of trees on soils and vegetation. Support for this comes from the weak effect of grazing on soil properties that would normally be expected to be strongly influenced by high levels of grazing (e.g. those surface variables that formed the PCA analysis; Eldridge et al. 2011), and the fact that grazing enhanced species richness, which is typically observed from low to moderate levels of grazing. Future studies should consider larger gradients in grazing intensity in order to improve our understanding of potential thresholds in grazing pressure that would likely influence the effect of understorey microsites, particularly those close to the trunk, on plants and soils.

In the present study we detected contrasting interactions between rainfall and different tree canopy positions on their understorey community, which partially contrast with a previous meta-analysis (Dohn et al. 2013), empirical work (Tewksbury & Lloyd 2001) and our own previous research with *Eucalyptus* trees (Soliveres et al. 2011, 2012a). These interactions significantly affected plant cover and similarity (Figs 1–3), but did not have significant effects on plant richness, soil attributes or the percentage of facilitation-obligates (Figs 1 and 2, Appendix S6). We found a significant, although weak, rainfall × distance interaction on the first component of the MDS ordination. However, both rainfall and distance to the trunk had stronger effects on plant composition when acting indepen-

dently of each other, as they influenced different axes (rainfall: mainly MDS1; distance to the trunk: MDS2 and MDS3). The most important distance to the canopy × rainfall interaction we found was a reduction in the similarity in the plant community between tree and open microsites towards drier environments. This accords with a reduction in facilitation under wetter environments generally found in previous studies (e.g. Tewksbury & Lloyd 2001; Soliveres et al. 2011; Dohn et al. 2013; Moustakas et al. 2013).

Three separate yet complementary explanations arise to explain the differences between our results and those from other studies. First, it is well known that the performance measure used as a response variable can drastically affect the reported relationship between plant–plant interactions and environmental conditions (Suding & Goldberg 1999; Maestre et al. 2005), and this is clearly shown with our own results, where some response variables were significantly affected by the rainfall × distance interaction (cover, MDS1 and similarity) whereas others were not influenced at all (richness, soils, percentage of obligate species). Second, it has been demonstrated recently that larger gradients (i.e. bigger differences between the wettest and driest sites) might reduce the strength of environment–plant community interactions (Soliveres & Maestre 2014), and our gradient spanned a larger annual precipitation range than many gradients studied previously (~1000 mm difference in annual rainfall, compared with, e.g. 400 or ~650 mm; Soliveres et al. 2011, 2012a), which found significant interactions between tree effects and rainfall on plant species richness. Third, the strength of the relationship between the percentage of facilitation-obligate species and rainfall increased and became marginally significant ($r = 0.17$; $P < 0.10$) when we compared the average tree effect with open microsites rather than spatial variation across the tree canopy. This relationship waned, however, when we considered different canopy positions separately. The latter results also suggests that the relatively low sample size within each site was not likely to cause these contrasting results, as we found a (weak) relationship similar to previous studies when joining all tree canopy positions within a single microsite. We argue, therefore, that (1) including nurse canopies as a single microsite may add up a large number of niches provided by separate parts of the canopy, rendering a more positive and significant effect of trees on diversity overall, and (2) if we consider separate canopy positions, the lack of a relationship between the percentage of species only found under the canopy (canopy obligate species) and rainfall reflects a high species turnover amongst the different canopy positions. It is known that different plant species respond differently to environmental conditions provided by neighbours across environmental gradients

(e.g. Greiner La Peyre et al. 2001; Liancourt et al. 2005; Gross et al. 2010) and that this likely obscured the relationship between rainfall and plant interactions (Soliveres et al. 2011; Soliveres & Maestre 2014). It is intuitive and reasonable, therefore, to consider that species-specific responses to canopy position would change as environmental conditions change. Thus species that are obligate (i.e. exclusive) for mid-canopy or trunk positions under low rainfall might be found at edge or even open positions at higher levels of rainfall. Indeed, we found that those species occurring in several of the sites preferred different canopy positions, or even open areas, depending on the site. An example is *Einadia nutans*, a sprawling bird- and ant-dispersed species that is almost trunk-obligate in the arid zone, but occurs in edge and open microsites at high levels of rainfall. The directionality of these changes across rainfall gradients is extremely variable among different species, and this might obscure the relationship with rainfall when more microsites or species are considered (Liancourt et al. 2005; Soliveres et al. 2012b).

Concluding remarks

Our results demonstrate that a substantial percentage (~30%) of species within a site depends on different niches provided across the different tree canopy positions. We show that tree effects are mostly unrelated to prevailing environmental conditions in our study system, and these effects are only partially driven by effects on soil properties. Overall, these results reveal the importance of considering the different positions across tree canopies to fully understand their role on ecosystem structure and function, and to partially explain the contrasting results of tree effects on their understorey found in previous studies. Our results help us to improve current theoretical models on the role of plant–plant interactions in response to changing environmental conditions by highlighting two potential mechanisms obscuring the relationships between environmental conditions and plant–plant interactions: the length of the gradient and the number of different microsites considered.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Location of the 100 study sites.

Appendix S2. Details on the MDS ordination performed for plant composition

**Appendix S3.** Soil surface features measured

Appendix S4. Details on the PCA ordination

Appendix S5. *A priori* model structures for the SEM

Appendix S6. Results for the linear models performed with similarity and the percentage of facilitation-obligate species.

Graphical Abstract

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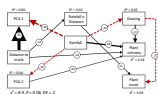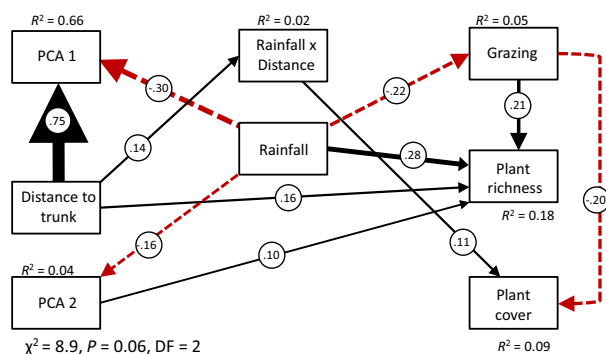
By sampling 100 sites across a wide environmental gradient in Australia we found that position within tree canopies, grazing and rainfall influenced understorey species richness and soil attributes, but independently of each other. However, canopy position × rainfall interactions importantly affected the similarity between tree and open plant communities. Our results help to better understand plant-plant interactions in tree-dominated ecosystems.