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Environmental and spatial drivers of spider diversity at contrasting microhabitats

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Abstract The relative importance of environmental and spatial drivers of animal diversity varies across scales, but identifying these scales can be difficult if a sampling design does not match the scale of the target organisms' interaction with their habitat. In this study, we quantify and compare the effects of environmental variation and spatial proximity on ground-dwelling spider assemblages sampled from three distinct microhabitat types (open grassland, logs, trees) that recur across structurally heterogeneous grassy woodlands. We used model selection and multivariate procedures to compare the effects of different environmental attributes and spatial proximity on spider assemblages at each microhabitat type. We found that species richness and assemblage composition differed among microhabitat types. Bare ground cover had a negative effect on spider richness under trees, but a positive effect on spider richness in open grassland. Turnover in spider assemblages from open grassland was correlated with environmental distance, but not geographic distance. By contrast, turnover in spiders at logs and trees was correlated with geographic distance, but not environmental distance. Our study suggests that spider assemblages from widespread and connected open grassland habitat were more affected by environmental than spatial gradients, whereas spiders at log and tree habitats were more affected by spatial distance among these discrete but recurring microhabitats. Deliberate selection and sampling of small-scale habitat features can provide robust information about the drivers of arthropod diversity and turnover in landscapes.

Key words: Araneae, arthropods, beta diversity, eucalypt woodland, spatial scale, species turnover.

INTRODUCTION

Heterogeneity in vegetation composition and structure is an inherent feature of landscapes and an important driver of variation in animal communities (Atauri & de Lucio 2001; Tews *et al.* 2004). Different attributes of vegetation, be it structural or floristic, determine how different taxa perceive and interact with their habitat, but the importance of the different attributes can vary with spatial scale (Field *et al.* 2009). Many studies have examined drivers of diversity at large scales (e.g. Bohning-Gaese 1997; Ribera *et al.* 2003) or between different vegetation types (e.g. Woodcock *et al.* 2010; Fahr & Kalko 2011). Yet, studies of animal assemblages at fine spatial scales can reveal new ways that attributes of vegetation structure can influence patterns of species diversity and distributions (Koivula *et al.* 1999; Rypstra *et al.* 1999). This can be particularly important, as analyses of environmental drivers of animal diversity at one scale may be contingent upon factors operating at much smaller scales (Allen & Hoekstra 1992; Barton *et al.* 2009).

Awareness of the issue of scale in studies of biodiversity has led to an increase in multi-scale studies, where patterns are quantified explicitly at different spatial scales (Cushman & McGarigal 2002; Manning *et al.* 2006). Indeed, spatial processes *per se* can be important drivers of biodiversity, with geographic distance often a useful predictor of assemblage turnover (Koleff & Gaston 2002; Ferrier & Guisan 2006). Isolated habitats in particular, such as mountain valleys (Moir *et al.* 2009) or remnant vegetation patches (Boulinier *et al.* 2001), can affect assemblage turnover by acting as specialized habitat where species aggregate, or by limiting dispersal across landscapes. Untangling the relative influence of both spatial and environmental drivers of assemblage diversity is therefore a core challenge in the study of biodiversity in landscapes (Davies *et al.* 2003; Cottenie 2005; Fattorini & Baselga 2012).

Matching the scale of sampling with the size or dispersal capacity of the study taxon is often done implicitly in the design of ecological studies (Barton *et al.* 2013). For example, birds are commonly sampled using single point counts among multiple vegetation patches, whereas smaller arthropods might be sampled using multiple pitfall traps, but within a single vegetation patch. Choice of sampling location is

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often quite specific for large organisms, such as birds, where particular landscape features are targeted to identify how variation among sites affects communities (e.g. Garcia *et al.* 2011; Cunningham *et al.* 2014). Sampling at fine spatial scales, however, is important when considering small-bodied or dispersal-limited organisms that may perceive and interact with habitat at spatial scales much smaller than many vertebrates (Koivula *et al.* 1999; De Mas *et al.* 2009). Many studies of arthropods, for example, do not clearly identify what unit of habitat is actually being studied, or the degree to which it is a sensible unit of habitat from the perspective of the organism of interest. Sampling of small arthropods often uses non-specific methods, such as grids of pitfall traps or sweep nets along transects, despite good evidence that these smaller organisms often respond to environmental heterogeneity at scales of individual plant species (Burns *et al.* 2015) or habitat structures (Krawchuk & Taylor 2003). Whereas randomized sampling approaches may be suitable for understanding general diversity patterns at broader scales, a targeted and non-random approach has greater potential to give insight into fine-scale patterns. Failure to tailor sampling to these smaller scales creates the risk that we will overlook important drivers of variation in arthropod communities (Sereda *et al.* 2014).

Knowledge of how fine-scale structuring of habitat affects animal assemblages is also important from a biodiversity conservation perspective. Manipulation of key structural features of habitat, such as trees (Stenchly *et al.* 2011) or woody debris (Castro & Wise 2010; Barton *et al.* 2011), can provide a tractable approach to the management of habitat to benefit biodiversity. However, this requires an understanding of what habitat structures are associated with the diversity and composition of animal assemblages. For example, it is well established that coarse woody debris and individual trees provide localized hotspots of ecological function in landscapes by retaining soil moisture and nutrient content (McElhinny *et al.* 2010; Goldin & Hutchinson 2013). Further, these structures provide distinct microhabitats for a variety of taxa (Harmon *et al.* 1986), yet how they contribute to assemblage turnover across landscapes is only just becoming apparent (Barton *et al.* 2009, 2010).

Arthropods comprise the bulk of terrestrial species richness (Stork 1988), and fill numerous ecological roles as herbivores, detritivores, pollinators, parasites and predators of other arthropods (Samways 2005; Yang & Gratton 2014). Ground-dwelling arthropods are likely just as diverse as canopy-dwelling arthropods (Stork & Grimbacher 2006), but may have weaker associations with particular plant species. Instead, ground-dwelling arthropods can be sensitive

to habitat attributes that provide appropriate microclimates, food resources and shelter. Spiders are an abundant group of ground-dwelling arthropod, and are obligate predators of other arthropods, thus performing an ecologically important role in terrestrial ecosystems (Riechert 1974). Ground-dwelling spiders are mostly comprised of cursorial species that do not use webs for prey capture (Uetz 1979; Cobbold & MacMahon 2012), and therefore are less dependent on habitat structures that are necessary for web placement (Gollan *et al.* 2010; Gibb *et al.* 2015). Instead, individual spiders are free to wander across diverse microenvironments (bare ground, leaf litter) in search of their preferred prey. Ground-layer habitat attributes, such as coarse woody debris (Castro & Wise 2010) and litter depth (Uetz 1979), are known to be key determinants of spider assemblage diversity and composition as they affect microclimate and prey abundance (Birkhofer *et al.* 2010). Examination of the relative importance of these environmental features at fine spatial scales can therefore be useful for understanding how they contribute to landscape-scale diversity patterns.

In this study, we examined the diversity and composition of ground-dwelling spider assemblages in one of the largest and best condition examples of yellow box (*Eucalyptus melliodora*) – red gum (*Eucalyptus blakelyi*) grassy woodland in the Australian Capital Territory, south-eastern Australia. This vegetation type is listed nationally as a critically endangered ecological community (Australian Government 2006), with very little unmodified grassy woodland remaining. To date, few studies of ground-dwelling spiders have been conducted in Australian eucalypt woodlands (but see Martin & Major 2001; Harris *et al.* 2003; Major *et al.* 2006; Recher & Majer 2006). The broad aim of this study was to determine the effects of environmental variation and spatial proximity among samples on the species richness and composition of ground-dwelling spider assemblages. We sampled spider assemblages from three distinct microhabitats: (i) in open grassland, (ii) near logs and (iii) under trees. This approach to sampling builds on work by (Sereda *et al.* 2014), and is quite different from most other studies of fine-scale arthropod diversity patterns, as it targeted different components of the ground-active fauna. As for studies in forest canopies that target fauna associated with individual epiphytes or tree crowns (e.g. Yano-viak *et al.* 2007; Burns *et al.* 2011), our study allows for the identification of fauna associated with distinct microhabitats at ground level. This allows for a comparative approach to the analysis of spider diversity, and can potentially reveal how the spatial and environmental structuring of assemblage diversity and composition at fine scales contributes to large-scale diversity (Barton *et al.* 2009, 2010). We asked the following questions:

1. To what extent do spider assemblages differ in richness and composition between microhabitat types?
2. Which environmental attributes affect spider species richness and do they differ among microhabitat types?
3. Is variation in spider assemblage composition most strongly affected by environmental variation or spatial distance, and does this differ among microhabitat types?"

We synthesize our findings into a broader perspective on how deliberate sampling at scales relevant to organisms' perception of habitat heterogeneity can reveal the drivers of beta-diversity in animal communities.

METHODS

Study area

We conducted the study at the Mulligans Flat Nature Reserve located in the Australian Capital Territory, south-east Australia (Fig. 1a). The reserve comprises yellow box – red gum grassy woodland, which is a critically endangered

ecological community in Australia (Department of the Environment and Heritage 2006). The reserve covers an area of approximately 500 ha, mean daily temperatures range from 6.5°C in winter to 19.7°C in summer, and mean annual rainfall is 615.9 mm (Manning *et al.* 2011). Within the reserve, 48 one-hectare sites were established for long-term monitoring of biodiversity and habitat composition and structure.

Spider sampling

Our sampling design consisted of a hierarchical nested arrangement (Barton *et al.* 2009). We sampled arthropods using pairs of pitfall traps, separated by 1 m, and placed in one of three microhabitats: (i) next to the base of a tree, (ii) adjacent to a log and (iii) in open grassland. Pitfall traps at trees were placed under a yellow box or red gum with a diameter at breast height (DBH) of more than 0.25 m. We selected logs only if they were more than 0.10 m in diameter and 1 m in length. Traps in open grassland were at least 2 m from the dripline of the canopy of a tree. Data from each pair of pitfall traps were pooled to give one sample per microhabitat, and all sampled microhabitats were at least 10 m apart to minimize complications of non-independence of samples.

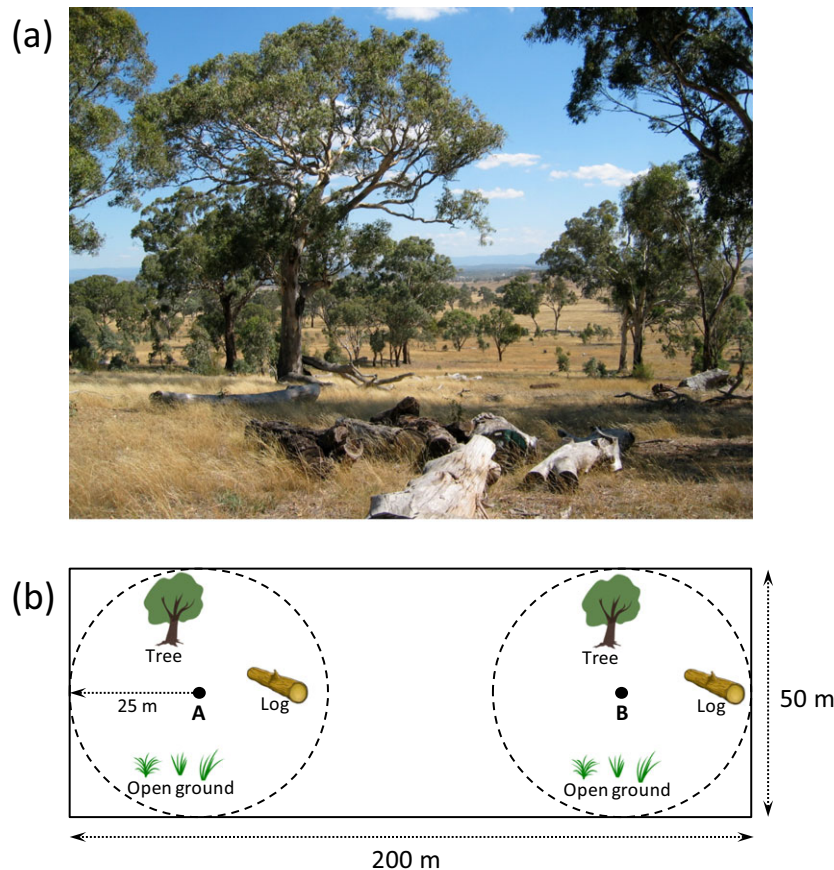


Fig. 1. (a) Photograph of a typical site showing the heterogeneous distribution of trees, logs and open grassland. (b) 48 one-hectare sites were surveyed for spiders, with a patch of open grassland, a log and a tree microhabitat sampled in a plot located at each end of every one-hectare site. All microhabitats were >10 m apart. [Colour figure can be viewed at wileyonlinelibrary.com]

The benefits and limitations of pitfall traps are well established in the literature (e.g. Melbourne 1999). In particular, trap captures are known to reflect both the density and activity of individuals, and are influenced by differences in habitat structure that could facilitate or impede the movement of individuals. With this in mind, we improved comparability among the three microhabitat types in three ways (i) we used two traps at each microhabitat, and then pooled these data to increase total captures, (ii) we examined sampling completeness using accumulation curves and richness estimators (details below) and found similar levels of observed *versus* expected richness for each microhabitat type and (iii) we square-root transformed our count data before compositional analysis to reduce the influence of abundant species on among-sample differences.

Each of the microhabitats was sampled once within a plot of 25 m radius, with two plots per 1-ha site (Fig. 1b). In a few cases, we could not locate a suitable tree or log within 25 m of the centre of the plot so that microhabitat element was not sampled. We deployed the pitfall traps for 3 weeks during March–April 2007. Traps consisted of 200 mL plastic jars dug in flush with the soil surface, each with 100 mL of propylene glycol as a preservative. All spiders (including adults, sub-adults and identifiable juveniles) were sorted to morphospecies (*sensu* Oliver & Beattie 1996) and counted. A reference collection of type specimens were identified to family, genus and species (where possible) by an expert taxonomist at the Australia Museum, Sydney.

Vegetation and soil surveys

Every site was surveyed during 2007 to quantify the volume of coarse woody debris, number of plant stems and ground-layer plant biomass. All woody debris over 10 cm in diameter was identified and their length and diameter recorded and converted to a volume (m³). All tree stems greater than 10 cm in diameter at breast height (DBH) were recorded. Ground-layer plant biomass was estimated from 30 quadrats (0.5 × 0.5 m) placed systematically in each site, and multiplied by a factor to give a total biomass per hectare (McIntyre *et al.* 2010). Percentage cover of leaf litter and bare ground was estimated from the same quadrats as plant biomass, and soil C:N ratio was derived from soil cores taken from quadrats, with full details given in McIntyre *et al.* (2010).

Statistical analysis

To what extent do spider assemblages differ between microhabitat types?

We compared spider assemblages among the three microhabitat types in three different ways. First, we compared estimates of observed and ‘total’ species richness of spiders using species accumulation curves produced with the software EstimateS 9.1 (Colwell 2013). We used the Chao 1 estimator for total species richness as it is both robust to small grain sizes (Hortal *et al.* 2006) and appropriate for abundance data (Colwell 2013). We used 1000

randomizations of the data to produce means and standard deviations, and extrapolated to 96 samples to make fair comparisons among the microhabitat types relative to sampling effort. Second, we tested for differences in spider assemblage composition among microhabitats using a multi-response permutation procedure (MRPP, PC-Ord 6, McCune & Mefford 2011). This test compares the average within-group distance with the overall average distance between samples in multivariate space. Greater within-group agreement among samples of a pre-defined group (i.e. microhabitat type) indicate they share greater similarity, and are therefore distinct from the overall set of samples (Zimmerman *et al.* 1985; McCune & Grace 2002). Third, we used Indicator Species Analysis (Dufrene & Legendre 1997) to look for individual species of spider that had associations with particular microhabitat types more than expected by chance. We used Monte-Carlo tests of significance using 999 permutations of the data.

Do environmental attributes associated with spider species richness differ among microhabitat types?

We next looked at whether associations between site-level environmental attributes and spider species richness differed among the three microhabitat types. We used a model selection procedure with Akaike Information Criterion adjusted for small sample sizes (AICc, Burnham & Anderson 2002) to examine which set of environmental variables best explained spider species richness for each of the log, tree and open microhabitats. We used the ‘lme4’ (Bates *et al.* 2015) and ‘MuMIn’ (Barton 2016) packages in R (R Core Team 2014) to fit models with all combinations of the environmental variables of bare ground cover, litter cover, soil carbon, soil nitrogen, coarse woody debris, total biomass, total basal area and total stems, rescaling variables to a scale between 0 and 100 to ensure directly comparable model effect sizes. We used a Poisson error distribution and a logarithmic link function for spider richness data. To account for potential spatial autocorrelation within our models, we fitted plot nested within site as a random effect in the generalized linear mixed models. For each habitat element, we ranked all the resulting models, considering those within two AICc units of the lowest AICc score (Burnham & Anderson 2002). Using model averaging, we summarized the relative importance of the habitat predictor variables by summing the Akaike weights of the highest ranked models ($\Delta AICc < 2$) that included the given variable (Johnson & Omland 2004).

Is variation in spider assemblage composition associated with spatial or environmental distance, and does this differ among microhabitats types?

We investigated the effect of spatial proximity and environmental distance on spider assemblage composition in two ways. First, we used partial Mantel tests (Smouse *et al.* 1986) to test for significant correlations between among-site spider assemblage dissimilarity and either (i) among-site spatial distance while controlling for among-site environmental distance, or (ii) among-site environmental distance while controlling for spatial distance. Second, we plotted correlograms of the partial Mantel statistic (*r*) as a measure

of spatial dependency of spider assemblages from samples among defined distance classes. These analyses were performed using the 'ecodist' package (Goslee & Urban 2007) in R (R Core Team 2014). We used Bray-Curtis dissimilarity metric for square-root transformed spider data, and Euclidean distances for spatial and environmental distances. We relativized our environmental data so all variables had mean 0 and standard deviation 1. Calculations of significance were performed using 9999 permutations of the data.

RESULTS

To what extent do spider assemblages differ between microhabitat types?

We collected 86 species of spiders (2324 individuals) across our study sites. The families Gnaphosidae (14 spp.), Lycosidae (14 spp.), Zodariidae (12 spp.) and Miturgidae (11 spp.) dominated the spider fauna. The majority of species were active hunters (72 species), followed by sit-and-wait predators (9 species), as well as three species of burrow users and two of web builders.

We found that spider assemblages were distinct among the three microhabitat types in terms of species richness, assemblage composition and individual species occurrences. For species richness, both observed and estimated total species richness was highest for spiders from tree litter, intermediate near logs and lowest in open grassland (Fig. 2). MRPP tests revealed significant differences in assemblage

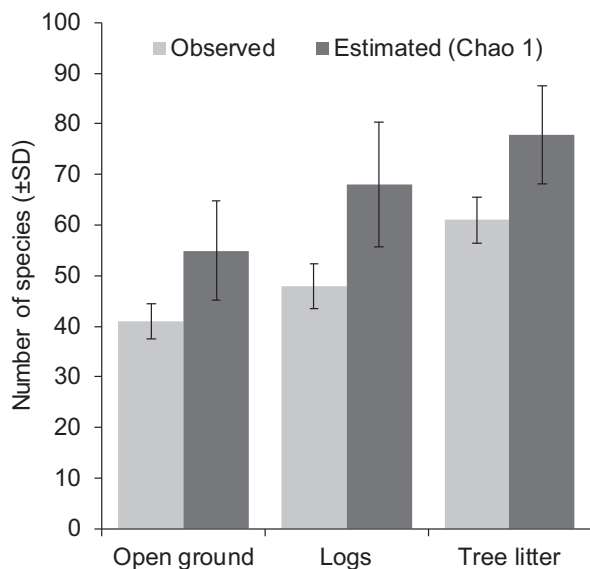


Fig. 2. Observed and estimated 'true' species richness of spiders from open grassland, logs and tree litter microhabitats. Means and standard deviations were derived from 1000 randomizations of the data, and extrapolated to 96 samples for each microhabitat.

composition among the microhabitat types ($T = -20.248$, $A = 0.029$, $P < 0.001$), with pairwise comparisons indicating the greatest difference was between open grassland and tree litter ($T = -21.187$, $A = 0.034$, $P < 0.001$), and open grassland and logs ($T = -17.204$, $A = 0.026$, $P < 0.001$). The smallest difference was between logs and trees ($T = -4.067$, $A = 0.006$, $P = 0.002$). Indicator Species Analysis identified several common species with significant non-random occurrence among the three microhabitats (Table 1). For example, *Habronestes helenae* was more common at trees, whereas *Habronestes pseudoaustraliensis* and *Habronestes ungari* were more common in open grassland.

What environmental attributes are associated with spider richness at each microhabitat type?

We found that different combinations of variables best explained species richness of spiders at each microhabitat (Table 2). The species richness of spiders at trees was best explained by a strong negative association with bare ground cover, with coarse woody debris and litter cover also included in the next best models but with smaller effects (Fig. 3). Best models for the richness of spiders in open grassland always included a positive effect of bare ground and leaf litter cover (Table 2, Fig. 3). The top models for spiders at logs included a wider range of variables, but a negative effect of bare ground and a weaker positive effect of tree basal area were the two most common variables (Table 2, Fig. 3).

Is variation in spider assemblages correlated with spatial proximity or environmental distance, and does this differ among microhabitats types?

Partial Mantel tests revealed a significant overall correlation between the spatial proximity of sites and corresponding spider assemblage dissimilarity at logs ($r = 0.151$, $P < 0.001$) and trees ($r = 0.102$, $P = 0.003$), but not for open grassland ($r = -0.035$, $P = 0.823$). The converse was true for environmental distance, with spider assemblages in open grassland significantly correlated with environmental distance ($r = 0.127$, $P = 0.007$), but not at logs ($r = -0.064$, $P = 0.909$) or trees ($r = 0.039$, $P = 0.207$). This was confirmed with the partial correlograms, which revealed a significant linear pattern of the spatial structuring among spiders at logs and trees (Fig. 4). This was most strong for logs to a distance of approximately 750 m, and then trees at a distance of approximately 250 m. By contrast, open grassland had correlations that were not linear across the full

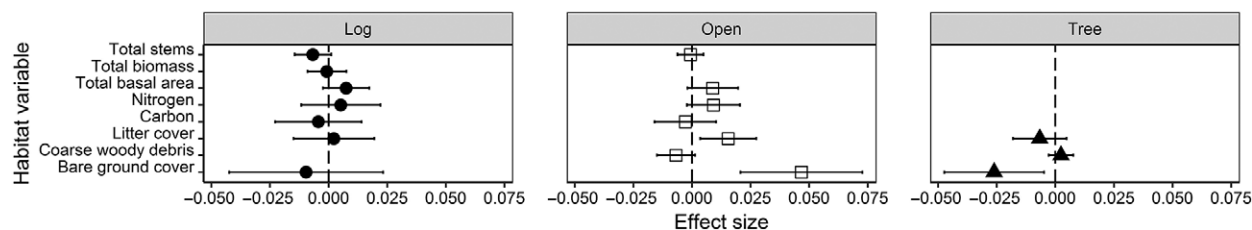
Table 1. Summary of Indicator Species Analysis showing the species of ground-active spider that were significantly associated with either open grassland, log, or tree microhabitat types

Species	Family	Preferred microhabitat	No. of individuals	P	No. of samples with this species		
					Open (n = 88)	Logs (n = 86)	Trees (n = 93)
<i>Gnaphosidae</i> sp2	Gnaphosidae	Logs	189	0.001	13	53	42
<i>Habronestes helenae</i>	Zodariidae	Trees	292	0.023	48	36	60
<i>Habronestes pseudoaustraliensis</i>	Zodariidae	Open grassland	253	0.001	50	14	11
<i>Habronestes ungaris</i>	Zodariidae	Open grassland	120	0.001	41	9	12
<i>Storosa</i> sp1	Zodariidae	Logs	81	0.025	3	41	25
<i>Nyssus albopunctata</i>	Corinnidae	Logs	56	0.010	2	15	14
<i>Tuxoctenus</i> sp1	Miturgidae	Trees	35	0.002	4	4	15

Table 2. Summary of the relative importance of habitat variables explaining species richness of spiders at each of the log, open and tree microhabitats

Microhabitat	Bare ground cover	Carbon	Coarse woody debris	Litter cover	Nitrogen	Total biomass	Total basal area	Total stems
Log	0.52	0.06	0.00	0.07	0.19	0.06	0.38	0.34
Open	1.00	0.24	0.19	1.00	0.76	0.00	0.36	0.00
Tree	1.00	0.00	0.21	0.28	0.00	0.00	0.00	0.00

Numbers are based on the sum of the Akaike weights of the highest ranked models ($\Delta AICc < 2$) that include the variable (a value of one indicates that the variable appears in all highest ranked models).

**Fig. 3.** Effects of seven environmental variables on spider species richness at each of the log, open grassland and tree litter microhabitat types. Effect sizes were determined from mixed models using only the variables that appeared in the best model. Error bars not overlapping zero are significant (e.g. bare ground cover under trees and in open grassland).

range of distances, including weak correlations at smaller distance classes, and an unexplained large correlation at the largest distance class.

DISCUSSION

Habitat structure and composition are important drivers of the diversity of arthropod communities, but are typically examined across broad environmental gradients (Carvalho *et al.* 2011), at landscape scales (Hendrickx *et al.* 2007), or with a focus on plant-dependent taxa (Schaffers *et al.* 2008). By focusing on the distinct microhabitat structures within a vegetation type, we were able to show that the richness and composition of ground-dwelling

spider assemblages not only differ between microhabitat types within a landscape, but that the environmental and spatial processes associated with each assemblage are themselves different for each microhabitat type. This provides new insight into the factors affecting fine-scale arthropod diversity within landscapes, and highlights the importance of the spatial proximity of microhabitat structures in driving assemblage turnover.

Logs, trees and open grassland as distinct microhabitats

We found that spider assemblages were different in richness and composition among the three

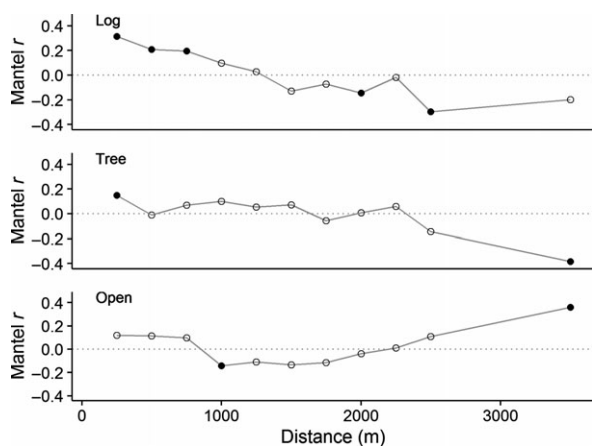


Fig. 4. Partial correlograms showing the mean correlation (r) between among-site spider assemblage dissimilarity and geographic distance (m) for log (top), tree (middle) and open (bottom) microhabitats, after accounting for environmental distance. Solid black points indicate that the spider assemblage of sites within that distance class were significantly more (positive Mantel r), or less (negative Mantel r) similar than expected by chance.

microhabitats, indicating that a distinct set of spiders were associated with these fine-scale structural components of our landscape. Species richness was highest at trees, intermediate at logs and lowest at open grassland, which matches the pattern of observed species richness of beetles (Barton *et al.* 2009) at these same microhabitats in similar nearby woodland. This gives further support for the general importance of these different woodland microhabitats as drivers of arthropod diversity and turnover. It also highlights the importance of considering microhabitat associations in sampling design, particularly if the processes of interest might be overlooked if sampling were to be pooled or randomized across the whole habitat (Herrmann *et al.* 2010).

All pairwise comparisons revealed differences in spider assemblage composition between microhabitats. Each of the microhabitats is characterized by distinct set of abiotic conditions and candidate prey species. For the eucalypt trees in our study area, this includes large amounts of leaf litter (McElhinny *et al.* 2010), which is known to affect spider assemblages (Uetz 1979), and litter-dwelling arthropods more broadly (Niemelä *et al.* 1996; Barton *et al.* 2010). For spiders associated with coarse woody debris, this habitat preference might be the result of greater soil moisture and reduced temperature extremes (Goldin & Hutchinson 2013, 2014). This can create a more favourable microclimate for both spiders and their prey compared with relatively more exposed open grassland (Birkhofer *et al.* 2010). Further, many species of saproxylic arthropods are found at logs (Ulyshen & Hanula 2009), and these likely form the part

of the diet of spiders. Notably, the amount of bare ground was an important variable affecting spider species richness in open grassland, and this might be because of greater visibility via reduced habitat complexity, and a greater chance of encountering prey (Barbosa & Castellanos 2005). However, greater amounts of bare ground had a negative effect on spiders under trees, and this may be because their preferred prey requires more complex litter environments. Testing this explanation would require manipulative experiments that added or removed litter under trees, and assessment of spider responses (Lawrence & Wise 2000). This could lead to differential exclusion or facilitation of spiders and their prey based on their body size and relative coarseness of the litter (Kaspari & Weiser 1999). Nevertheless, our study provides additional knowledge of the importance of fine-scale patchiness in bare ground and litter cover for the maintenance of spider diversity in grassy woodland ecosystems.

There are two important caveats to our findings of environmental drivers of spider richness. First is the distinct possibility that the patterns we observed at each microhabitat may change through the year as assemblages respond to seasonal forces. We sampled spiders in March, which is after summer, is warm and dry, and when many arthropods are likely to have retreated into their preferred sheltering and foraging habitat. This may contrast strongly with Spring, for example, which is characterized by increased food availability, reproduction and dispersal in many arthropods and pulses of plant growth that may alter vegetation structure. Second is the large amount of variation in spider species richness that was unexplained by our environmental variables. This suggests that the variables we examined were limited, and that other variables may be useful, such as soil moisture or grass sward structure. Exploration of other variables may perhaps provide further evidence of environmental effects contingent on microhabitat.

Geographic distance is a driver of spider assemblage heterogeneity

We found that spatial proximity of logs and trees explained similarity among samples of spiders, and that environmental distance explained variation in spider samples from open grassland. The spatial patterning of spiders at logs and trees, but not open grassland, suggests these microhabitat structures play a key role in generating spatial turnover and heterogeneity in arthropods in temperate eucalypt woodlands. Our results corroborate the findings of spatial dependence in beetle assemblages in a neighbouring woodland (Goorooyarroo Nature Reserve), an area of

similar grassy woodland habitat (Barton *et al.* 2009). Studies on predatory carabids elsewhere have also found spatial structuring at a scale of up to 800 m (Judas *et al.* 2002), but as far as we are aware, no other studies have identified spatial dependence in spider assemblages associated with logs or tree litter. Previous work on spiders has shown that assemblages adjacent to logs are different from assemblages farther away from logs (Varady-Szabo & Buddle 2006), and that log decay stage can be an important factor affecting spider richness (Varady-Szabo & Buddle 2006). Other work has shown that the volumes of woody debris on forest floors are important for spider species richness (Castro & Wise 2010). Although previous work has demonstrated scale-dependent associations with habitat (Drapela *et al.* 2008), our study is the first to show that the spatial proximity of logs is important for the turnover of spider assemblages within a single vegetation type at distances of only 100s of metres.

Dispersal may partly explain the spatial distribution patterns of some spider species (Cobbold & MacMahon 2012), and often occurs via ballooning whereby spiderlings cast fine trails of web into the air and use air currents to passively disperse (Turnbull 1973). However, ballooning is most effective for dispersal at larger landscape scales (Samu *et al.* 1999), and is more common among species with lower habitat specificity because of the haphazard nature of ballooning as a dispersal strategy (Bell *et al.* 2005). Higher beta-diversity has also been found among less vagile spider assemblages where movement is more restricted (Jimenez-Valverde *et al.* 2010), such as might be expected for species associated with spatially discrete, but stable and resource-rich microhabitats such as logs. We suggest the assemblage turnover observed in our study is driven by 'island hopping', where spiders move among and aggregate at individual logs or trees like islands in a sea of open grassland.

Explicit sampling provides insight into the contribution of microhabitat to beta diversity

The microhabitat concept, as we have used it, requires being explicit about what is sampled, and combining this with existing scaling theory about organism's perceptions of landscapes (Wiens 1989; Manning *et al.* 2004). We do not know if we have compartmentalized the environment in the most powerful way possible, but we have shown that our choice of compartmentalization (i.e. selection of microhabitat categories) explained a useful amount of variation in the spider community. Few studies make the distinction between random and deliberate sampling of arthropods in this way (Sereda *et al.* 2014).

Many studies pool data from many different microhabitats when sampling along environmental gradients, or perhaps use transects or grids that incorporate several microhabitats, thus losing the ability to assign diversity to different microhabitats and reveal unique fine-scale drivers of community variation within the context of a larger vegetation type. While researchers often scale the sampling grain and extent with the size of the organisms being studied, becoming larger for bigger organisms (Barton *et al.* 2013), the precision with which sampling locations are selected is rarely scaled in the same way. We have shown that precise sampling of microhabitats can reveal differences in the drivers of beta-diversity that are likely to be overlooked with grid-based, or fully randomized approaches.

By being explicit about what is sampled, and scaling it with body size, the microhabitat concept applies to taxa of all sizes. For example, the concept could just as easily apply to microhabitat as viewed from a mammal or bird perspective, such as strips of riparian vegetation, scattered trees, or patches of grassland in the context of large woodland or agricultural landscapes. Careful consideration of non-random sampling designs could help to reveal the drivers of turnover in species assemblages at scales commensurate with the size of the organism. Specifically, the more spatially discrete a microhabitat, the more likely it is for there to be spatial turnover among the associated species. This was highlighted by our finding that spiders from discrete logs and trees were spatially structured, but spiders from widespread open grassland were not. A similar analogy might be higher turnover in arthropod assemblages found at discrete small-scale structures on the sea bed compared with assemblages found in the open sea bed (Hewitt *et al.* 2005). This apparently a straightforward concept and is deceptively simple, yet many studies do not clearly identify what unit of habitat that are actually studying, or the degree to which it is a sensible unit of habitat from the perspective of the study organisms. We therefore conclude that being explicit about the type of habitat sampled, whether that habitat is widespread or forms discrete patches, and considering the relevance of the scale of sampling to the study taxon, can provide a more robust way of investigating drivers of compositional variation among arthropod assemblages within landscapes.

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