
Disentangling the drivers of ant community composition:
integrating structural, spatial and inter-specific competition
at multiple scales.

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Abstract

Understanding the drivers of community composition are crucial to providing effective conservation of biodiversity. Currently, community or ecosystem-based conservation strategies are considered the best approach for conserving cryptic or otherwise poorly quantified diversity such as invertebrate fauna, under the logic that conserving some representative subset of all communities across the landscape we are also conserving all the species that inhabit that landscape. Communities are typically defined in terms of plant community composition, and unique assemblages of plants that are rare or subject to historically high rates of loss are often afforded legal protection under biodiversity conservation legislation. This form of plant community surrogacy assumes a strong correlation between patterns of plant community composition and assemblage patterns of purportedly represented taxa, however this assumption is rarely tested. Patterns of community composition may instead be the result of a variety of other drivers besides those tied to plant community composition, including inter-specific competition or stochastic processes resulting in spatially structured assemblages.

My thesis seeks to evaluate the efficacy of plant community-based strategies for conserving cryptic biodiversity, using ants as a model system. I investigate the roles of environmental and spatial drivers of ant community composition, and also the influence of inter-specific competition in shaping assemblages of ants. I first evaluated the success of a regional plant community-based conservation strategy for representation of ant assemblages across the Sydney region, Australia. I sampled ant and plant assemblage composition, and structural attributes of habitat across 40 sites from five distinct plant communities, including four listed as Endangered or Critically Endangered under state and national legislation. I found a weak association of ant assemblages with plant community composition, with only those community pairs varying strongly in structural composition of vegetation supporting unique

assemblages. Despite the weak associations, plant community composition was the strongest predictor of ant assemblages, however structural variation amongst samples also contributed to observed assemblage composition. Spatial turnover amongst ants was low overall, however I found stronger within-community turnover patterns, and the strength of this relationship also varied greatly amongst community types.

I then investigated the relative importance of plant community, habitat structure and spatial drivers of ant assemblage composition at fine scales in a mosaic of plant communities within the NSW South-West Slopes bioregion. I used Multiple Regression on Distance matrices to partition explained variation amongst assemblage drivers. Spatial turnover was the strongest predictor of ant assemblage composition, with assemblages also showing some association with habitat structure. Plant community composition alone showed weak significant association with ant assemblages, however this association was driven entirely by shared spatial autocorrelation of assemblages and structural differences amongst plant communities. Habitat complexity was found to influence assemblages by reducing the fine-scale abundances of highly aggressive competitively dominant species. Abundances of dominant species at fine-scales in turn negatively affected the abundances of competitively subordinate ant species. The abundance of dominant species had a negative effect on species richness of subordinate species at fine scales, however they had no effect at intermediate or coarse spatial scales.

I found competitive exclusion between the two most abundant dominant species in the study area, *Iridomyrmex purpureus* and *I. chasei*. To investigate the potential influence of variable competitive influences on ant community assemblages, I sampled ant assemblages along well-defined territory boundaries. I also compared the strength and uniformity of competitive dominance at food resources within territories of the two species. I found very strong inter-specific competition between dominant species, resulting in rapidly shifting territory

boundaries with *I. chasei* consistently encroaching into the territory of *I. purpureus* and regularly usurping nests. Food resources were more consistently won by the numerically dominant *I. chasei*, resulting in lower species richness of affiliate ant species attending baits, and significantly different assemblage composition of species attending baits between territories occupied by the two species.

In conclusion, I found that plant community surrogacy provided only weak representation of ant assemblages, and only at coarse scales when comparing broadly different plant community classes. Within communities, and amongst structurally similar plant communities, spatial turnover in assemblages was strong and resulted in highly spatially structured ant communities. Assemblages also appear to be structured in part by inter-specific competition, both in terms of non-random patterns of spatial association amongst dominant species, but also through suppression of competitively subordinate species by dominant ants. These findings are especially important to the implementation of biodiversity offsetting strategies, as ant assemblages represented in compensatory habitat would likely be compositionally distinct from those lost through development if offsets are located large distances from lost habitat.

Declaration

The research described in this thesis, except where acknowledged, is all my own original work. Conceptual ideas were developed in collaboration with my supervisors Associate Professor Dieter Hochuli and Dr Mathew Crowther.

Signed:



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Chapter 1

General introduction

1.1 Diversity and distributions of species

The question of what drives the distribution and abundances of species has been central to ecology for over a hundred years, and drove the development of fundamental theories of ecology. The niche concept was originally formulated to relate the distribution, behaviour and morphology of species to aspects of their environment, including the availability and type of food resources and climatic requirements (Grinnell 1917). This concept was later expanded to incorporate aspects of trophic position and inter-specific interactions, particularly in recognising the functional influences species can have on their environment (Elton 2001). It was then further developed to recognise the differences between a species' potential niche based on abiotic restrictions and resource availability (the 'fundamental' niche) and the actual, reduced niche breadth occupied by a species (the 'realised' niche) (Hutchinson 1957). The difference between fundamental and realised niche space are introduced by interspecific interactions, most notably negative associations due to competition for resources and predation (Hutchinson 1957). Niche theory remains central to explanations of both species occurrences and community assembly (Chase and Leibold 2003).

Ultimately, species occurrences are also influenced by biogeographical processes. The current distribution and abundance of a species is a function of speciation, dispersal and historical distributions at a continental scale (Ricklefs 1987, Gaston 2000, Webb et al. 2002), all interacting to determine suitability to local environmental and competitive conditions. Biogeographical processes are also responsible for broad patterns of species diversity and endemism across the globe, such as the increase in diversity at lower latitudes (Dirzo and Raven 2003). At more local levels, the island biogeography theory enables prediction of species occurrences based on probabilistic models of chance dispersal, extinction and colonization (MacArthur and Wilson 1963, 1967). Although the application of island

biogeography theory to fragmented terrestrial systems has been criticised in some quarters owing the fundamental differences in the systems being compared, key principles outlining the roles of spatial turnover and habitat composition remain central to understanding the distribution of species across landscape types.

1.2 Community assembly

The interplay between environmental associations of species and inter-specific interactions (including positive associations) are crucial in integrating individual species into communities. Early developments in community theory came from the field of vegetation science, and sought to relate patterns of association amongst plant species to their environment. Early studies of successional processes following disturbance lead to the development of the concept of plant communities as entities analogous to individual organisms (Clements 1916, 1920). This formulation of the community concept proposed strong inter-connectedness of species leading to discrete community units associated with climate (Clements 1936). In sharp contrast, the Continuum theory of plant communities emphasises the individual responses of species to environmental gradients in determining fundamental patterns of association (Gleason 1926). Under this model, each species within a community responds to their environment independently, and observed associations between species are therefore a result of indirect shared association with a common set of environmental factors (Gleason 1926, Goodall 1963). Although our understanding of the drivers of community assembly have progressed considerably, questions of inter-connectedness of species in communities versus individualistic association are still relevant from a practical perspective.

Explanations for co-occurrence of species in communities, particularly those sharing a common resource base, account for much of the community ecology literature. Niche theory

predicts that the number of co-occurring species should be limited, and that this limit is a function of the degree of similarity between competing species (MacArthur and Levins 1967). Limits to the co-occurrence of competing species may even guide community assembly to the extent that certain species combinations are ‘forbidden’ (Diamond 1975). Contemporary niche theory explanations of community assembly derived from individual-level responses to environment and competition and are still central to community theory (Chase and Leibold 2003). Neutral theories however emphasise the role of stochastic processes in shaping community structure, and argue that coexistence amongst species occupying the same trophic levels can be explained without the need for niche differentiation or differences in competitive abilities (Hubbell 2001). Chief amongst stochastic processes guiding community assembly is dispersal limitation, resulting in high rates of spatial turnover (Hubbell 2001, Condit et al. 2002, Volkov et al. 2005).

It is now widely supported that community assemblage patterns are a combined result of both niche-based drivers resulting in environmental associations, and stochastic processes such as dispersal limitation leading to spatial structure in assemblages (Condit et al. 2002, Tuomisto et al. 2003, Gravel et al. 2006, Steinitz et al. 2006, Thompson and Townsend 2006, Smith and Lundholm 2010). The relative degree to which communities are assembled by niche-based drivers (resulting in environmental associations in communities) and stochastic drivers (resulting in spatial structure in communities) varies across taxonomic groups (Chase and Myers 2011). Primarily, spatial structure in communities driven by dispersal limitation is related to the traits of species within those groups (Thompson and Townsend 2006).

1.3 Beyond species-level conservation: utilizing ecological communities as conservation units

Conserving habitat is central to protecting biodiversity and preventing species loss (Margules and Pressey 2000). Species-level conservation is unrealistic for conserving all species due to incomplete knowledge of species distributions, abundances and sensitivity to threatening processes. For example, the threat status of invertebrate species has been assessed for only 1% of described species, despite invertebrate species often comprising the bulk of diversity across the landscape, and many invertebrate groups facing similar levels of threat to vertebrate species (Collen et al. 2012). For this reason, conservation strategies aim to maximise the number of species represented by utilizing habitat units as a basis for practical conservation management. Community-level conservation strategies employ ecological community-based units as a basis for allocating conservation priority across the landscape. This approach partitions landscapes into fine-scale management units based on biotic patterns of species associations tied to abiotic factors (Ferrier and Guisan 2006).

Most often, plant communities are utilized as a surrogate for ecological communities due to their close associations with underlying abiotic factors (Ferrier and Guisan 2006), and as existing, well-developed vegetation classification systems provide an ideal basis for practical conservation management (Keith 1999, Tozer 2003). In Australia, plant communities that have suffered disproportionately high rates of historical loss, such as those associated with soils and climates with high agricultural land use potential or urban development (Auld and Tozer 2004), are afforded legal protection under biodiversity conservation legislation at national (DOE 2015) and state levels (NSW Office of Environment and Heritage 2015). This legislation acts to restricts development in high conservation value areas to limit impacts on ‘threatened ecological communities’ alongside threatened species, including on private land to allow conservation to extend beyond the protected area network.

Central to this approach is an assumption that conserving some representative portion of all plant communities will also conserve all underlying components of biodiversity across the landscape. This implies that all purportedly represented components of ecological communities, such as invertebrate species, show strong community-level congruence with plant community associations. The direct associations between plant community composition and structural components of habitat (Mac Nally et al. 2002), and the strong congruence between plant communities and underlying bioclimatic variables (Ferrier and Guisan 2006) provide a conceptual basis for predicting assemblage-level congruence. The degree to which underlying species assemblages respond to niche-based (environmental) drivers versus stochastic drivers resulting in spatially structured assemblages may relate directly to how well they are represented by plant community surrogacy strategies.

Assemblages showing strong niche-based associations with underlying abiotic conditions, particularly those conditions that also shape plant community composition, will be well represented by plant community surrogacy strategies. Assemblages that are predominantly stochastically driven and that show strong spatial assemblage structure however will be less likely to show strong congruence with plant community composition across the landscape.

Previous studies have demonstrated strong spatial turnover patterns amongst invertebrate assemblages compared to vertebrate assemblages (Oliver et al. 1998, Ferrier et al. 1999), and weak representation of invertebrate species by broad community or landscape-based surrogates (Ferrier 1997, Mac Nally et al. 2002, Rodrigues and Brooks 2007). It is therefore critical to evaluate the effectiveness of practical plant community surrogacy strategies in conserving the breadth of biodiversity across landscapes.

1.4 Study system: ant communities

Ants comprise a large proportion of ground-dwelling invertebrate fauna, and are particularly diverse both at a continental scale (Dunn et al. 2009) and at local scales across Australia

(Andersen 2007). Ants provide an ideal model system for assessing congruence with plant communities not just due to their diversity and abundances. Ant communities also have parallels with plant communities due to aspects of life strategies and the structuring of communities (Andersen 1991). Both plants and ants have mobile dispersal agents during reproduction (seeds in plants, winged reproductives in ants) but are otherwise sessile during maturity. Australian ant species also conform to discrete functional group categorizations that may be analogous with plant growth forms with respect to competition for resources and structural influences on other groups (Andersen 1995). For example, competitively dominant species are analogous to trees as both monopolize resources (light, space, nutrients and water in plants, foraging territory and food resources in ants) and have strong regulating effects on other community components. By contrast, competitively subordinate opportunistic species are analogous to grasses, both being highly sensitive to and dominating only in the absence of other growth forms or functional groups.

Competition is a central theme in ant community ecology (Hölldobler and Wilson 1990), with highly aggressive and competitively dominant ants often monopolizing resources and suppressing abundances of competitively subordinate species (Savolainen and Vepsäläinen 1988, Andersen 1992, Andersen and Patel 1994). Consequently, competitively subordinate ant species display a range of adaptations to minimise direct competition, including shifting peak foraging to suboptimal times (Briese and Macauley 1980, Cerdá et al. 1998b) and behavioural adaptation to rapid discovery and exploitation of resources (Fellers 1987).

Strong interference competition can also occur between dominant ant species, sometimes resulting in mutually-exclusive territories between dominant species (Greenslade 1976a, Fox et al. 1985, Greenslade 1987, Savolainen and Vepsäläinen 1988). Despite the strong aggressive dominance exerted at the local scale, manipulative experiments have failed to replicate predicted structuring effects of dominant ants on community composition (Andersen

and Patel 1994, Gibb and Hochuli 2004, Gibb and Johansson 2011). Local ant species richness also appears to not be negatively affected by dominant ant abundances (Andersen 2008). The role of inter-specific competition in shaping assemblage composition and species richness is therefore unclear.

1.5 Aims and structure of thesis

The aim of my research is to investigate the roles of environmental and stochastic assemblage drivers, and also inter-specific interactions in shaping ant community composition across the landscape. The primary goal of this research is to evaluate the efficacy of plant community surrogacy for conserving poorly known or cryptic fauna such as invertebrates, using ants as a model system.

In chapter two I evaluate the efficacy of plant community surrogacy for representation of ant assemblages in a practical regional conservation strategy. I compare the assemblages of ants across five plant communities in the Sydney region, Australia, including four listed as threatened under biodiversity conservation legislation. I compare observed assemblage patterns to the plant community composition and structural attributes of vegetation across sites, and also the geographical distances between sites, to determine the relative contributions of environmental and spatial assemblage drivers in shaping ant assemblage patterns. I relate these findings to the efficacy of this approach to landscape-scale conservation. This chapter is currently in review for the journal *Ecological Applications*.

In chapter three I compare the influences of environmental drivers (plant community composition and habitat structural attributes of vegetation) against stochastic drivers of ant assemblage composition. I utilize a spatially-explicit sampling design to effectively partition the spatial and environmental components of variation in assemblage composition of ants, to

further evaluate the efficacy of plant community surrogacy, and also evaluate neutral theory predictions of community assembly in ant communities.

In chapter four I investigate the effect of inter-specific competitive pressures exerted by competitively dominant ant species in structuring ant assemblages, and the role of fine-scale microhabitat complexity in mediating this effect. I compare the abundances of dominant, sub-dominant and subordinate ant species sampled at three spatial scales (individual traps, plots and sites), and relate these to patterns of microhabitat complexity. I then relate observed fine-scale relationships between microhabitat complexity and abundances of dominant and subordinate ants to observed patterns at higher levels of spatial organisation. I also compare co-occurrence patterns of dominant ant species at fine and intermediate scales to identify patterns of non-random association. This chapter utilizes ant abundance data collected as part of the previous chapter (Chapter 3) to answer fundamentally different ecological questions.

In chapter five I investigate the effects of dominant ant identity in structuring ant assemblage composition, by comparing assemblages of ants across the mutually-exclusive territories of two highly aggressive dominant ant species identified in the previous chapter. I sample ant assemblages and also compare performance of ants at tuna baits across territory boundaries, to investigate assemblage composition responses to the competitive dominance effects of two dominant species highly divergent in traits. I also compare the relative uniformity of dominant ant competitive pressures across space by measuring the proportion of tuna baits monopolized by the two dominant species within their respective territories, and relate this to site-level assemblage composition and species richness of ant species recorded at baits between territories.

A note on redundancy and authorship

My thesis has been written as a series of manuscripts intended for publication, and as such there is redundancy in the introductions and discussions of the individual papers. As these manuscripts have been prepared to represent collaborative research between myself and my supervisory team, I use the collective active voice ('we') in Chapters 2-5.

Chapter 2

**Threatened plant communities as surrogates
for affiliated invertebrates: structural,
compositional and spatial drivers**

Abstract

Practical biodiversity conservation strategies often employ ecosystem or community-level surrogacy to represent total biodiversity. Unique plant communities facing disproportionate threat may be given legal protection through restriction on development. Impacts of development are often mitigated through biodiversity offsetting strategies, where habitat is conserved and managed to compensate for losses elsewhere. Plant community conservation however assumes congruence between plant community composition and underlying cryptic or rarely quantified aspects of ecological communities, and this assumption is rarely tested empirically. We compared assemblages of ants amongst five plant communities (including four listed under threatened species legislation) across 40 sites within the Sydney region, Australia. We used Multiple Regression on Distance Matrices (MRM) to partition the effects of plant community composition, structural attributes of vegetation and spatial turnover on ant assemblage composition.

At a coarse scale, plant communities supported unique assemblages of ants independently of structural composition of vegetation and spatial autocorrelation of sites. Co-occurring and structurally similar plant communities however did not support distinct ant assemblages. The overall strength of congruence between plant communities and ant assemblage composition was weak, limiting representation of ant species through plant community surrogacy in a practical context. Although spatial assemblage patterns were weak across all communities, some communities showed strong within-community turnover patterns. It is therefore important to conserve communities across their extent rather than just within high integrity remnants, particularly when implementing biodiversity offsetting strategies as assemblages of cryptic fauna conserved in compensatory habitat may be compositionally distinct from those lost through development.

Keywords: plant communities, threatened ecological communities, biodiversity
offsetting, arthropod conservation, ants, BioBanking, ant conservation, Cumberland
Plain.

2.1 Introduction

Habitat-based approaches are central to practical conservation of biodiversity (Margules and Pressey 2000, Brooks et al. 2006). As information on species occurrences and threats is incomplete in all cases, surrogate systems must be employed to represent rarely quantified biodiversity, such as invertebrate fauna or non-vascular plants (Rodrigues and Brooks 2007). Landscape-based surrogacy (the “coarse-filter”) partitions landscapes into biogeographical units based on shared environmental and abiotic traits, such as ‘ecoregions’ at very coarse spatial scales (Olson and Dinerstein 1998), or ‘landscape systems’ at intermediate scales (Oliver et al. 2004). Fine-scale partitioning of landscapes for biodiversity conservation management is often achieved through incorporating biological assemblage information into management units, most often through identification and mapping of distinct plant communities (Ferrier et al. 2002).

Plant communities (recurring patterns of associated plant species occurring across the landscape) present a theoretically ideal surrogate measure as they are strongly tied to underlying environmental variables such as soil, rainfall, slope, aspect and elevation (Ferrier and Guisan 2006), and may even directly influence availability of microhabitat elements through variation in the growth forms and densities of plant species within communities (Mac Nally et al. 2002). Historical plant community distributions also correlate strongly with agricultural land use potential, meaning some plant communities have suffered disproportional rates of loss over time (Tozer 2003). The development of methods for identifying distinct plant communities based on recurring patterns of plant assemblages, and relating these communities to underlying abiotic environmental variables has enabled the development of complex predictive models of historical plant community extent (Keith 1999, Tozer 2003, Ferrier and Guisan 2006), from which the historical losses and contemporary

threats to each plant community can be derived. The strong representation of underlying environmental variation achieved through plant community surrogacy suggests strong representation of underlying cryptic fauna (particularly invertebrate animals) in landscape-scale conservation strategies. As the task of assessing the extinction threat to the breadth of invertebrate species is an insurmountable task (Collen et al. 2012), community-level strategies for representation of biodiversity have gained favour. Recently, the IUCN Red List criteria have been expanded to incorporate ecosystems, enabling globally-consistent assessment of threat to communities (Keith et al. 2013). This new IUCN Red List criteria has been successfully applied at the plant community level (Tozer et al. 2014).

Designated conservation reserves form an integral part of regional conservation strategies. However, incorporation of areas into the reserve system has often been based on opportunistic acquisitions rather than strategic regional conservation planning (Pressey et al. 1993). High economic value areas such as productive agricultural land are typically beyond the reach of acquisition, leading to those plant communities of highest conservation significance being under-represented in reserve systems. Hence, protected habitat often needs to extend beyond the formal reserve system and into private land through restrictions on land use. Legal protection of plant communities or collections of related plant communities has been implemented within Australia in varying forms, including protection of ‘threatened ecological communities’ nationally (DOE 2015) and through a range of state-level legislative frameworks. Although typically described through a combination of plant assemblage composition, parent geology and geographical extent, the ‘ecological community’ is defined under the New South Wales *Threatened Species Conservation Act 1995*, as “an assemblage of species occupying a particular area”, meaning threatened ecological communities aim to represent the breadth of taxonomic diversity (NSW Office of

Environment and Heritage 2015). While mechanisms of protection vary, all require formal assessment of developments to prevent or minimise impacts. Conservation of threatened ecological communities is particularly prevalent around coastal and urban centres (Auld and Tozer 2004) where pressures on remnant native vegetation are often greatest. Native vegetation within urban centres also face a myriad of other threatening processes, most notably habitat loss and fragmentation leading to small remnant sizes, edge effects and invasion by weeds (Fahrig 2003, Fischer and Lindenmayer 2007). These processes can lead to reductions in species richness and changes in assemblage composition of species in smaller remnants (Gibb and Hochuli 2002, Drinnan 2005).

Impacts on plant communities through habitat loss are often mitigated through biodiversity offsetting strategies (Alvarado-Quesada et al. 2014). For example, the BioBanking scheme operational in New South Wales allows for the offsetting of plant community or threatened species habitat losses under a “no net loss” framework, whereby acquired land is protected and managed in perpetuity to compensate for losses elsewhere (DEC 2006). Despite the attractiveness of this practice from a planning perspective, several key issues surrounding its implementation have been identified (Gonçalves et al. 2015), particularly the determination of ‘equivalence’ and appropriate land area in matching offsets (Maron et al. 2012), the required spatial fidelity of offset sites (Gordon et al. 2011), and the trading of immediate loss over uncertain future gains (Morris et al. 2006, Gibbons and Lindenmayer 2007, Bekessy et al. 2010). In spite of these issues, the scope of biodiversity offsetting in New South Wales is likely to be expanded based on the recommendations of a recent review of biodiversity legislation (Byron et al. 2014).

The key assumption of surrogacy based on plant communities (and derived biodiversity offsetting strategies) is that conserving some representative subset of all plant communities

across the landscape also conserves the breadth of unquantified biodiversity occurring within that same landscape. This assumption implies a degree of homogeneity amongst purportedly represented taxa within plant communities, and strong assemblage-level cross-taxon congruence with plant community composition (Su et al. 2004). Evaluation of plant community surrogacy therefore requires consideration of patterns of change in species composition of target taxa across the landscape (β -diversity) (Whittaker 1960, 1972).

Patterns of β -diversity are governed predominantly by two different assembly processes: spatial turnover driven primarily by stochastic processes such as dispersal limitation; and niche-based processes driven by environmental heterogeneity (Condit et al. 2002, Freestone and Inouye 2006, Steinitz et al. 2006, Thompson and Townsend 2006). Different taxonomic groups however differ markedly in patterns of β -diversity, based on differences in the strength and scale at which they adhere to these two assembly processes, and the specific environmental filters of assemblage patterns within groups (Ferrier et al. 1999, Chase and Myers 2011). Observed patterns of congruence will therefore be a result of either shared environmental filters, direct influence of plant communities on assemblages (e.g. through variation in habitat structure and microhabitat availability), or simply shared spatial autocorrelation due to spatially confounded plant community distributions. The relative strength of spatial turnover in target taxa is particularly relevant to biodiversity offsetting, as taxa showing strong spatial assemblage patterns would likely be unrepresented in compensatory habitat, particularly when located some distance from the impacted areas (Johst et al. 2011). Consequently, evaluations of plant community surrogacy must evaluate both environmental and spatial variation in assemblage composition of target taxa.

Our understanding of the effectiveness of plant community surrogacy is grounded in studies of cross-taxon surrogacy of plant assemblages and other data-rich groups, particularly

vertebrate animals (Grantham et al. 2010, Barton et al. 2014). Despite a wealth of literature on congruence of species richness patterns, evaluations of compositional congruence of plant assemblages with cryptic or otherwise rarely quantified diversity (particularly invertebrate taxa) are rare and typically focus on coarse vegetation classes and/or regional spatial scales (Oliver et al. 1998, Ferrier et al. 1999, Mac Nally et al. 2002), rather than specific plant communities within a local legislative context. Studies have evaluated broad-scale environmental and spatial drivers of invertebrate assemblage patterns (Ferrier 1997, Ferrier et al. 1999), however the role of fine-scale structural drivers in shaping assemblage patterns have been overlooked. Other investigations of the relative contributions of plant species composition and structural drivers of invertebrate assemblages have neglected the role of stochastic spatial patterns in assemblage composition (Stoner and Joern 2004, Schaffers et al. 2008).

We sought to evaluate the efficacy of plant community surrogacy for conserving underlying ant assemblages within a legislative framework of conserving ‘threatened ecological communities’. Ants provide an ideal target group for evaluating plant community surrogacy for invertebrate conservation in an Australian context, as they typically comprise the majority of ground-dwelling arthropod fauna and show characteristically high local diversity across the continent (Andersen 2007, Dunn et al. 2009). Ants also show consistent functional group level responses to a range of habitat disturbances at a continental scale (Hoffmann and Andersen 2003), as well as local assemblage and species richness responses to fragmentation and urbanisation (Gibb and Hochuli 2002). Additionally, ant assemblages show compositional responses to variation in habitat complexity within plant communities (Lassau and Hochuli 2004, Lassau et al. 2005a).

We sampled ant and plant assemblages and structural attributes of habitat in remnant native vegetation within the Sydney region, NSW, Australia to address the following questions: (i) Do structural habitat traits of vegetation vary amongst plant communities? (ii) What are the drivers of ant species richness within urban remnant native vegetation, and what are the relative strengths of these drivers? Are these drivers congruent with structural differences amongst vegetation communities? (iii) Do different plant communities support unique assemblages of ants? (iv) To what degree are ant assemblages spatially structured, and does this vary among different community types? (v) What are the relative strengths of association of ant assemblages to spatial or environmental drivers?

2.1 Methods

Study area and conservation significance

We conducted our study within the Cumberland Plain (and associated Hornsby Plateau), of the Sydney region, NSW, Australia (lat., long.: 33° 53'S, 151° 7'E. The study area supports 22 unique plant communities (Tozer 2003), of which 14 are currently listed as threatened under NSW and/or National legislation (Table 1). The Cumberland Plain is bounded by the Blue Mountains to the west, the Hornsby Plateau to the North and the Woronora Plateau to the South (Figure 1). It stretches east into current-day metropolitan Sydney, where few remnants of native vegetation currently remain. The Cumberland Plain is characterised by a gently undulating low plain of primarily clay soils derived from the Wianamatta Shale formation, bounded by elevated plateaus of sandy-loams derived from the Hawkesbury and Woronora sandstone formations, which underlay the Wianamatta formation (Chapman and Murphy 1989). The Wianamatta formation also extends into to the Hornsby Plateau, where

Table 1. Attributes and underlying abiotic predictors of plant communities sampled in this study. Information adapted from Tozer (2003).

Community	Form	Status (TSC Act/ EPBC Act)	Tozer (2003) map unit(s)	Parent geology	Typical soils	Extent (pre- 1788/ 1997)(Ha)	Rainfall (mm) (Mean/ Range)
Blue Gum High Forest (BHGF)	Tall wet sclerophyll forest	Critically Endangered/ Critically Endangered	152 - Bluegum High Forest	Wianamatta shale, Hawkesbury Sandstone, Mittagong formation	Shale-derived clays on Hornsby Plateau	3720/ 165 (4.5%)	1050/ 816-1250
Cooks River/ Castlereagh Ironbark Forest (CCIF)	Dry sclerophyll open forest to low woodland	Endangered/ Endangered (nominated)	3 - Castlereagh Ironbark Forest	Tertiary alluvium, Holocene alluvium, Wianamatta shale	Alluvial clays	12211/ 1012 (8.3%)	853.6/ 799-960
Cumberland Plain Woodland (CPW)	Dry sclerophyll woodland or open forest	Critically Endangered/ Critically Endangered	10 - Shale Plains Woodland 9 - Shale Hills Woodland	Primarily Wianamatta shale	Shale-derived clays	125449/ 11054 (8.8%)	823.7/ 722-923
Sandstone Ridgetop Woodland (SRW)	Structurally variable shrubby woodland to open forest	Not listed	31 - Sandstone Ridgetop Woodland	Hawkesbury Sandstone, Mittagong formation	Loamy sands and sandy loams	Not calculated	1178/ 837-1509
Shale/sandstone Transition Forest (SSTF)	Grassy or shrubby woodland to open forest	Endangered/ Endangered	1 - Shale/sandstone transition Forest (Low-sandstone influence) 2 - Shale/sandstone transition Forest (High-sandstone influence)	Wianamatta shale, Hawkesbury Sandstone, Mittagong formation	Transitional sandy-clays and clayey-sands	45355/ 9960 (21.5%)	870.7/ 26-28.9

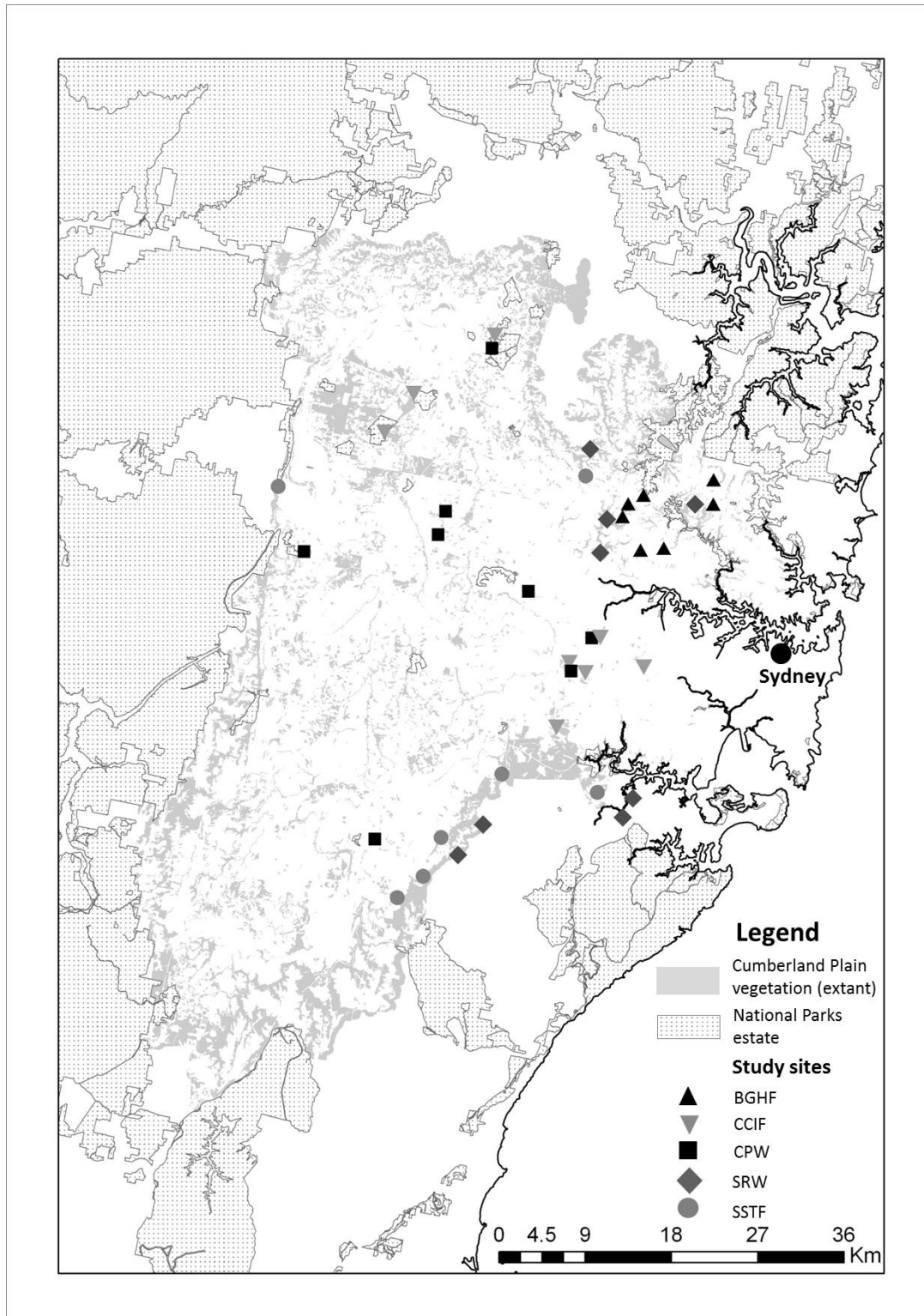


Figure 1. Location of study sites within the Cumberland Plain and Hornsby Plateau. BGHF = Blue Gum High Forest, CCIF = Cooks River/Castlereagh Ironbark Forest, CPW = Cumberland Plain Woodland, SRW = Sandstone Ridgetop Woodland, SSTF = Shale/Sandstone Transition Forest.

shale outcroppings overtop underlying Hawkesbury Sandstone. A variety of other soils also occur within the study area, most-notably transitional sandy-clay and clayey-sand soils on the boundaries of the Cumberland Plain, and clays formed from Tertiary-alluvium (Chapman and Murphy 1989).

Since the establishment of Sydney in the late Eighteenth Century, the vegetation of the Cumberland Plain has been cleared first through the establishment of rural satellite towns, followed by more recent expanding of urban development enveloping most of the remaining areas. The deep clays soils of the Cumberland Plain were much more fertile than the surrounding sandstone-derived soils, and served as the “food bowl” of Sydney (Benson 1990, Haworth 2003). The ongoing expansion of urban development of Sydney continues to impact on native vegetation, with only 13.1% of the original extent remaining (Tozer 2003). The remaining vegetation forms a matrix of largely disconnected fragments (see Figure 1). To diminish the rate of loss of native vegetation, many of these vegetation communities have been listed for protection under the New South Wales *Threatened Species Conservation Act 1997* (TSC Act) and National *Environmental Protection and Biodiversity Conservation Act 1999* (EPBC Act).

We selected five vascular plant communities (out of 22) for comparison, due to their conservation significance, large and often overlapping spatial extents, and representation of the broad compositional and structural variation of vegetation within the study area. We sampled 40 sites, comprising eight sites of each vegetation community. Remnants ranged from 1.9 to 5414 ha in extent, with some sites connected to the largely continuous network of vegetation surrounding the Sydney basin. Some larger reserves contained a number of distinct vegetation communities and where possible two different communities were sampled within the same reserve. Owing to the congruence of vegetation communities to underlying

soil and climatic conditions, remaining examples of each vegetation community were often spatially clustered (see Figure 1). Hence, where possible, we chose sites that maximised the geographical spread of samples within each community, and provided the greatest possible spatial overlap between communities sampled. Sites were restricted to national parks or designated public reserves. Management of sites varied though most had some form of active weed eradication at either a commercial or community-based volunteer level.

Vegetation communities sampled

The five communities sampled were Bluegum High Forest (BGHF), Cooks River/Castlereagh Ironbark Forest (CCIF), Cumberland Plain Woodland (CPW), Sandstone Ridgetop Woodland (SRW) and Shale/sandstone Transition Forest (SSTF). Where relevant, these communities conform to relevant Final Determinations under the State TSC Act and National EPBC Act. These communities are summarized in Table 2. Full community characterisations are detailed by Tozer (2003).

Sampling

Plant community composition was sampled in 20x20 metre quadrats. Two plots were established per site: 'edge' being <20m from the edge and subject to edge effects, and 'interior' being mostly >60m from the edge of the reserve, however in some smaller sites this was not possible. All plant species present were recorded and allocated a cover-abundance score using a modified Braun-Blanquet score (Poore 1955) following Tozer (2003).

Structural attributes of vegetation within the 20x20m quadrat were also recorded (see Table 2). Attributes of vegetation condition, such as extent of native vegetation in the patch and distance to nearest native vegetation (a proxy measure of isolation) were calculated using GIS in ArcMap version 10 (ESRI Software 2010). Sites connected to the largely continuous

Table 2. Predictor variables collected within 20x20 vegetation plots for inclusion in models for ant species richness and ant assemblage composition.

Variable	Description
Categorical	
Vegetation community	Identity of vegetation community sampled
Sample	Interior or edge sample
Reserve	Identity of reserve or patch sampled
Vegetation structure	
Canopy height	Mean upper canopy height (m)
Sub-canopy height	Mean sub-canopy height (m)
Shrub height	Mean shrub layer height (m)
Ground height	Mean ground vegetation height (m)
Canopy cover	Projected foliage cover of canopy (%)
Sub-canopy cover	Projected foliage cover of sub-canopy (%)
Shrub cover	Foliage cover of shrub layer (%)
Ground cover	Foliage cover of ground vegetation (%)
Bare ground cover	Cover of bare ground (%)
Litter cover	Cover of leaf litter and fine woody debris (%)
Coarse woody cover	Percentage cover of coarse woody debris (>2.5cm diameter) and logs (%)
Vegetation condition	
Reserve extent	Total area of native vegetation in reserve or patch (Ha)
Nearest native vegetation	Distance to nearest native vegetation (km)
Nearest continuous vegetation	Distance to nearest continuous (>6000 Ha) vegetation (km)
Native species richness	Total native plant species in sample
Exotic species richness	Total exotic plant species in sample

system of National Parks and reserves surrounding the Sydney basin were allocated a size value of 6000 Ha (larger than the largest isolated fragment) in statistical analyses.

Ant assemblages were sampled in the same 20x20m quadrat using nine pitfall traps (small 150mL cylindrical plastic vials (diameter 45mm) containing 50mL of 100% Ethylene Glycol) placed in a 3x3 grid spaced at 10m. Traps were left for a minimum of five days before opening to minimise ‘digging in’ effects (Greenslade 1973). All traps were opened over a three day period commencing 10th May 2011 and left open for eight days. Traps were then closed and collected in the order they were opened, over three days. Ants were sorted from the traps and transferred to 70% ethanol, then identified to species or morphospecies in the lab. Species-level identifications were confirmed or conducted by Alan Andersen (CSIRO Tropical Ecosystems Research Centre, Winellie NT). Abundances of each species were recorded at the trap level, and pooled to plot level for analyses.

Analyses

Plant community composition

Validation of assigned plant communities was confirmed using cluster analysis based on group average of raw Braun-Blanquet abundance scores using Primer v. 6 (Clarke and Gorley 2006). Dissimilarity was calculated using Bray-Curtis dissimilarity to maximise comparability with the ant data collected. Exotic plant species were excluded from samples for all community analyses.

Structure of vegetation communities

We compared structural attributes of vegetation amongst vegetation communities using multiple analysis of variance (MANOVA) in R version 3.0.2 (R Core Team 2013), using sequential Bonferroni corrections to account for multiple comparisons. Tukey’s HSD *post-*

hoc tests were carried out on individual one-factor ANOVAs to identify community-level differences between each pair of vegetation communities.

Ant species richness

A substantial number of traps (94 out of 720) were removed from the ground during the sampling period., with chew marks on discarded traps suggesting canine interference. Species richness across all samples was estimated by standardising sampling effort to nine traps across all samples using extrapolation of sample-based rarefaction in EstimateS program (Colwell and Elsensohn 2014). We used un-biased chao-1 and chao-2 estimates. Only samples with five or more intact traps were used for further analyses (only 65 of the 80 samples were used for all species richness and community composition analyses). The number of samples employed in the final analysis did not vary significantly across plant communities, with between 12 and 14 samples in either 7 or 8 sites per community.

We compared estimated species richness of ants amongst vegetation communities using a three-factor blocked ANOVA for vegetation community, sample and reserve. We compared amongst vegetation communities using Tukey's HSD. We used linear mixed-effect models to compare estimated species richness against structural attributes of vegetation, using a model averaging approach to account for model uncertainty (Burnham and Anderson 2002). Predictor variables were standardized with a mean of zero and a variance of one. A manageable subset of predictor variables (n=9) was then selected based on lowest Akaike's Information Criterion (AICc) values (Burnham and Anderson 2002). We generated a set of models using all combinations of remaining variables using a Gaussian distribution, and ranked them based on AICc values using the R package 'MuMIn' (Bartoń 2012). We calculated the Akaike weight and AICc difference (Δ AICc) for each model, then applied model averaging to models with a Δ AICc of less than two (Burnham and Anderson 2002).

We used the model-averaged parameter estimates from all models, weighted by the Akaike weights, to determine the direction and magnitude of effect sizes for each variable (Burnham and Anderson 2002). Uncertainty of parameter estimates was based on the unconditional standard error for each variable.

Plant community relationships with ant assemblages

We visually represented similarity in ant assemblages amongst vegetation communities, using non-metric multidimensional scaling (nMDS) based on Bray-Curtis dissimilarity matrix. We also compared ant assemblages across samples using permutational multivariate analysis of variance (PERMANOVA) based on 999 permutations. We used a three-factor model for vegetation community type, reserve, and sample (interior or edge), with reserve nested within community. We used single-factor PERMANOVAs to identify significant comparisons between vegetation community pairs. We identified ant species contributing to the dissimilarity amongst vegetation communities using SIMPER analysis. These analyses were performed in Primer (and Permanova) v. 6 (Clarke and Gorley 2006). We also compared multivariate dispersion amongst vegetation communities with the PERMDISP2 procedure (Anderson 2006) in the Vegan package in R. We used a Tukey's HSD test to compare dispersion between all community pairs.

Spatial drivers of assemblages

Spatial autocorrelation of plant and ant species composition (similarity of samples based on distance between them) was examined using Mantel tests based on Bray-Curtis dissimilarity. Spatial autocorrelation of ants within plant communities (using only pairwise distances from the same community type) were also performed. The scale of autocorrelation in ant assemblages was also examined using a Mantel correlogram, using Sturge's rule to determine

the appropriate number of lag matrices classes used (Legendre and Legendre 2012). We generated appropriate distance classes based on the distribution of site-pair distances in our dataset. These analyses were performed using the ‘ecodist’ package in R (Goslee and Urban 2007). We adjusted p-values using sequential Bonferroni corrections.

Comparing spatial and environmental drivers of ant assemblages

We used Multiple Regression on Distance Matrices (MRM) (Smouse et al. 1986, Lichstein 2007) to compare the relative influence of plant community composition, structural attributes of vegetation and spatial autocorrelation of samples on ant community composition. MRM generates a multiple regression model for a response matrix (here Bray-Curtis dissimilarity amongst ants samples) against any number of predictor matrices, using a permutation procedure to perform statistical significance testing. MRM is able to account for the hierarchical structure of vegetation community relationships, and also the within-community variability in plant species composition through comparing relationships amongst samples in Bray-Curtis dissimilarity of plant assemblages rather than broad community classifications. By generating distance matrices for each variable of interest, MRM is able to compare ant assemblage dissimilarity directly against structural predictors and geographical distance amongst samples. Distance-based linear model analyses are known to suffer from low statistical power, however the spatially-explicit nature of our question makes it an appropriate analysis for our data (Legendre and Fortin 2010).

We generated Euclidean distance matrices for each variable, then standardized all matrices for a mean of zero and variance of one to allow direct comparison of coefficients in the final model. We generated a subset of predictor matrices by first identifying pairs of variables showing strong linear correlations, then removing those showing the weakest linear correlations with ant assemblage dissimilarity (lowest Mantel-R) (Mantel 1967) from the

MRM model. We also generated a series of lag matrices based on the lag distance classes used for the Mantel Correlogram above. Lag matrix values were coded as zero for all distances falling within the given distance range, and one for all distances outside that range. A global MRM model was then generated in the ‘ecodist’ package, incorporating all lag classes showing significant spatial autocorrelation in the Mantel Correlogram, plant assemblage dissimilarity, and structural variables. Models were run based on Pearson correlation and 1999 permutations.

2.3 Results

We recorded 526 plant species (including 103 exotic species and four species listed as threatened under NSW and/or Commonwealth legislation) in the sampled vegetation communities. We caught 4199 ants in 87 species in pitfall traps, representing 37 genera in six subfamilies. No exotic ant species were recorded.

Plant community composition

Samples represented their purported vegetation community classes well as shown by cluster analysis (Figure 2), with some exceptions. These exceptions were typically basal to groupings and represented borderline examples or transitional communities. For example, vegetation sampled at Lake Parramatta Reserve was associated with outcropping sandstone and deep sandy soils, however some shale influence is apparent in the composition of shrub and understorey species. The canopy was also primarily *Eucalyptus pilularis*, a species present in a number of communities but common in Blue Gum High Forest, explaining the loose affiliation with this community in the cluster analysis. We retained our original community classification as these largely represent the best possible interpretations of legal

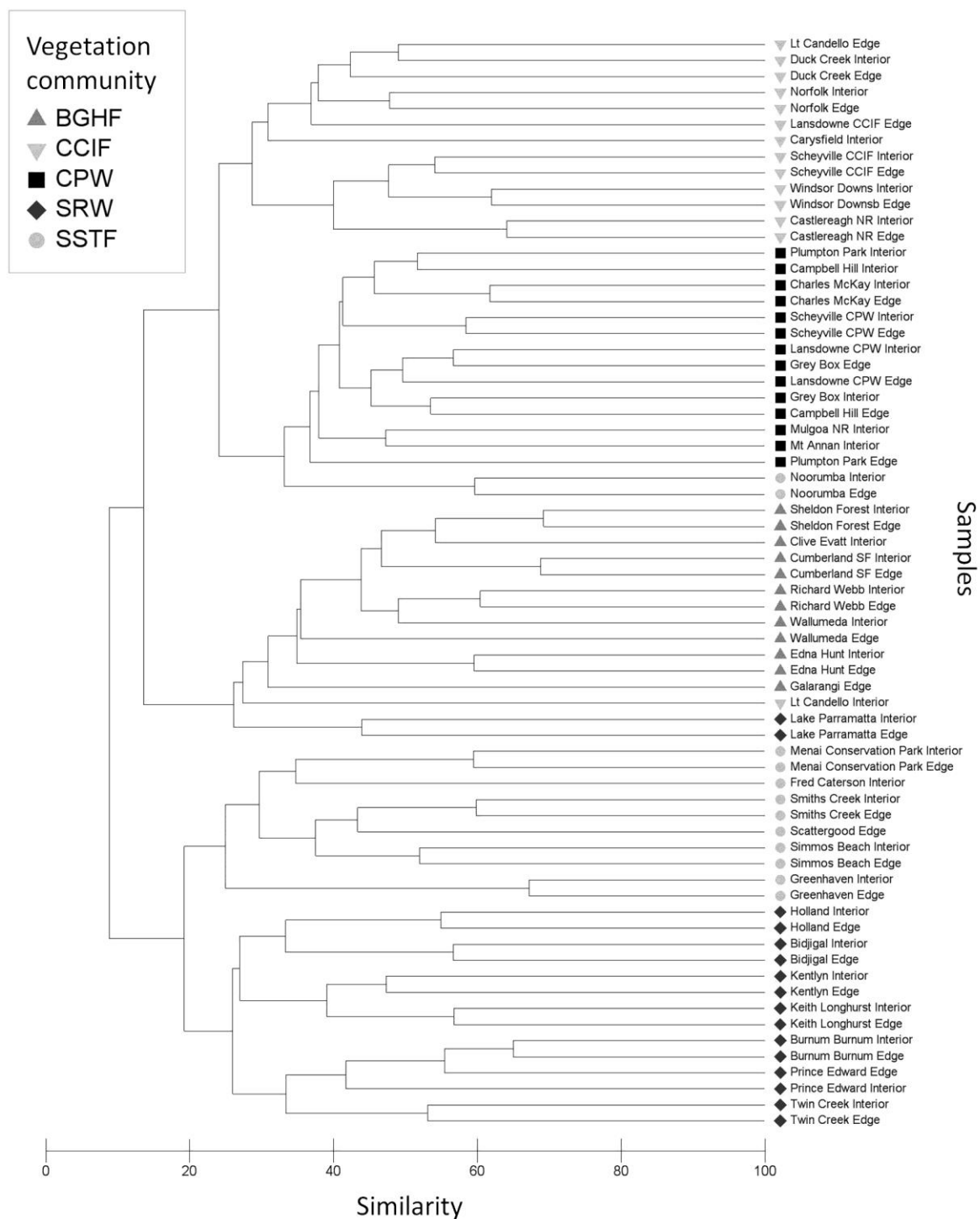


Figure 2. Cluster analysis of plant community samples based on Bray-Curtis dissimilarity of raw Braun-Blanquet abundance scores.

definitions of these communities based on the Final Determinations for State (TSC Act) and National (EPBC Act) legislation. Our samples also revealed a hierarchy of relatedness amongst communities, with Cumberland Plain Woodland and Cooks River/Castlereagh Ironbark Forest are the most similar communities, grouped more broadly with Blue Gum High Forest. Sandstone Ridgetop Woodland and Shale/sandstone Transition Forest form a separate cluster. Samples taken from the same reserve were typically more closely related in species composition than other samples within community type.

Structure of vegetation communities

Several structural attributes of vegetation varied amongst communities (Table 3), for example Blue Gum High Forest had a much taller and denser canopy than all other communities (Table 4). Other distinct community differences include significantly lower litter cover in Cumberland Plain Woodland than all other community types, offset by a characteristically taller ground vegetation cover.

Species richness

Estimated ant species richness was significantly different among vegetation communities ($F_{4,65} = 6.4$, $P < 0.001$) and sample ($F_{1,65} = 5.34$, $P < 0.005$) but not reserve ($F_{32,65} = 1.8$, $P = 0.062$). CPW sites were significantly more species-rich than CCIF (diff=3.23, $P < 0.01$), SRW (diff=4.32, $P < 0.001$) and SSTF (diff=3.04, $P < 0.05$) sites. There were no significant differences in species richness among other communities. The total number of species recorded in each community varied from 39 in BGHF to 48 in CPW, with both SRW and CCIF supporting 44 species, and SSTF supporting 41 species.

Five linear mixed-effect models returned a ΔAIC value of < 2 from the best model (Table 5), which were then used for model averaging. Parameter estimates and standard error of

Table 3. MANOVA results of vegetation structural variables compared amongst plant community classifications. Presented P-values adjusted using sequential Bonferroni corrections.

	Df	Sum of Squares	Mean Square	F-value	P-value (Bonf.)	Resid. Mean Sq	Resid. F-value
Height (m)							
Canopy	4,60	2619.92	654.98	63.43	<0.001	619.53	10.33
Sub-canopy	4,60	22.44	5.61	1.02	0.663	328.62	5.48
Mid-storey	4,60	1.12	0.28	1.66	0.515	10.10	0.17
Ground-storey	4,60	0.22	0.05	6.62	<0.001	0.50	0.01
Cover (%)							
Canopy	4,60	2089.20	522.31	7.96	<0.001	3939.20	65.65
Sub-canopy	4,60	1241.90	310.48	2.16	0.338	8629.60	143.83
Mid-storey	4,60	1192.50	298.12	1.17	0.663	15232.90	253.88
Ground-storey	4,60	15987.00	3996.70	13.50	<0.001	17770.00	296.20
Bare ground	4,60	971.80	242.96	4.10	0.026	3555.20	59.25
Litter	4,60	17624.00	4406.00	13.42	<0.001	19698.00	328.30
Log	4,60	864.93	216.23	8.60	<0.001	1509.32	25.16

Table 4. Mean value differences and significance levels for pairwise Tukey's HSD test results for vegetation structural variables between plant community pairs. Negative values indicate a larger value for plant communities listed in the horizontal row. Asterisks denote statistically significant comparisons (*= <0.05 , **= <0.01 , ***= <0.001).

Height (m)	Cover (%)				Cover (%)	Cover (%)			
	BGHF	CCIF	CPW	SRW		BGHF	CCIF	CPW	SRW
Canopy					Canopy				
CCIF	-14.95***				CCIF	-14.20***			
CPW	-15.16***	-0.21			CPW	-13.85***	0.36		
SRW	-17.22***	-2.27	-2.06		SRW	-9.68*	4.52	4.17	
SSTF	-15.89***	-0.94	-0.73	1.33	SSTF	-15.51***	-1.31	-1.67	5.83
Ground					Ground				
CCIF	-0.105*				CCIF	-40.85***			
CPW	-0.103*	0.002			CPW	-4.78	36.07***		
SRW	0.029	0.134**	0.132**		SRW	-31.09***	9.76	26.31**	
SSTF	0.008	0.113*	0.111*	-0.021	SSTF	-20.67*	20.18*	15.89	10.42
					Bare ground				
					CCIF	7.12			
					CPW	9.4*	2.29		
					SRW	9.62*	2.50	0.21	
					SSTF	10.87**	3.75	1.46	1.25
					Litter				
					CCIF	-2.03			
					CPW	-42.39***	-40.36***		
					SRW	-2.21	-0.18	40.18***	
					SSTF	-17.63	-15.6	24.76**	-15.42
					Log				
					CCIF	-0.41			
					CPW	-1.13	-0.71		
					SRW	9.06***	9.48***	10.19***	
					SSTF	2.15	2.56	3.27	-6.92*

Table 5. Coefficients of the five best linear mixed-effect models for estimated species richness of ants (change in AIC values (Δ) of less than two).

Intercept	Ground-layer vegetation height	Litter cover	Nearest cont. native vegetation	Nearest native vegetation	df	log- Likelihood	AICc	Δ	weight
9.557 +/- 0.381	-	-1.375 +/- 0.378	-	-0.695 +/- 0.394	7	-157.542	331.049	0.000	0.151
9.547 +/- 0.396	-	-1.223 +/- 0.381	-	-	6	-159.023	331.495	0.446	0.121
9.564 +/- 0.378	-0.419 +/- 0.353	-1.359 +/- 0.377	-	-0.707 +/- 0.392	8	-156.962	332.496	1.447	0.073
9.554 +/- 0.385	-	-1.279 +/- 0.395	0.360 +/- 0.410	-0.740 +/- 0.403	8	-157.136	332.844	1.795	0.062
9.554 +/- 0.395	-0.400 +/- 0.360	-1.206 +/- 0.380	-	-	7	-158.510	332.984	1.935	0.058

Table 6. Parameter estimates of model-averaged linear mixed-effect models for estimated ant species richness.

	Estimate	Standard Error (adj.)	Z-value	P-value	Relative importance
Intercept	9.555	0.4011	23.823	<0.001	
Litter cover	-1.299	0.4062	3.198	<0.01	1.000
Nearest vegetation	-0.708	0.4104	1.724	0.085	0.620
Ground height	-0.410	0.3741	1.097	0.273	0.280
Nearest cont. vegetation	0.360	0.4253	0.846	0.397	0.130

predictor variables based on model averaging are shown in Table 6. Only litter cover was significantly (negatively) associated with estimated ant species richness, and was included in all five of the best models. Distance to nearest native vegetation also showed a non-significant negative association and was included in three of the best models.

Plant community relationships with ant assemblages

Two-dimensional ordination of relationships amongst samples (nMDS, Figure 3) shows some vegetation communities supported unique assemblages of ants. However, the observed stress value for the 2D ordination is high (0.28, hence should not be over-interpreted). There was a strong dissociation between CPW and SRW. However there was substantial overlap between some of these communities in assemblage composition, with some communities (particularly BGHF and SSTF) showing broad within-community variation.

Ant assemblages were significantly different between vegetation communities (Pseudo-F= 1.902, $P < 0.001$) and reserves (Pseudo-F= 1.632, $P < 0.001$), however there was no effect of sample (Pseudo-F= 1.142, $P = 0.295$). Only four out of ten community comparisons were significantly different (Table 7). Ant assemblages from BGHF sites showed greatest dissimilarity amongst the communities, being significantly different from all other communities except SRW. The nMDS shows a large spread of BGHF sites relative to the other communities, and a lack of separation BGHF sites from other communities. However, the BGHF group showed similar dispersion to all other communities. Only the CPW-SRW pairwise PERMDISP2 Tukey's HSD comparison being statistically significant (diff. = 0.097, $P < 0.05$), with SRW sites showing greater dispersion.

Most species (79.3%) were recorded in fewer than ten samples, and half (50.6%) were recorded in three or fewer samples. Thirty species (34.5% of recorded species) were

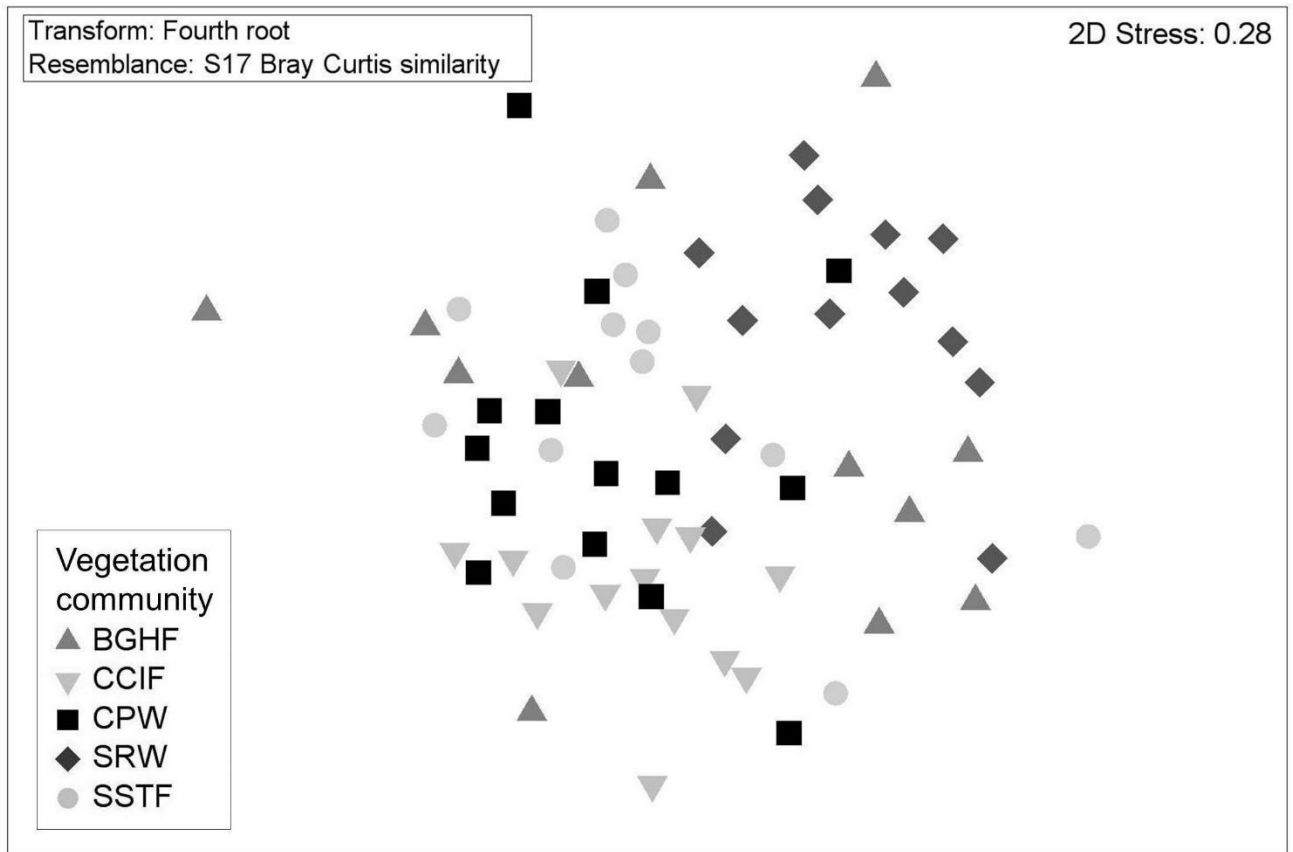


Figure 3. Non-metric multidimensional scaling (nMDS) ordination of ant assemblage composition based on vegetation community.

Table 7. Pseudo-F values for pairwise comparisons of Bray-Curtis dissimilarity of ants amongst plant communities based on single-factor PERMANOVA. Asterisks denote statistical significance of comparisons (*= <0.05 , **= <0.01 , ***= <0.001).

	BGHF	CCIF	CPW	SRW
CCIF	1.90**			
CPW	1.89***	1.12		
SRW	1.25	1.13	1.31*	
SSTF	1.40*	1.19	1.25	1.04

recorded in a single sample. Only one species (*Rhytidoponera metallica*) was recorded in more than half of samples (n=58). Thirty-five species (40.2%) were recorded in only one plant community, and only 13 (14.9%) were recorded in all communities. Of those species restricted to one community, four were from SRW, five from BGHF, eight from SSTF and nine from each of CCIF and CPW. Eight relatively abundant species (mean 4th-root abundance of > 0.4) were absent from one or more plant communities. Samples from CCIF sites were missing five out of these eight abundant species. Only one abundant species was not present in SRW sites. *Pheidole* sp. C was abundant in BGHF (mean 4th-root abundance 0.77) but absent from three of the other four communities.

The species contributing the most to these differences amongst communities were typically the most abundant species overall. The opportunist species *Rhytidoponera metallica* was the most abundant species in all of the communities sampled, and variation in the magnitude of their abundance was the strongest driver of assemblage differences in seven of the ten pairwise tests. This species was most abundant in Cumberland Plain Woodland (mean 4th-root abundance 2.36) and least abundant in Sandstone Ridgetop Woodland (1.09). The second most abundant species was *Pheidole* sp. E, being second-most abundant in four of the five communities and third-most in the remaining community, and contributed the most to community differences in the remaining three pairwise community comparisons. Other species contributing most to community-level differences were *Aphenogaster longiceps*, *Anonychomyrma* sp. A (*nitidiceps* group), *Tapinoma* sp. A, *Pheidole* sp. A and *Notoncus* sp. A (*enormis* group).

Table 8. Total and within-community Mantel test results for ant assemblage similarity (Bray-Curtis dissimilarity) against geographical distance between site pairs.

Subset	Number of comparisons	Mantel R	P-value
Total	2078	0.058	0.098
BGHF	78	0.149	0.088
CPW	91	0.564	<0.001
CCIF	91	0.136	0.084
SSTF	66	0.282	0.075
SRW	66	0.067	0.243

Spatial drivers of assemblages

We found significant spatial autocorrelations of samples based on plant species composition (Mantel- $r = 0.259$, $p < 0.001$). No spatial autocorrelation was detected in ant species composition in the Mantel test (Table 8). Spatial patterns within-communities however showed varied responses amongst plant communities (Table 8). CPW sites showed stronger spatial assemblage patterns than other communities studied, particularly SRW (Figure 4).

Sturge's rule determined 12 lags were appropriate for the Mantel Correlogram of ant assemblage dissimilarity. We determined the appropriate lag class break points to be 0, 3, 7, 12, 15, 18, 21.5, 25, 29, 32, 36, 43 and 60km, with between 73 and 231 site pairs within each class (greater resolution was given to the shortest distance classes due to the expected stronger positive spatial autocorrelation at these distances). Positive spatial autocorrelation was detected in the first distance lag (lag midpoint 1.5km, see Figure 5).

Comparing spatial and environmental drivers of ant assemblages

Four structural variables were retained for the final MRM model: canopy height, ground-storey height, litter cover and shrub cover. Only the first lag distance matrix (representing distances of 0-3km) was included in the model to represent geographical distance between samples. Plant assemblages similarity was the best variable for predicting ant community composition in the MRM model (Table 9), with ground-layer vegetation height also significantly associated. As all predictor matrices were standardised to have a mean of zero and variance of one (besides the spatial lag matrix), coefficients are directly comparable as a relative strength of association (Lichstein 2007).

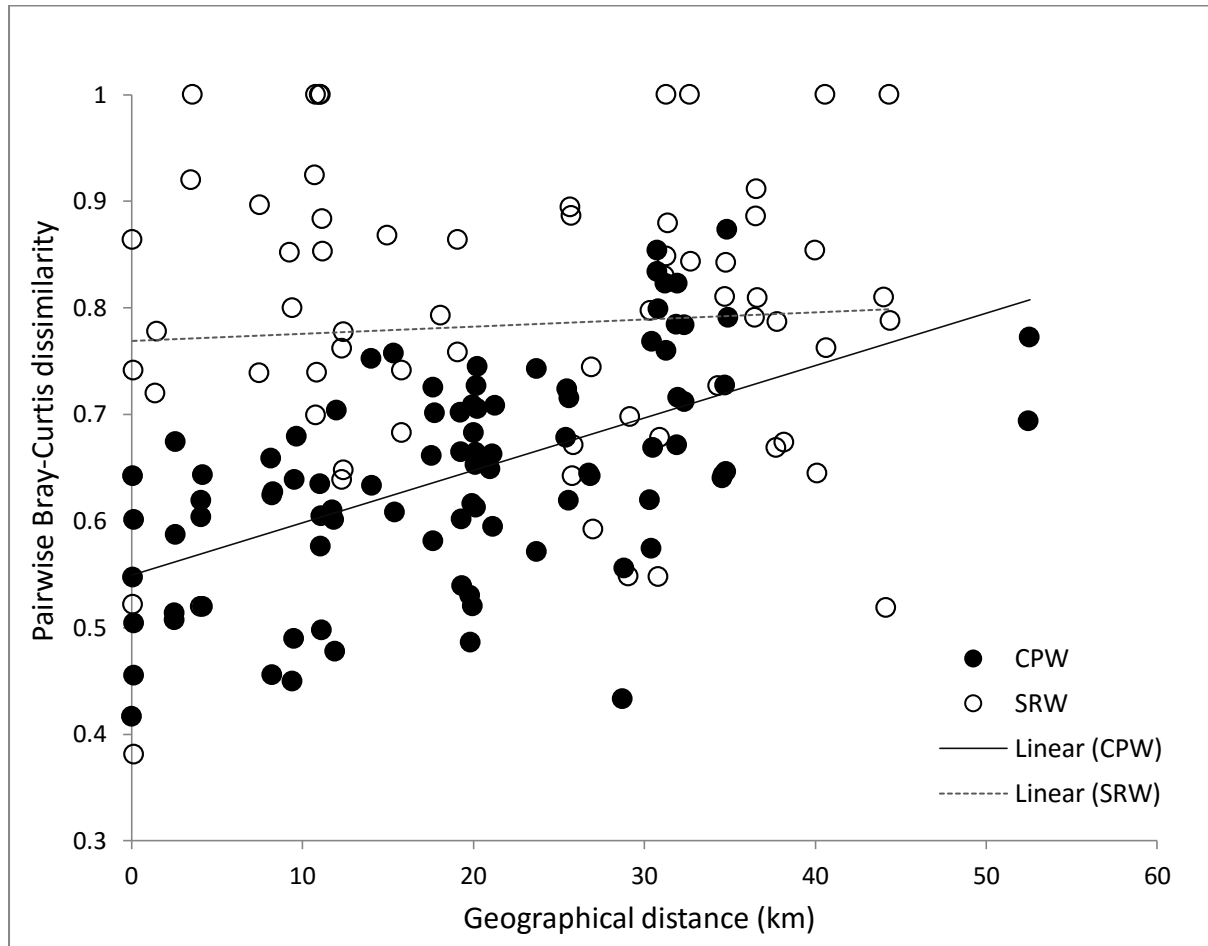


Figure 4. Comparison of within-community pairwise differences in ant assemblage composition across geographical distance for Cumberland Plain Woodland sites (closed circles) and Sandstone Ridegetop Woodland sites (open circles).

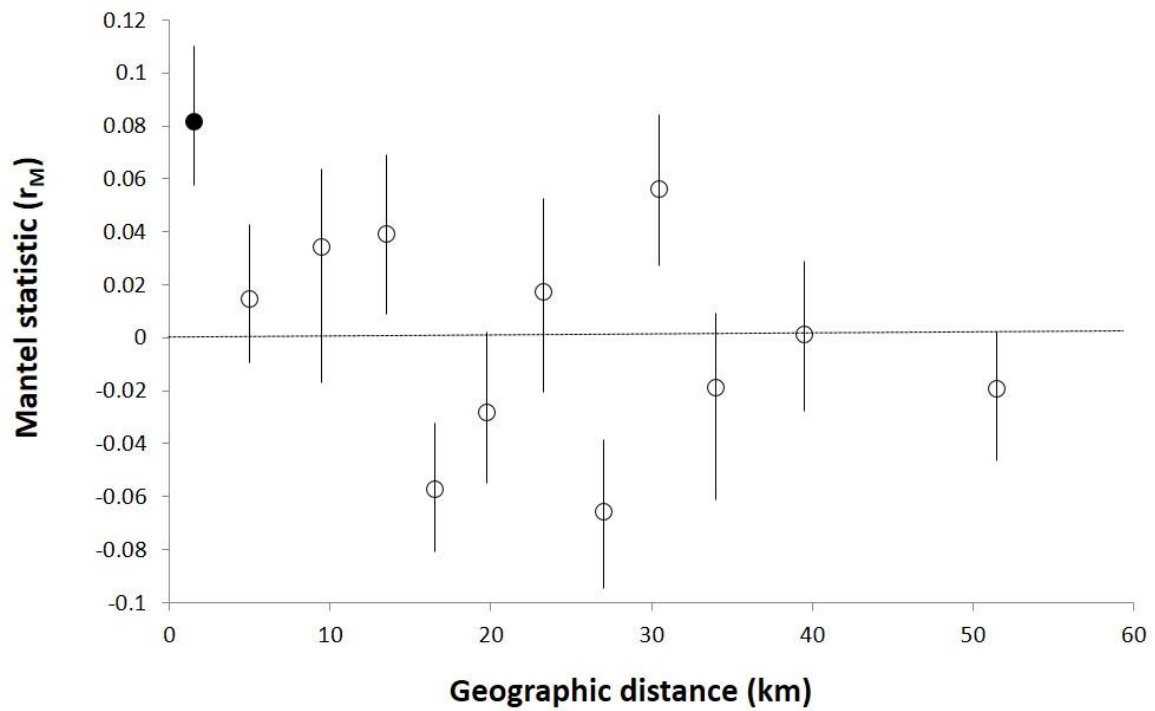


Figure 5. Mantel Correlogram of Bray-Curtis distance in ant assemblages against geographic distance between samples. Solid circles indicate sequential Bonferroni corrected P-values of <0.05.

Table 9. Results of Multiple Regression on Distance Matrices (MRM) model for ant assemblage Bray-Curtis dissimilarity. Coefficients are based on distance matrices standardized for equal variances and means of zero.

Model R ² = 0.095	Coefficient	P-value
Intercept	-0.102	0.420
Plant assemblage dissimilarity	0.208	<0.001
Geographic distance (lag 1)	0.106	0.420
Canopy height	0.109	0.083
Ground-storey height	0.107	<0.05
Litter cover	0.024	0.545
Shrub cover	-0.027	0.572

2.4 Discussion

Plant community-level assemblage patterns

Our results provide some limited support for the use of plant community surrogacy for conserving ants within a local legislative framework, as: (i) different plant communities occurring within a local context supported distinct assemblages of ants; and (ii) pairwise dissimilarity in plant community composition was found to be the strongest predictor of ant assemblage dissimilarity amongst samples. For example, ant assemblages within CPW sites were significantly different from assemblages supported by the surrounding matrix of vegetation on soils derived from the Hawkesbury Sandstone, and from assemblages within BGHF on the Hornsby Plateau. Comparisons of communities co-occurring within and on the peripheries of the Cumberland Plain (CPW, CCIF and SSTF) however showed a largely homogenous ant assemblage composition. These communities, while showing some community level differences in structural variables (ground vegetation height and cover, and litter cover) all conform to a broad dry-sclerophyll woodland or open forest form. The community supporting the most distinct ant assemblages, Blue Gum High Forest, was in contrast a tall wet-sclerophyll forest form. For this reason, our results do not provide any evidence of increased representation of underlying species assemblages through partitioning of native vegetation into discrete units derived solely from unique associations of plant species, as compared to simply basing conservation units on broad vegetation forms.

Structurally distinct but co-occurring vegetation forms have long been known to support different assemblages of ants, for example between woodland and heathland (Andersen 1986a, Andersen 1986b) and between tropical savanna and rainforest (Andersen et al. 2008). These examples however relate to vastly different community types, varying dramatically in microhabitat availability and even microclimate at the scales encountered by ground-dwelling

invertebrates. Variation in the complexity of habitat at the ground level can dramatically affect its suitability for invertebrate species through regulation of foraging success (Gibb and Parr 2010), favouring species displaying particular morphological traits, such as large size and long legs, in more complex microhabitats (Kaspari and Weiser 1999). Our results show strong community level differences amongst plant communities in litter cover, which was greater in BGHF samples than all other communities sampled. The mesic environments encountered by ground-dwelling invertebrates in BGHF sites (moist and structurally complex microhabitats featuring deep leaf litter) support specialized genera such as *Leptomyrmex* which were found only in this community in our study.

Structural complexity of vegetation within Sandstone Ridegetop Woodland sites in our study area has been shown to affect assemblage composition of ants (Lassau and Hochuli 2004), as well as wasps (Lassau and Hochuli 2005) and beetles (Lassau et al. 2005b). We found that structural variation in vegetation responsible for ant assemblage differences was well represented by the surrogate measure of variation in plant assemblage composition, however one structural variable (height of ground vegetation) showed a significant independent contribution to explaining ant assemblage composition. This finding suggests that incorporating structural diversity alongside compositional diversity in landscape-based assessments of conservation significance may provide an additional dimension to representation of underlying biodiversity. Incorporating a range of species compositional and richness data, as well as environmental data into classification of conservation units has been shown to maximise the representation of communities in a protected area network (Arponen et al. 2008).

Spatial turnover of ant assemblages

The observed weak spatial structure of ant assemblages across all samples contrasts with our strong within-community structure in Cumberland Plain Woodland samples. The pattern within CPW sites is very strong, with a Mantel-R value of 0.564 (explaining 56% of the variation in pairwise dissimilarities amongst samples), compared to the non-significant Mantel-R of 0.054 in the comparison of all samples. Three other communities (BGHF, CCIF and SSTF) also show stronger spatial association however are only statistically significant at the $\alpha=0.1$ level. Statistical significance in these comparisons is likely limited by the low power characteristic of Mantel tests (Legendre and Fortin 2010) combined with the low number of within-community pairwise comparisons available.

Our results demonstrate that patterns of spatial turnover in assemblages were not constant amongst plant communities within the landscape. This finding limits the generality of studies of β -diversity patterns, including comparative studies of β -diversity across taxonomic groups. The identities of the communities showing the greatest and weakest spatial turnover in ant assemblages are also counter-intuitive. Cumberland Plain Woodlands, prior to European settlement, occurred within a single largely continuous flat plain without significant barriers to dispersal, whereas the Sandstone Ridgetop Woodland community is a much more structurally and compositionally variable community occurring within more topographically complex sandstone-derived landscapes (Tozer 2003). In addition, sites of Sandstone Ridgetop Woodland occurring within the South and North of the study area are dissected by the Cumberland Plain. The within-community variability in assemblages reflects this degree of topographical heterogeneity, with SRW sites having greater multivariate dispersion than CPW. This greater degree of heterogeneity suggest a larger pool of species and more rare species occurring within the SRW community leading to the greater pairwise dissimilarities,

however this community supported the smallest number of unique species not found in other communities of all the communities sampled. Conversely, CPW supported the greatest number of species overall, the equal greatest number of unique species, and the highest sample-level species richness of all the communities sampled.

Plant community surrogacy as a strategy for conserving ant communities

Our MRM model explained only 9.5% of the variation in ant assemblage dissimilarity amongst samples. This may be due the Mantel-based MRM model used may be under-fitting our spatial turnover component (Legendre and Fortin 2010). Regardless, the observed lack of strong congruence between ant and plant assemblages means attributing conservation significance to vegetation based on plant community identity is little better than arbitrary for representing underlying ant species in conserved areas in a practical context. These results support previous findings of poor performance of surrogacy methods for representing invertebrates (Ferrier 1997, Rodrigues and Brooks 2007). Considering both this lack of prediction based on plant community and the observed high degree of heterogeneity in ant assemblage composition within some plant communities, conserving a small representative portion of all plant communities will likely be an inadequate conservation strategy for representing the breadth of ant diversity occurring across the landscape. The validity of offsetting losses of native vegetation will therefore depend on spatial fidelity of offset sites, and the within-community spatial turnover and compositional heterogeneity of the particular plant community being offset.

Effectiveness of conserving 'threatened ecological communities' in the Sydney region

The plant community that showed the greatest spatial turnover in ant assemblages is also the community under greatest pressures from urban development (Auld and Tozer 2004). The

construction of approximately 180,000 housing lots in western Sydney through the Growth Centres initiative is expected to clear up to 1765Ha of native vegetation, including 1252Ha of Cumberland Plain Woodland and six other Threatened Ecological Communities (NSW Office of Environment and Heritage 2014). The strategic plan for offsetting this loss is through a \$530 million fund for acquiring and managing high-value remnant native vegetation. While a stipulated minimum of 205ha of “high management viability” Cumberland Plain Woodland must be conserved as part of the offsetting package, the bulk of the required offsets (2,400Ha) need only conform to a broad “grassy woodland” vegetation class and occur within the broader Sydney Basin bioregion (NSW Office of Environment and Heritage 2014). The Sydney Basin bioregion is an area covering over 3.6 million hectares and stretching over 250km north-south. While broadly similar grassy woodlands occur within this region outside of the Cumberland Plain, for example in the Central and Upper Hunter Valley, they are geographically and compositionally distinct from those to be impacted (Keith 2004). Our observed patterns of spatial turnover within Cumberland Plain Woodland suggest that assemblages of ants and potentially other taxonomic groups supported within these geographically separated grassy woodland communities would likely be compositionally very different from those lost as a result of the Growth Centres initiative.

Patterns of β -diversity vary amongst invertebrate taxa, with previous studies showing lower spatial turnover patterns in ants than ground beetles and spiders (Ferrier et al. 1999), and flies at coarse spatial scales (Oliver et al. 2004). Species turnover patterns are however scale dependent (Barton et al. 2013), and as demonstrated here also dependent on the specific habitats studied, limiting the validity of extrapolation between studies and contexts. Further studies of turnover patterns amongst taxonomic groups should therefore employ sampling at a

range of spatial scales and sampling grains to examine spatial patterns across the landscape (Olivier and van Aarde 2014).

Remnant native vegetation on the Cumberland Plain faces a range of threats (Auld and Tozer 2004, Hill and French 2004), most notably weed invasion facilitated through urbanisation and historical land use (Hill et al. 2005, Cuneo and Leishman 2013). These threats are generally more pronounced in isolated fragments (Fischer and Lindenmayer 2007) and active management is often required to guarantee long-term persistence (Cuneo and Leishman 2013). Although we found species richness of samples to be related predominantly with structural factors (cover of leaf litter) and found no effect of remnant size, species richness was negatively associated with the degree of fragmentation (represented by the surrogate measure of distance to nearest native remnant vegetation). Biodiversity offsetting has a place in mitigating the impacts of development through consolidating remnant native vegetation into large, well-managed remnants with high persistence potential. However the criteria for evaluating “like for like” in offsets clearly need to incorporate spatial fidelity of offsets into selection criteria. This is particularly true as prior to the implementation of biodiversity offsetting strategies in NSW, assessments of impacts to threatened ecological communities through 7-part tests under the Environmental Planning and Assessment Act 1979 failed to sufficiently halt the loss of these communities in the Sydney Basin (Auld and Tozer 2004). The potential for enhancement of native vegetation through active management however is highly variable and context-dependent (Maron et al. 2012). Attempted restoration of Cumberland Plain Woodland through revegetation of non-native managed pastureland has achieved some restoration of functional ecosystem processes such as seed dispersal by ants (Lomov et al. 2009) and pollination (Lomov et al. 2010), however restored sites have failed to achieve convergence in plant species composition with remnant vegetation.

Conclusion

Our results demonstrate a characteristically poor representation of ant assemblages within a practical plant community surrogacy framework. This is evident in the degree of heterogeneity within plant community units and the observed strong spatial assemblage patterns within plant communities. While protecting threatened ecological communities provides a greater representation of underlying species assemblages than random selection of conservation significance, the high rates of spatial turnover seen within some communities means that biodiversity offsetting strategies (such as the BioBanking scheme in NSW) need to take into account the spatial fidelity of offset sites into assessment of impacts to communities. While threatened ecological communities are defined exclusively through their assemblages of plant species, the broader definition of ecological communities under the NSW *TSC Act 1995* encompasses the breadth of taxonomic diversity within communities. As such, it is important to conserve threatened plant communities across their extent, rather than just within high integrity examples. The determination of ‘like-for-like’ in biodiversity offsets should incorporate other taxonomic components of total diversity into the concept of ‘threatened ecological communities’.

Chapter 3

Spatial turnover in ant communities limits the effectiveness of plant community surrogacy and supports stochastic models of ant community assembly

Abstract

Habitat-based conservation strategies are central to conservation of biodiversity. Plant community surrogates are often employed to represent the breadth of biodiversity in conservation planning. This approach assumes a strong degree of congruence between plant community composition and assemblage patterns of other underlying taxa such as cryptic invertebrate fauna, however this assumption is rarely tested. Underlying species assemblages may alternatively be driven by structural components of habitat unrelated to plant community composition, or be highly spatially structured limiting the effectiveness of plant community surrogacy. We sampled floristic composition, structural attributes and ant assemblage composition in native vegetation in South-Eastern Australia, to partition the relative influences of plant community, structure and spatial turnover in driving ant assemblage patterns across the landscape. We found that spatial turnover was the strongest driver of ant assemblage patterns. While ant assemblages were independently associated with structural attributes of vegetation, there was no effect of plant community composition once spatial location of sites was taken into account. These results indicate that in structurally homogenous landscapes, ant communities show weak or no associations with plant community identity, severely limiting the efficacy of plant community surrogacy strategies. Instead, ant communities appear to be structured by stochastic processes, providing evidence of neutral community assembly.

Keywords: Beta-diversity, spatial turnover, ants, plant communities, surrogacy, vegetation surrogacy, BioBanking

3.1 Introduction

Conservation of biodiversity requires representation of species within protected habitat (Margules and Pressey 2000, Brooks et al. 2006). Practical conservation efforts often employ community-level strategies, where landscapes are partitioned at local scales based on assemblages of species inhabiting distinct sets of climatic and other abiotic conditions (Ferrier 2002). By conserving some representative portion of all ecological communities inhabiting a landscape, we should theoretically be conserving all species inhabiting that landscape, including cryptic and otherwise seldom-quantified biodiversity. Ecological communities are typically defined by their floristic assemblages, as plant species are readily quantifiable and contribute to the structure and microhabitat availability within communities (Mac Nally et al. 2002). Plant community identity is also strongly tied to fine-scale climatic and abiotic factors including rainfall, soils, aspect and slope (Ferrier and Guisan 2006), meaning predictive plant community distribution models (and mapping) can be generated based on abiotic data and aerial photography (Keith 1999, Tozer 2003).

Using plant communities as a surrogate measure for representing ecological communities assumes congruence between plant community classifications and assemblage patterns of all other taxonomic groups across the landscape (Su et al. 2004). This assumption implies a degree of shared association with the set of climatic and other abiotic factors driving plant community patterns. Assemblage patterns of species typically reflect a combination of both environmental filtering and spatial structuring due to processes such as dispersal limitation (Weiher et al. 2011). The degree to which assemblage patterns are influenced by each process however is taxon-dependent (Chase and Myers 2011). Groups showing strong environmental filtering should display strong congruence with plant community classifications through either shared environmental determinants of species turnover (β -

diversity) patterns, or even directly through responses to the unique habitat structures associated with each plant community. Assemblages of taxa responding mostly to stochastic processes however may show only weak associations with plant communities through shared patterns of spatial turnover.

Mobile and behaviourally specialised taxa such as mammals and birds often show strong patterns of association with plant community classifications or broad vegetation classes (Ferrier 1997, Oliver et al. 1998, Mac Nally et al. 2002). However, plant community surrogacy, along with other forms of surrogacy, generally performs poorly for representing ground-dwelling invertebrate taxa (Ferrier 1997, Oliver et al. 1998, Mac Nally et al. 2002, Santi et al. 2010). Ant assemblages show weak associations with spatially and structurally distinct plant communities representing broadly different vegetation forms (Chapter 2). Plant communities co-occurring in space and providing similar habitat structural composition meanwhile supported largely homogenous assemblages of ants (Chapter 2). Additionally, ants showed strong patterns of spatial turnover for within some plant communities. These results indicate that ant assemblages respond to coarse environmental filters, but assemblage patterns may be determined primarily through stochastic assembly processes in the absence of strong environmental heterogeneity.

While the processes shaping assemblage patterns have direct relevance to applied conservation, studies partitioning the relative influences of environmental versus stochastic processes typically do so in the context of evaluating rival theories of community ecology (Smith and Lundholm 2010, Chase and Myers 2011, Tuomisto et al. 2012). Niche theory proposes that assemblage composition and diversity are determined through individual species' interactions with their environment, through behavioural, morphological and physiological adaptation to local environmental conditions, and through behavioural

specialisation facilitating co-occurrence among species (Grinnell 1917, Chase and Leibold 2003, Soberón 2007). By contrast, Neutral theory proposes that rather than through functional differences amongst species, assemblage patterns are directed predominantly through stochastic processes such as random dispersal, extinction and speciation events, resulting in spatially-structured assemblages (Hubbell 2001). Both niche-based and stochastic processes are now recognised as contributing to shaping communities of species (Tuomisto et al. 2003, Freestone and Inouye 2006, Thompson and Townsend 2006, Farnon Ellwood et al. 2009, Rominger et al. 2009, Weiher et al. 2011).

The relative strength of niche-based and stochastic processes in structuring assemblage composition of ants relates directly to the efficacy of plant community surrogacy in representing the breadth of ant diversity across the landscape. If ant assemblages respond strongly to environmental drivers, especially those related to plant community composition, then ant communities will be well represented in regional conservation strategies based on representation of plant communities. However, strong spatial turnover in assemblage composition and weak associations with plant communities, as detected in our previous study (Chapter 2), indicates poor representation of ants within a plant community surrogacy strategy. In this study, we compare the plant community, vegetation structural and spatial drivers of ant assemblage patterns across the landscape, using a model system comprising a mosaic of co-occurring but compositionally distinct plant communities. This study system allows for the partitioning of spatial and environmental drivers at fine and intermediate scales, enabling effective evaluation of the processes in shaping ant assemblage composition at local scales. Based on our previous findings, we expect that while plant community composition and microhabitat structure will have some impact on structuring ant assemblages, stochastic drivers will have a strong structuring effect on assemblages.

3.2 Methods

Study area

We sampled ant and plant assemblages within two conservation reserves (Big Bush and Ingalba Nature Reserves) and several adjoining private properties near Temora, New South Wales, Australia. These reserves occur within the NSW South West Slopes Bioregion, a highly modified landscape characterised by broad-scale agriculture dominated by grain cropping and grazing. Only 1.2% of the original native vegetation is currently conserved in formal conservation reserves (NSW National Parks and Wildlife Service 2003). Remnant native vegetation within this landscape is highly fragmented and typically associated with geological features such as rocky hills or other land unsuitable for agricultural production. The two reserves show strong similarity floristically, with both occurring predominantly on Upper Silurian geology with shallow soils and surface shales and siltstones on crests, and slightly deeper soils on slopes and flats. The surrounding cleared landscape is characterised by deeper, richer soils.

Sampling

We sampled ants and plant assemblages within the two Nature Reserves using a nested sampling design (see Figure 3.1). We established five sites oriented on a roughly linear north-south transect along the two reserves, over a distance of around 19km. This spanned the greatest possible distance of largely continuous native vegetation in the local context. There is no significant rainfall or climatic gradient across our sites (the rainfall gradient occurs on an east-west axis in this location, decreasing in a westerly direction). Within each site, we established 16 plots, located at points on a 4x4 grid spaced at 0.02 decimal degrees.

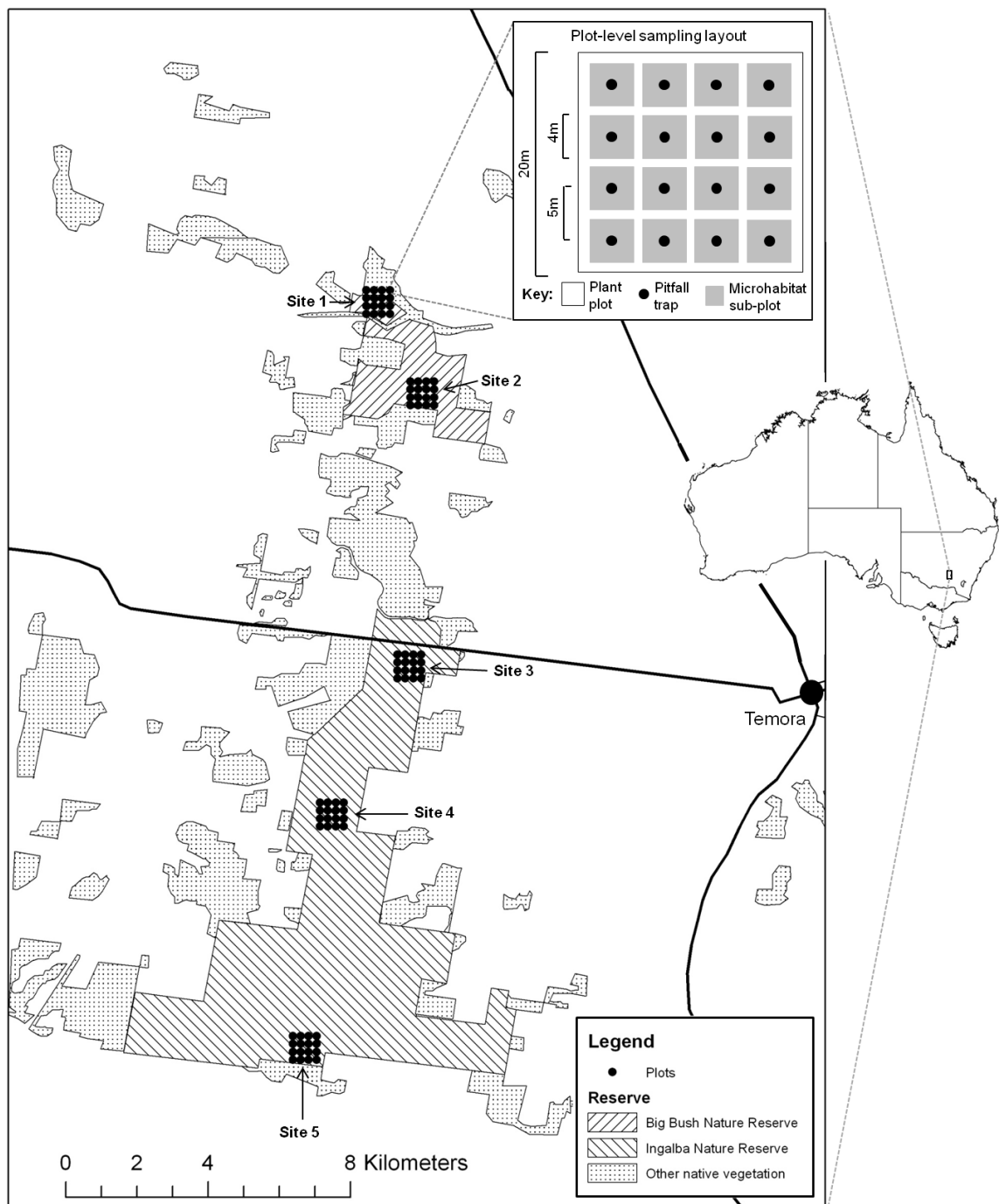


Figure 3.1. Location of sites within the study area and layout of plot-level sampling procedure.

This distance varied on latitudinal (~187m) and longitudinal (~222m) axes. Plant assemblages were sampled within each 20x20m plot. All plant species present were recorded and allocated a cover-abundance score based on a modified Braun-Blanquet scale (after Tozer 2003).

Ants were sampled within each plot using 16 pitfall traps (1280 traps in total across the 80 plots in five sites). Pitfall traps were 150mL cylindrical plastic vials (45mm diameter) containing 50mL of 100% Ethylene Glycol. Traps were located on a 4x4 grid within the plot, spaced at 5m. Traps were left for a minimum of five days before opening to minimise 'digging in' effects (Greenslade 1973). Traps were opened on the 5th and 6th of February 2012 and left for eight days, then closed and collected in the order they were opened. Ants were sorted from the traps and transferred to 70% ethanol. Representatives of each species were mounted and identified to species groups in the lab where possible. Species-level identifications were conducted and/or confirmed by Alan Andersen (CSIRO Tropical Ecosystems Research Centre, Winellie NT). Trap-level data were pooled for plot-level analyses.

Habitat variables were recorded within a 2x2m sub-plot centred on each pitfall trap, by estimating the height and percentage cover of canopy, sub-canopy, shrub, dicot forb and monocot forb vegetation layers. We also recorded the estimated depth and cover of leaf litter, and cover of woody debris in three classes (<2.5cm, 2.5-10cm and >10cm), bare ground, moss, gravel, rocks, and percentage of the sub-plot occupied by tree bases. Plot-level habitat data were produced by averaging the 16 trap-level measurements for each plot.

Analyses

Plant community classification

We performed cluster analysis on collected plant data to define distinct floristic assemblages representing unique plant communities. Analyses were performed on Braun-Blanquet cover/abundance scores using the PATN program (Belbin 1991). Pairwise dissimilarity of samples was calculated using a symmetric Kulczynski coefficient. We then performed hierarchical agglomerative clustering using an unweighted pair group average arithmetic (UPGMA) (Belbin and McDonald 1993) and a beta value of -0.1. The appropriate number of groups was then determined through visual inspection of the resulting dendrograms.

Plant community structural differences

We used Principal Component analysis (PCA) to produce orthogonal Principal Components from our set of structural variables due to the large number of strong correlations amongst our recorded structural variables. We included only variables represented in all plots, hence canopy height and sub-canopy height were not used in the calculation of Principal Components. The first principal components contributing to 90% of the variation in structural variables amongst sites were used for further analysis. We compared structural microhabitat variation across our derived plant communities using multiple analyses of variance (MANOVA) of principal component scores from each plot. We then performed univariate post-hoc Tukey's HSD tests on significant Principal Components showing significant community-level differences in habitat structure.

Ant assemblage patterns

Many traps were removed from the ground during the survey period (N=184 out of 1280) concentrated mainly in Site 4, most likely by dogs or foxes. We therefore excluded any plots

sampled with fewer than eight pitfall traps from all further analyses. This reduced our sample size to 1030 traps in 71 plots. We produced non-metric multidimensional scaling (nMDS) ordinations to visualise patterns of similarities in ant species. We applied fourth-root transformation to abundances and generated Bray-Curtis dissimilarity matrices. We also compared ant assemblage composition amongst our derived plant communities using Permutational Multiple Analysis of Variance (PERMANOVA) based on Bray-Curtis dissimilarities, with site included as a random factor. We identified ant species contributing the greatest amount to observed assemblage differences across factors in the PERMANOVA model using Similarity Percentages (SIMPER). These analyses were performed in Primer V.6 (Clarke and Gorley 2006).

Comparing spatial and environmental drivers of species turnover

We compared spatial turnover of ant and plant assemblages using Mantel Correlograms (Oden and Sokal 1986) on plot-level data, based on Bray-Curtis dissimilarity. Mantel Correlograms are an effective method for detecting changes in the strength of spatial autocorrelation at different scales (Borcard and Legendre 2012). We used fourth-root transformed ant assemblage data due to the large variation in abundance amongst species in our samples, and raw Braun-Blanquet cover-abundance scores for plant data. Pairwise geographical distances were calculated using the ‘fossil’ package in R. Ten distance classes were chosen, based on the relatively staggered distributions of distances amongst samples. Break points used were 0.17, 0.3, 0.5, 0.9, 4, 6, 8.5, 9.5, 12, 16 and 18.5km, with between 155 and 334 plot pairs within each lag distance class. Greater resolution of lag distance classes was given to within-site comparisons (the three shortest distance classes) due to the expected strongest spatial patterns at shorter distances. Significance levels were adjusted

using sequential Bonferroni corrections (Holm 1979). Mantel Correlograms were produced in the 'ecodist' package (Goslee and Urban 2007) in R.

We also investigated the spatial turnover patterns of specific ant functional groups. Ant species were partitioned into functional groups based on a widely used framework of Australian ant functional groups based on shared behavioural and morphological traits, and responses to disturbance (Andersen 1995, Hoffmann and Andersen 2003). These functional groups, and the genera assigned to these groups in this context were Dominant Dolichoderinae (*Iridomyrmex*, *Anonychomyrma*, *Froggattella* and *Papyrius*), Generalized Myrmicinae (*Monomorium*, *Pheidole* and *Crematogaster*), Opportunists (*Doleromyrma*, *Nylanderia*, *Rhytidoponera*, *Paraparatrechina*, *Tapinoma* and *Tetramorium*), Subordinate Camponotini (*Camponotus* and *Polyrhachis*), Cryptic Species (*Epopostruma*, *Solenopsis*, *Austroponera*, *Brachyponera*, *Colobostruma*, *Heteroponera*, *Hypoponera*, *Mayriella*, *Mesostruma*, *Myrmecina* and *Strumigenys*), Specialist Predators (*Bothroponera*, *Myrmecia* and *Cerapachys*), Cold Climate Specialists (*Notoncus*, *Stigmacros*, *Ochetellus*, *Podomyrma*, *Dolichoderus* and *Prolasius*) and Hot Climate Specialists (*Melophorus*, *Meranoplus* and *Ochetellus*). We generated Bray-Curtis dissimilarity matrices based on fourth-root transformed abundance data for each functional group. Due to the large number of plot pairs containing no shared species in some functional groups, we used extended dissimilarity to extend saturated pairwise dissimilarities using flexible shortest path adjustment (De'ath 1999). This method alleviates the problems of saturation associated with datasets showing high β -diversity amongst samples, and is effective for matrices containing fewer than 60% saturation (Tuomisto et al. 2012). We compared our extended dissimilarity matrices against geographical distance between sites using individual Mantel-tests (Mantel 1967).

We used Multiple Regression on Distance Matrices (MRM) (Smouse et al. 1986, Lichstein 2007) to evaluate the strength of plant community, habitat structural factors and spatial drivers in shaping ant assemblage composition. MRM models allow for the comparison of an $n \times n$ response matrix (comprising pairwise distance/dissimilarity measures amongst sample pairs) against multiple predictor $n \times n$ distance matrices (representing pairwise geographic, environmental or other distance metrics) using standard multiple regression. Statistical hypothesis testing is however performed through a permutation procedure as per Mantel and partial-Mantel tests (Legendre and Legendre 2012). Several potential issues exist with the use of MRM, including low statistical power to detect spatial patterns in assemblages (Legendre and Fortin 2010) and problems with saturation of dissimilarity values when pairs of samples share no species (Tuomisto et al. 2012). MRM is however the most appropriate analysis for these data as our specific research questions are best expressed in terms of multiple dissimilarity values (spatial, structural and plant community) amongst sample pairs. Additionally, the large sample sizes obtained in ant community datasets should prevent saturation effects.

We generated predictor matrices based on Euclidean distances between pairwise plot-level habitat structural values and Principal Component scores, and also Bray-Curtis dissimilarity in plant species composition amongst samples. Each matrix was unfolded into a vector of length $n(n-1)/2$ (representing pairwise values of n observations), and values were scaled for equal variance and mean of zero. We then compared each predictor matrix against ant pairwise Bray-Curtis dissimilarity using simple Mantel tests, with all non-significant variables excluded from further analyses. We also generated geographic distance lag matrices based on the distance classes used for the Mantel Correlograms. For each lag matrix, each distance value falling within the lag class was coded as zero, and all other values as one. We included only lags showing significant autocorrelation in the Mantel Correlogram

in models to avoid a linear dependency encountered when vector values sum to one

(Rawlings et al. 1998, Lichstein 2007).

We first evaluated the combined explanatory power of all included habitat structural variables against Principal Component scores for the six best PCs, with the model showing the greatest R^2 value retained for further analysis as the best representative of structural variation in habitat amongst plots. We then evaluated each variation components separately, with models for each combination of (a) plant assemblage composition, (b) habitat structure and (c) lag matrices spatial model, including a three-way global model. Due to the three variation components in our model, we could not perform standard variance partitioning based on R^2 values (Borcard et al. 1992). MRM models were run in the ‘ecodist’ package in R. We performed sequential Bonferroni corrections for each model.

3.3 Results

We recorded 109,622 individual ants of 142 species within our plots. Ant species recorded represented 38 genera in eight subfamilies. Our reduced dataset for analyses (excluding plots sampled with fewer than eight traps) included only 104,924 ants. One species of ant, *Iridomyrmex chasei*, represented over half of individuals recorded (55,151). The ten most abundant species represent 87.45% of individuals (95868). 40% of species (57) were however represented by fewer than eight individuals, including 23 represented by a single individual. Similarly, 27 species were present in only a single trap, and 37 species were recorded in a single plot only. Only two species (*Rhytidoponera metallica* and *Rhytidoponera punctiventris*) were recorded in all plots, and only 20 species were recorded in more than half of plots. Total ant species richness at site-level were 100, 94, 86, 75 and 70 from site one through site five. Up to 40 species were recorded in plots, and up to 18 species

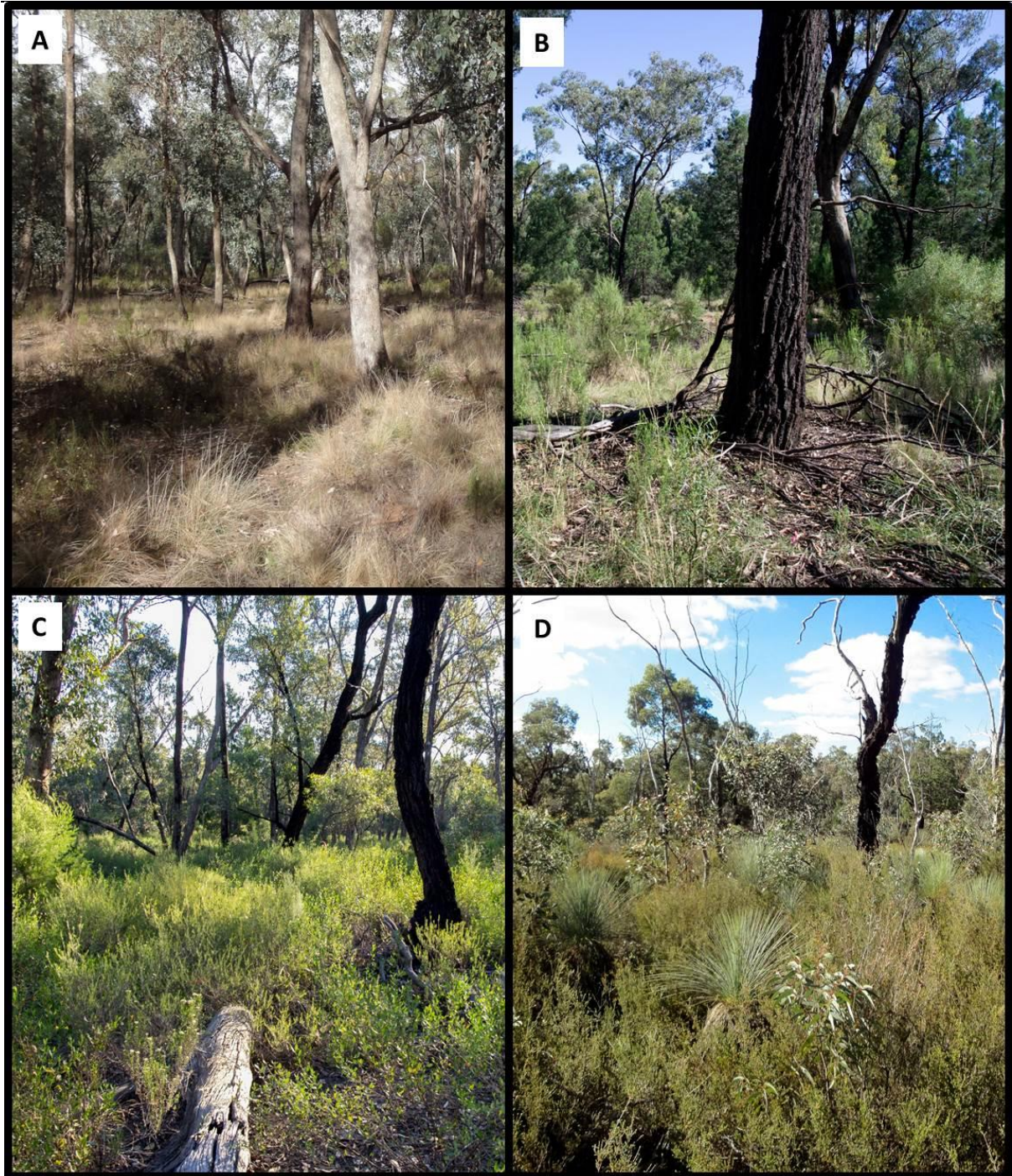


Figure 3.2. Vegetation communities developed through hierarchical agglomerative clustering of plot-level plant assemblage data. A = ‘Woodland form A’, B = ‘Woodland form B’, C = ‘Woodland form C’, D = ‘Heathland’.

at trap-level. Plants recorded represented 114 species in 76 genera and 36 families. One plant species listed under threatened species legislation, *Tylophora linearis*, was recorded.

Plant communities

Samples clustered into four distinct plant communities based on assemblage composition (Figure 3.2). Broadly, our samples separate into two very distinct groups representing a heathland/low open woodland community (hereafter “heathland”), and a collection of three distinct forms of Box/Ironbark woodland. The heathland community is characterised by a sparse or absent canopy of Dwyer’s Red Gum (*Eucalyptus dwyeri*), Inland Scribbly Gum (*Eucalyptus rossii*) and Black Cypress Pine (*Calitris endlicheri*), and relatively diverse shrub layer including *Calytrix tetragona* and *Platysace lanceolata*, occurring predominantly on low shale ridges particularly in the North of the study area. This community corresponds with the “Dry Heathland/Low Open Woodland” community (Portners 2001) and has affinities with the “*Allocasuarina diminuta* (she oak) – *Calytrix tetragona* (Five Fringe Myrtle) shrubland” community (ID292) identified by Benson (2008).

The three woodland communities identified here share a characteristic canopy of Mugga Ironbark (*Eucalyptus sideroxylon*), Inland Grey Box (*Eucalyptus microcarpa*) and Black Cypress Pine (*Calitris endlicheri*) and have previously been collectively identified as “Mugga Ironbark/Grey Box Woodland” (Portners 2001) and “*Eucalyptus sideroxylon* (Mugga Ironbark) – *Eucalyptus microcarpa* (Inland Greybox) shrubby woodland” (ID217) (Benson 2008). We further recognise three distinct forms of this broad woodland community based on floristic composition of shrub and ground stratum. Form A is a grassy woodland form characterised by *Rytidosperma setaceum*, *Austrostipa scabra* subsp. *scabra*, *Calotis cuneifolia* and *Xerochrysum viscosum*. Form B is a shrubby form characterised by *Cassinia uncata*, *Lissanthe strigosa* subsp. *subulata* and *Melichrus urceolatus*. Form C is a shrubby

form characterised by *Goodenia ovata*, *Acacia flexifolia*, *Pultenaea largiflorens* and *Olearia floribunda*, and also a greater proportional abundance of *Eucalyptus microcarpa*. These four plant communities were distributed relatively evenly throughout the sites, except for Woodland form C, which was restricted to Site 4 only (see Table 3.1).

Plant community structural differences

The first five Principal Components contributed to 93.2% of the variation in structural variables. Principal Component weightings for each variable are presented in Table 3.2. PC1 was weighted positively for litter and canopy cover, and negatively for shrub and bare ground cover. PC2 was weighted positively for shrub and litter cover, and negatively for bare ground cover. PC3 was weighted positively for forb cover (particularly monocotyledon cover) and canopy cover, and negatively for sub-canopy and moss cover. PC4 was weighted positively for sub-canopy cover and forb (particularly dicotyledon forb) cover, and negatively for canopy cover. PC5 was weighted positively for bare ground and litter cover, and negatively for moss and canopy cover.

There were significant differences amongst plant communities for three of the five Principal Components (PC2, PC3 and PC4) (see Table 3.3). Pairwise comparison of communities showed significant differentiation in PC values in some cases (Table 3.4). For example, Heathland samples were not significantly different from either B or C woodland forms for any of the three Principal Component scores used. Woodland form A showed the greatest differentiation from other communities in structural attributes, being significantly different from all other communities in PC3 scores and different to Woodland form C in all three Principal Component scores.

Table 3.1. Distribution of plant communities amongst sites.

	Site 1	Site 2	Site 3	Site 4	Site 5	Total
Heathland	3	10	4		3	20
Woodland form A	6				2	8
Woodland form B	7	6	9	1	11	34
Woodland form C				9		9

Table 3.2. Principal Components explaining 93.2% of the variation in structural attributes of vegetation amongst samples. Warmer (red) colours indicate a positive weighting on variables, colder (blue) colours indicate negative weighting on variables.

	PC1	PC2	PC3	PC4	PC5
Cover					
Canopy	0.229	0.071	0.300	-0.586	-0.301
Sub-canopy	0.053	-0.150	-0.414	0.478	-0.141
Shrub	-0.482	0.820	-0.094	-0.061	0.159
Forb (dicotyledon)	-0.081	0.126	0.380	0.554	-0.019
Forb (monocotyledon)	0.106	0.097	0.696	0.283	-0.172
Litter	0.757	0.356	-0.154	0.106	0.354
Bare ground	-0.298	-0.380	0.183	-0.079	0.641
Woody debris (<2.5cm)	-0.006	0.024	-0.035	-0.102	-0.116
Woody debris (2.5-10cm)	0.008	0.024	-0.019	-0.015	0.002
Woody debris (>10cm)	0.010	0.017	0.004	0.008	0.014
Rock	0.002	-0.006	-0.009	0.004	-0.003
Gravel	-0.032	-0.042	-0.022	-0.065	-0.003
Moss	-0.174	-0.016	-0.202	0.072	-0.533
Tree base	0.014	0.002	-0.008	0.005	-0.016
Height					
Shrub	-0.003	0.009	0.002	0.021	-0.002
Forb (dicotyledon)	0.001	-0.001	0.005	0.006	0.004
Forb (monocotyledon)	0.000	-0.002	0.002	-0.002	-0.001
Litter depth	0.010	-0.001	0.026	0.009	-0.021
% variation explained	45.3	21.7	12.9	7.4	5.8

Ant community composition

We found a weak association of ant assemblages with plant community identity, besides a relatively tight grouping of samples from Woodland form C (Figure 3.3). Samples however show strong association based on site, with an almost total separation of sites one and two (Big Bush Nature Reserve) from sites three, four and five (Ingalba Nature Reserve). This strong spatial fidelity of ant assemblages explains the above clustering of Woodland form C samples, as this community occurred only within site four. There was a strong spatial pattern in ant assemblages, with assemblages significantly associated with site (Pseudo- $F_{4,59} = 4.87$, $P = 0.001$, perm=999) but no association with plant community (Pseudo- $F_{3,59} = 0.85$, $P = 0.66$, perm=998). There was a significant site*plant community interaction (Pseudo- $F_{4,59} = 1.50$, $P = 0.008$, perm=995).

There were no plant community differences between ant assemblages, hence we performed SIMPER analyses on site groups only. The ant *Iridomyrmex chasei* contributed the greatest amount to site-level differences in ant assemblages in seven of the ten pairwise site comparisons, contributing up to 9.27% to pairwise site differences. This species was the most abundant in the study area, accounting for over half of all captures ($n=55151$), however it was present in only 26 of the 80 total plots sampled, and only within sites one and two, plus one plot within site three. The ant *Monomorium* sp. B (*sordiden* species group) contributed the greatest amount to the remaining three pairwise community comparisons, and second-most in six other comparisons (contributing up to 4.73%). This species was almost entirely absent from sites one and two. Other ants contributing greatly to site differences were *Notoncus* sp. C (*ectatomoides* species group), *Doleromyrma darwiniana*, *Solenopsis* sp. A, *Iridomyrmex purpureus*, *Iridomyrmex* sp. A (*mjobergi* species group), *Monomorium* sp. J (*laeve* species group) and *Monomorium* sp. A (*sordiden* species group).

Table 3.3. Results of Multiple Analysis of Variance (MANOVA) comparison of Principal Component scores amongst plant communities.

PC	Df	Mean sq.	Residual mean sq.	F-value	P-value
PC1	3, 67	477.3	354.11	1.35	0.266
PC2	3, 67	453.1	159.51	2.84	<0.05
PC3	3, 67	352.4	91.31	3.86	<0.05
PC4	3, 67	247.2	50.47	4.90	<0.01
PC5	3, 67	99.7	43.94	2.27	0.088

Table 3.4. Pairwise Tukey-test comparisons of Principal Component scores across plant communities. Asterisks denote significance level (*= <0.05 , **= <0.01 , ***= <0.001).

	Heathland	Woodland (form A)	Woodland (form B)
PC2			
Woodland (form A)	-9.06		
Woodland (form B)	-4.00	5.06	
Woodland (form C)	7.10	16.15*	11.10
PC3			
Woodland (form A)	11.55*		
Woodland (form B)	-0.15	-11.70*	
Woodland (form C)	-2.37	-13.92*	-2.21
PC4			
Woodland (form A)	7.42		
Woodland (form B)	3.46	-3.96	
Woodland (form C)	-4.27	-11.69**	-7.73*

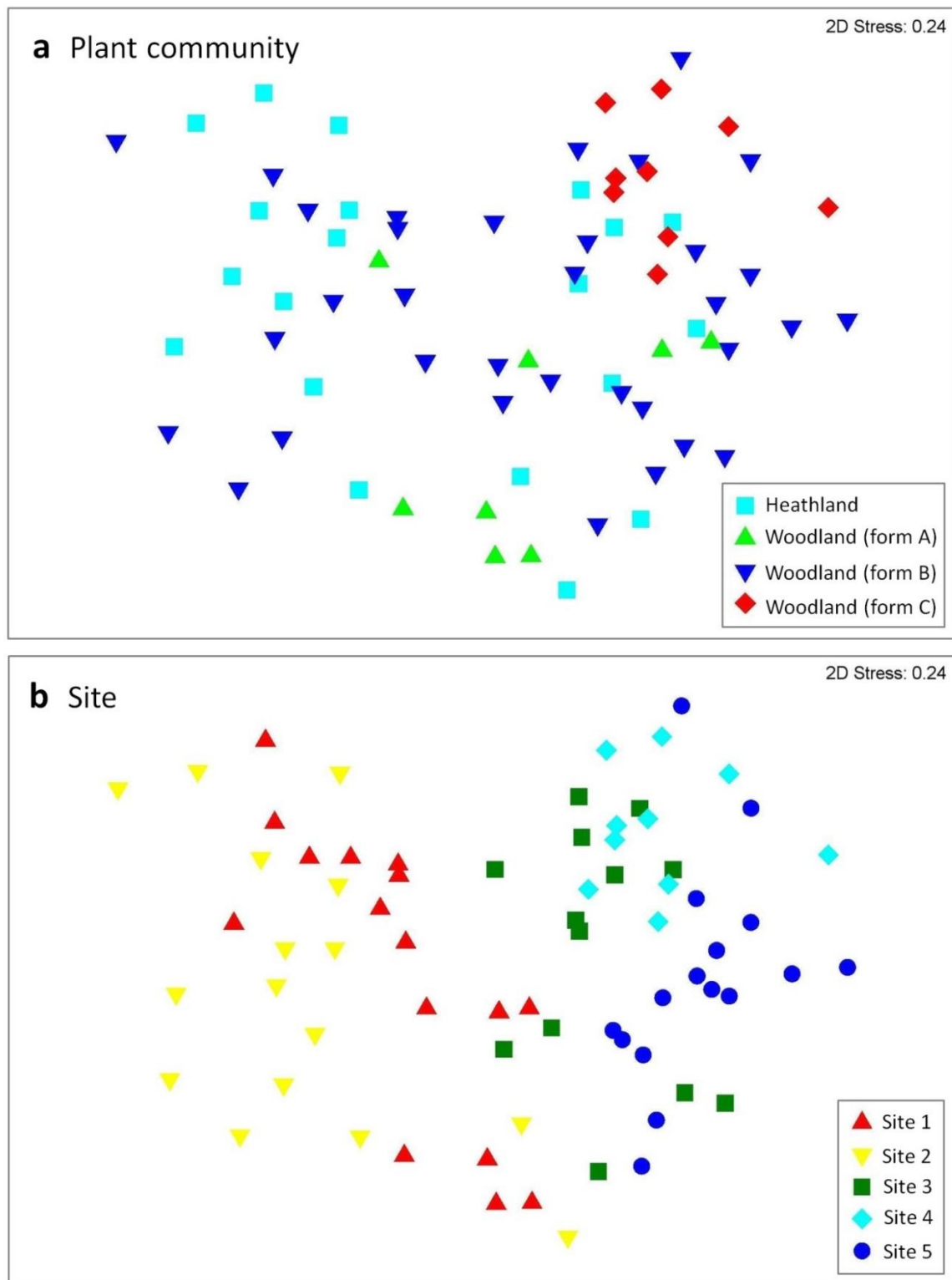


Figure 3.3. Non-metric multidimensional scaling ordination based on Bray-Curtis dissimilarity of 4th-root transformed ant assemblage data, compared amongst (a) plant communities and (b) sites.

Spatial patterns in assemblages

There was significant spatial autocorrelation in both plant and ant species assemblages in the Mantel Correlograms (Figure 3.4). Both groups show a similar pattern of strong positive spatial autocorrelation in the first three lags. Plant assemblages show a further negative autocorrelation at lags eight and nine, with no pattern detected in the greatest distance class. Ant assemblages show a greater degree of spatial association, with further positive spatial autocorrelation at lag five, and negative spatial autocorrelation at lags six, eight, nine and ten. This significant negative autocorrelation at the final lag indicates that spatial autocorrelation extends beyond the scale studied here.

Functional group-specific rates of spatial turnover were highest for the three functional groups with highest abundances (Generalized Myrmicinae, Dominant Dolichoherinae and Opportunists, see Table 3.5). The Subordinate Camponotini also showed significant, but weaker spatial turnover. We did not perform analysis of the Specialist Predators functional group due to the high number of saturated pairwise dissimilarities (93.16%, due to low numbers of captures).

Raw species turnover was greatest between site two and site four, with 55 species not shared from a combined total 112 species (49.11%, see Table 3.6). Overall, 31 species were unique to Big Bush Nature Reserve (sites one and two), while 24 were recorded only in Ingalba Nature Reserve (sites three, four and five).

Niche versus spatial assemblage processes

Seven habitat structural variables were significantly associated with dissimilarity in ant assemblages using simple Mantel tests. These variables (cover of canopy, shrub, litter,

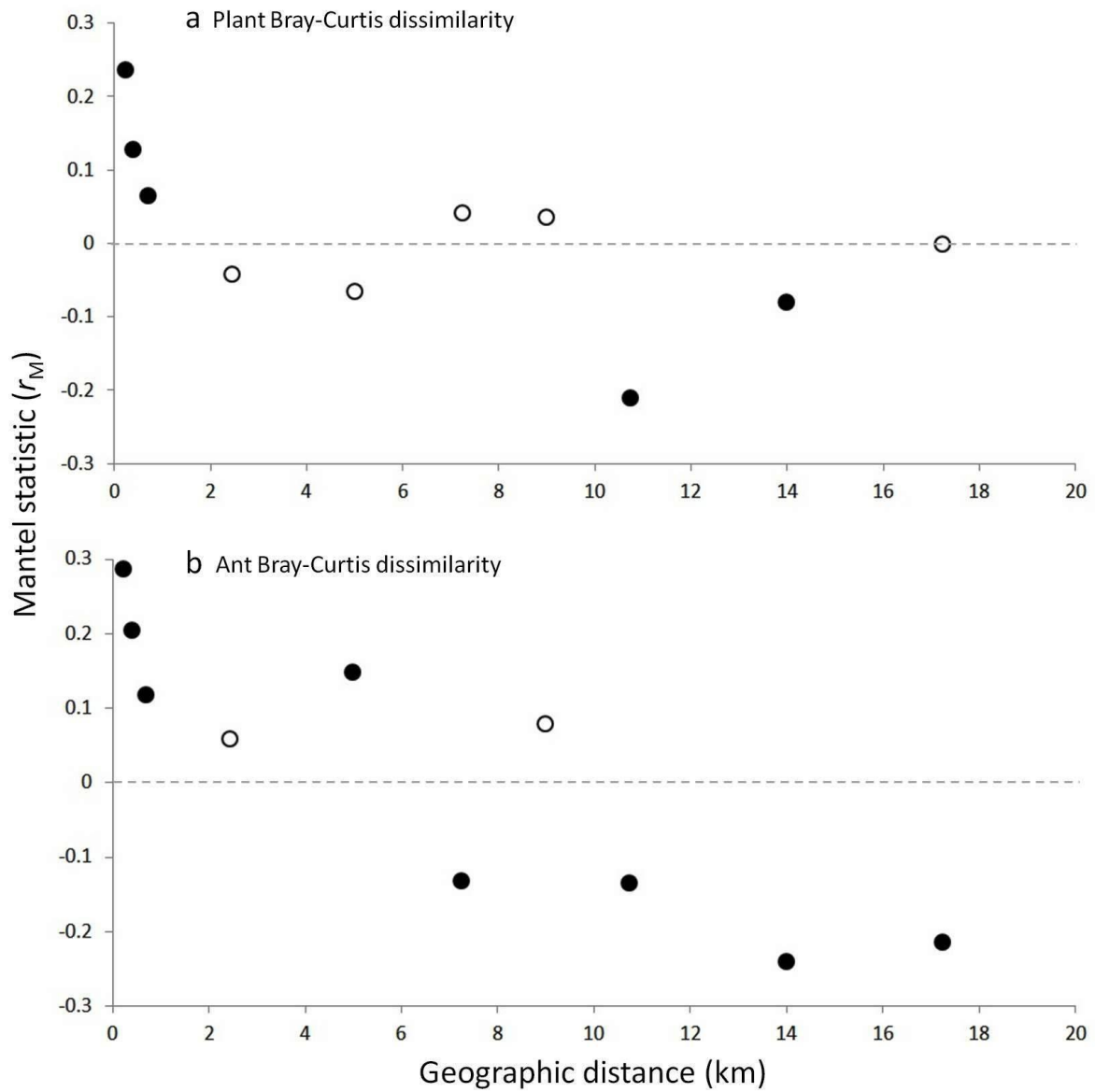


Figure 3.4. Mantel Correlograms for Bray-Curtis distance between (a) plant and (b) ant assemblages over geographical space. Solid circles indicate statistically significant spatial autocorrelation at that lag distance ($P < 0.05$).

Table 3.5. Comparison of species turnover patterns amongst ant functional groups based on Mantel tests of extended Bray-Curtis dissimilarity against geographical distance between site pairs.

Functional Group	# species	# individuals	Mantel-R	P-value	% saturation
All species	142	104924	0.455	<0.001	0.00
Generalized Myrmecinae	24	13715	0.368	<0.001	1.05
Dominant Dolichoderinae	11	60426	0.285	<0.001	46.64
Opportunists	18	16365	0.205	<0.001	0.00
Subordinate Camponotini	19	942	0.071	<0.05	11.39
Hot-climate Specialists	15	9166	0.052	0.074	0.28
Cold-climate Specialists	19	2005	0.036	0.154	27.89
Cryptic Species	21	2209	0.024	0.232	18.47
Specialist Predators	15	96	-	-	93.16

woody debris (2.5-10cm), gravel, moss and tree base) when combined in an MRM model explained 8.4% of the variation in ant assemblages (see Table 3.7). By comparison, the MRM based on scores from the best six Principal Components explained only 4.2% of the variation in ant assemblages. For this reason, raw structural variables were retained for inclusion in the global model to account for association of ant assemblages to the structure of vegetation. Our spatial component was best explained by our lag distances model ($R^2=0.279$) (incorporating the eight lag distance matrices showing significant associations in the Mantel Correlogram, see Figure 3.4) than our raw geographical distance matrix model ($R^2=0.207$).

Our component MRM models showed significant association of ant assemblages to plant community similarity ($R^2=0.0202$, $P<0.001$), combined habitat variables ($R^2=0.084$, $P<0.001$) and spatial lag matrices ($R^2=0.279$, $P<0.001$) models (Figure 3.5). Our combined models however showed very little independent contribution of plant assemblage similarity to explained variation in ant assemblage similarity (Figure 3.5). When combined, our plant assemblage model contributed only $R^2=0.013$ (1.3%) to our structural model, only $R^2=0.00044$ (0.044%) to our spatial model and only $R^2=0.000013$ (0.0013%) to our space + structure combined model. Our global model found no significant association of ant assemblages to plant assemblages after spatial drivers of assemblage composition were accounted for (see Table 3.8). Our global model also found that only one structural variable, cover of gravel, had a statistically significant effect when spatial autocorrelation was taken into account. Ant assemblages showed spatial assemblage patterns at seven of the eight lag distances included in the model, with model coefficients shifting from strong positive autocorrelation at close distances (lag 1 coefficient =0.775) to strong negative autocorrelation at the furthest distance (lag 10 coefficient =-0.828).

Table 3.6. Percentage of shared species (and combined total number of species) across site pairs.

	Site 1	Site 2	Site 3	Site 4
Site 2	63% (119)			
Site 3	60% (116)	59% (113)		
Site 4	54% (114)	51% (112)	59% (101)	
Site 5	56% (109)	53% (107)	51% (103)	56% (93)

Table 3.7. Results from three component MRM models (plant assemblage similarity model, habitat structure model and spatial model). All coefficients except lag matrices are based on distance vectors standardised for equal variance and mean of zero. Presented P-values adjusted using sequential-Bonferoni corrections for each component model.

	Coefficient	P-value
Environmental models		
Plant assemblages		
Model $R^2 = 0.0202$		
Intercept	-0.562	<0.001
Plants Bray-Curtis distance	1.018	<0.001
Habitat structure		
Model $R^2 = 0.084$		
Intercept	0.000	0.791
Canopy cover	0.094	0.266
Shrub cover	-0.014	0.791
Litter cover	0.071	0.791
Woody debris (2.5-10cm) cover	0.094	0.228
Gravel cover	0.186	<0.01
Moss cover	0.090	0.760
Tree base cover	0.050	0.791
Spatial model		
Model $R^2 = 0.279$		
Intercept	0.516	0.292
Geographic distance lag 1	0.691	<0.001
Geographic distance lag 2	0.446	<0.001
Geographic distance lag 3	0.229	<0.05
Geographic distance lag 5	0.273	0.094
Geographic distance lag 6	-0.458	<0.001
Geographic distance lag 8	-0.534	<0.001
Geographic distance lag 9	-0.594	<0.001
Geographic distance lag 10	-0.560	<0.001

Chapter 3: Spatial turnover in ant communities limits the effectiveness of plant community surrogacy and supports stochastic models of ant community assembly

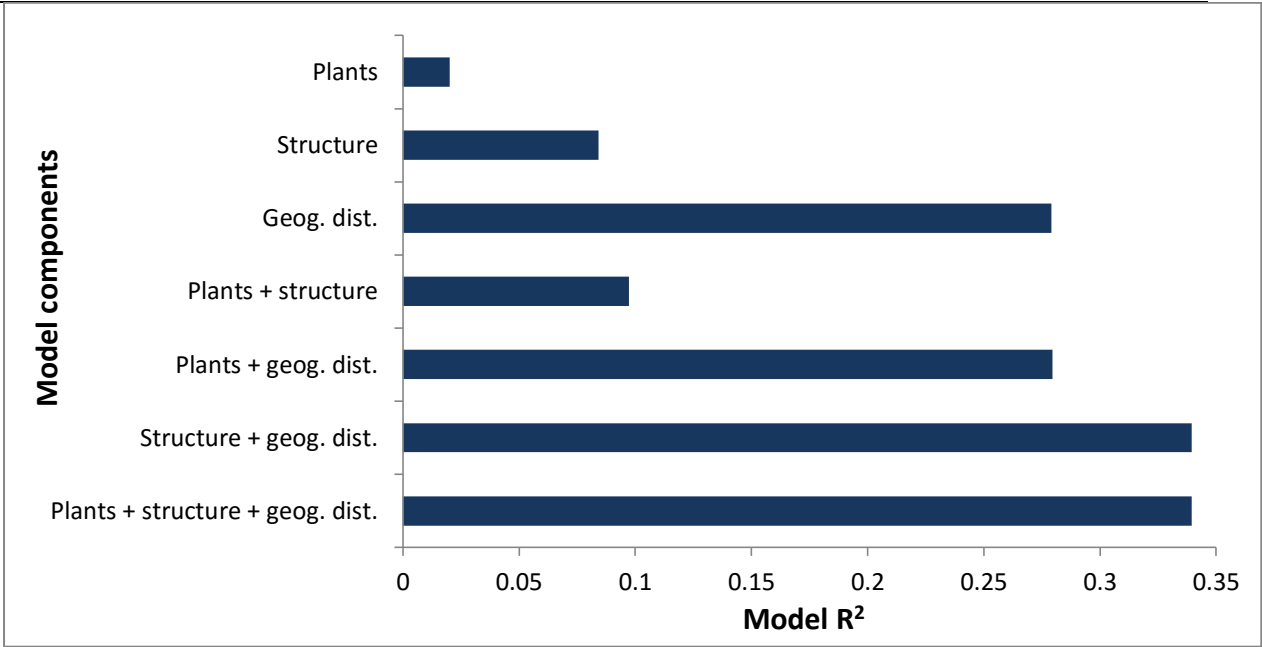


Figure 3.5. Model R² values from component MRM models and model combinations.

3.4 Discussion

Drivers of ant assemblage composition

Our results show no association of ant assemblages with plant community patterns across the landscape, beyond a relatively weak correlation due to shared spatial autocorrelation. Hence, plant communities are not a useful surrogate measure for representing underlying ant assemblages. Instead, we demonstrate that by-far, the greatest predictor for the degree of similarity between samples is the raw geographical distance between them. This result differs from other studies that have found significant association of ant assemblages with plant communities (Andersen 1986b, Ferrier 1997, Oliver et al. 1998, Andersen et al. 2008), as well as our own work (Chapter 2). These previous studies have compared association at broader scales, amongst often spatially disjunct and structurally very distinct plant communities. Our previous comparison of ant assemblages within structurally similar plant communities with overlapping distributions however showed only weak or no differences (Chapter 2). The structural variation amongst plant communities within this study was low, and plant community categorizations did not correlate strongly with our recorded vegetation structural variables or derived Principal Components. Rather, the greatest source of variation in structure amongst plots was related to cover of litter and shrub layers, independent of plant community identity. Ants showed compositional responses to variation in habitat structure across the landscape, independent of plant community structural differences. These results support our own findings of ant assemblage responses to structural variation in vegetation (Chapter 2), as well as previous findings of ant assemblages responses to within-plant community variation in habitat structural complexity (Lassau and Hochuli 2004, Lassau et al. 2005a). Although our plant communities showed some distinct structural differences, our

Table 3.8. Results of global Multiple Regression on Distance Matrices (MRM) model on ant assemblage similarity. All coefficients except lag matrices are based on distance vectors standardised for equal variance and mean of zero. Presented P-values adjusted using a sequential-Bonferroni procedure. Model $R^2=0.340$.

	Coefficient	P-value
Model intercept	0.859	0.50
Plant community drivers		
Plants Bray-Curtis distance	-0.028	1
Structural drivers		
Canopy cover	0.074	0.37
Shrub cover	0.003	1
Litter cover	0.028	1
Stick cover	0.095	0.10
Gravel cover	0.146	<0.05
Moss cover	0.122	0.19
Tree base cover	0.049	1
Spatial drivers		
Lag 1 (0.17-0.3km)	0.775	<0.002
Lag 2 (0.3-0.5km)	0.521	<0.002
Lag 3 (0.5-0.9km)	0.261	<0.05
Lag 5 (4-6km)	0.157	1
Lag 6 (6-8.5km)	-0.539	<0.002
Lag 8 (9.5-12km)	-0.593	<0.002
Lag 9 (12-16km)	-0.819	<0.002
Lag 10 (16-18.5km)	-0.828	<0.002

best principal component axes (explaining 45.3% of the variation in structural variables amongst plot samples) showed no differences amongst plant communities. Much of the structural heterogeneity of samples was therefore independent of plant community composition, and was attributable instead to within-community variation in structure.

The strongest driver of ant assemblage patterns was spatial turnover, independent of the effects of plant community composition or heterogeneity in vegetation structural composition. The strength of spatial turnover also varied amongst ant functional groups. The highest rates of turnover were generally amongst those groups with the highest overall abundances. This pattern is potentially due to unequal detection probabilities amongst functional groups, with low-abundance species more likely to be undetected when present than abundant species (Tuomisto et al. 2012), resulting in a large proportion of sites with no shared species (the saturation percentage) for these less abundant functional groups. Despite this abundance-turnover relationship, some functional groups showed disproportionately high Mantel-R values. For example, the Generalized Myrmecines showed highest overall rates, despite having overall abundances less than one-quarter of the Dominant Dolichoderinae group. Similarly, the Subordinate Camponotini had higher rates of turnover than groups with higher abundances including Hot Climate Specialists, Cold Climate Specialists and Cryptic Species.

Ant assemblage β -diversity patterns and plant community-based conservation

Ant assemblages here show a total mechanistic disconnect with plant community patterns across the landscape, and observed congruence of assemblages is due solely to shared spatial autocorrelation patterns. While this may provide some weak support for the use of plant community surrogacy generally, our data demonstrate that geographical location of native vegetation provides a superior criterion for allocating conservation significance.

Our previous work comparing ant assemblages amongst different plant communities in the Sydney region (Chapter 2) provided a greater degree of support for plant community surrogacy, with some plant communities supporting unique assemblages of ants independent of structural attributes of vegetation and the geographical location of sites. However these differences were limited to between broadly different plant community forms with spatially distinct geographical distributions. As with the current study, plant communities co-occurring within a common set of climatic conditions and providing broadly similar structural microhabitats supported homogenous assemblages of ants. Similarly, we found very high rates of within-community spatial turnover of ant assemblages.

The strength of spatial turnover in assemblages is particularly important for the implementation of biodiversity offsetting strategies (Chapter 2). In a hypothetical implementation of biodiversity offsetting (such as the NSW BioBanking scheme) (DEC 2006) in this context, the loss of some portion of the local extent of native vegetation would be traded against the legal protection and active management of some other portion, with the stated aim of ‘no net loss’ to local biodiversity. Choosing offset sites based purely on plant community composition would provide no better representation of lost species than arbitrary selection. The high spatial turnover of ant assemblages within this context however means that representation of species supported in lost habitat decreases with increasing distance from impacted areas. Therefore, strict spatial fidelity criteria should be incorporated into offset site selection in order to represent whole ecological communities.

The strong spatial turnover amongst ants observed here is likely to be representative of, or even an underestimate of the spatial turnover patterns of other invertebrate fauna taxa. Comparative studies with ants have found higher spatial turnover rates in flies (Oliver et al. 2004), and ground beetles and spiders (Ferrier et al. 1999). Several taxonomic groups of

invertebrates are recognised to show high levels of endemism and small geographical ranges at the species level, due to poor dispersal abilities and/or heavy reliance on spatially clustered habitats (Harvey 2002). Narrow-range endemism, defined as species occurring within an area of less than 100km x100km, is recognised to be common amongst species of freshwater crustaceans (particularly the Decapoda and Phreatoicidea), freshwater and terrestrial gastropods, mygalomorph ground spiders, earthworms and millipedes, among others (Harvey 2002). Recognition of these patterns of endemism has resulted in the requirement to formally assess the impacts of development on short-range endemic species under formal conservation legislation in the state of Western Australia (Harvey et al. 2011). Similarly, numerous invertebrate species associated with discrete geographical ranges or freshwater catchments are protected under Tasmanian biodiversity conservation legislation (DPIPWE 2015).

Stochastic assembly of ant communities

Traditionally, the study of ant community assembly has invoked niche-based explanations for the occurrences of ant species (Hölldobler and Wilson 1990). Fundamentally, ants are generalist omnivores and largely share a common resource base. Strong competition for resources has driven niche-partitioning through specialist foraging strategies in order to minimise competitive exclusion and facilitate co-occurrence. A variety of specialisations have been identified, including partitioning of foraging times through temporal and temperature-dependent cues (Briese and Macauley 1980, Cerdá et al. 1998a, Albrecht and Gotelli 2001, Schultheiss and Nooten 2013), partitioning of preferred food resources (Morrison 2000) or adaptation to fine-scale microhabitats enabling variable foraging success (McGlynn and Eben Kirksey 2000, Gibb and Parr 2010). Species may also co-occur through varying behavioural strategies for discovery and subsequent defence of food resources (Fellers 1987, Amarasekare 2003, Adler et al. 2007).

Although competitive interactions clearly facilitate niche differentiation among ant species, niche-based models make several predictions that are contradicted by empirical ant community data. Firstly, species co-occurring at a local scale should display only limited niche overlap (Levins 1979). Ant communities however often support much greater local diversity than can be explained through simple niche partitioning (Torres 1984, Andersen 2008). Secondly, closely related species are less likely to co-occur due to shared niche overlap in diet and foraging strategies (Mayfield and Levine 2010). Large numbers of closely related and ecologically similar species however can co-occur at fine spatial scales (Andersen et al. 2012). Thirdly, that in the absence of environmental heterogeneity, composition of assemblages should be largely homogenous across space (Tuomisto et al. 2003). We here demonstrate strong spatial structure within ant communities across plant communities, and previously demonstrated strong spatial assemblage patterns within plant communities (Chapter 2).

Stochastic assembly processes have been proposed as an explanation for ant species coexistence due to the inadequacy of niche-based models for explaining the often very high local species richness of ants, particularly in the presence of very strong competitive dominance (Andersen 2008). As ant colonies display strong persistence and longevity once established (Gordon and Kulig 1996), it is proposed that local species assemblages are a function of the availability of both mated queens and suitable nest microsites for establishment (Andersen 2008), rather than through niche-based competition for resources. Under neutral theory predictions, local assemblages of ant species should represent a stochastically selected subset of a larger regional pool of species similarly well adapted to the broad regional environment. The observed weak responses of assemblages to environmental drivers, very high species richness and strong patterns of spatial turnover in this study support this hypothesis of neutral processes shaping ant communities.

Conclusion

Our results demonstrate that in the absence of strong environmental heterogeneity, ant communities are structured primarily through stochastic processes resulting in strong spatial turnover. These results also demonstrate poor representation of ant assemblages within plant community-based conservation strategies, due to only weak patterns of assemblage-level congruence with plant community composition based on shared patterns of spatial autocorrelation. This study was carried out within an isolated remnant of native vegetation in a heavily modified landscape, with only 1.2% of the original land area formally conserved. The observed spatial turnover of assemblages within this study, with assemblages of the two most dispersed sites sharing only around half of their species, strongly suggests that the historical regional species pool is not fully represented in conserved native vegetation in this landscape. Consideration should therefore be given to maximising the spatial dispersal of conserved habitat within regional conservation strategies. Consideration of spatial assemblage patterns is particularly relevant in the implementation of biodiversity offsetting strategies, as assemblages conserved within offset sites would be unlikely to represent those lost through development if located far from the impacted habitat. These findings provide further support for our previous conclusion (Chapter 2) that biodiversity offsetting strategies must incorporate community composition of a broad range of taxonomic groups, along with strict spatial criteria in the determination of appropriate offset sites.

Chapter 4

**Fine-scale habitat complexity mediates
competitive dominance in ant communities**

Abstract

Competition is a fundamental key process guiding community assembly. This is particularly true for ant communities, as competitively dominant and aggressive ant species often exert strong control of competitively subordinate species abundances. However, local species richness of subordinate species can be high even in the presence of strong competitive dominance. Under the ‘interstitial’ hypothesis, subordinate species exploit fine-scale patchiness in the abundances of dominant species. However, empirical investigation suggests a positive association between dominant and subordinate ants at fine scales, mediated through a reduction of sub-dominant species capable of exerting competitive dominance in the absence of dominant species.

Habitat complexity negatively affects dominant species at broad scales, however the role of fine-scale microhabitat complexity has not been investigated as a potential factor driving patchiness in the fine-scale abundances of dominant ants. We compared abundances of dominant, sub-dominant and subordinate ant species at three spatial scales and related observed patterns to fine-scale microhabitat complexity to evaluate both the interstitial hypothesis and the hypothesis of a three-tiered competitive hierarchy. We found a strong negative influence of microhabitat complexity on dominant ant abundances at fine scales. In turn, the abundances of subordinate species were negatively associated with abundances of dominant species at fine, intermediate and coarse spatial scales. Species richness of subordinate ants however was affected at only fine scales (within individual pitfall traps). Our results therefore support the interstitial hypothesis as an explanation for the maintenance of species richness under strong competitive pressures.

Keywords: Competition, ants, interference competition, ant communities, dominant ants, interstitial hypothesis

4.1 Introduction

Competition is a fundamental process influencing the assembly of communities (HilleRisLambers et al. 2012). Competition has long been regarded as a major driver of ant community structure, particularly through the influences of competitively dominant species (Hölldobler and Wilson 1990, Cerda et al. 2013). Communities of ants worldwide comprise species conforming to discrete categories based on behavioural strategies (Wilson 1971, Andersen 1995), often forming linear hierarchies of competitive abilities with respect to monopolization and defence of resources (Savolainen and Vepsäläinen 1988). In the absence of adaptations enabling co-occurrence with dominant species, ant communities should consist of only the most competitively dominant species (Feener et al. 2008). However, depauperate ant communities are rare in nature (Hölldobler and Wilson 1990), and local species richness of ants may often be positively associated with strong competitive dominance (Andersen 1995, 2008).

Competitively subordinate ants coexist with dominant species by limiting direct competition. Many species co-occur spatially with dominant ants by partitioning of foraging times through adaptation to sub-optimal temperatures (Briese and Macauley 1980, Cerdá et al. 1998a, Albrecht and Gotelli 2001, Lessard et al. 2009, Schultheiss and Nooten 2013). Species co-occurring both temporally and spatially with aggressive dominant species often rely on behavioural and morphological adaptations enabling rapid exploitation of resources, resulting in a trade-off in the ability of ant species to locate resources against ability to achieve competitive monopolization, often termed the dominance-discovery trade-off (Fellers 1987). The outcomes of interactions between subordinate discoverers and dominant monopolisers however are typically highly asymmetrical, and dominant ants are often associated with reduced local abundances of competitively subordinate species (Savolainen and Vepsäläinen 1988, Andersen 1992, Andersen and Patel 1994). However, the role of dominant ants in

structuring communities remains unclear, as species richness of competitively subordinate ants can often be very high even under strong competitive dominance (Andersen 1992, 1995, 2008). Also, experimental reductions of dominant ant abundances often fail to achieve subsequent increases in subordinate forager abundances or shifts in assemblage composition (Gibb and Hochuli 2004, King and Tschinkel 2006, Gibb and Johansson 2011), however responses may be dependent successional stage of vegetation (Gibb 2011).

The exclusionary effects of competitively dominant species are perhaps most strongly exerted amongst rival dominant species. Non-random spatial associations between competitively dominant species are the norm in ant communities (Gotelli and McCabe 2002), often leading to total competitive exclusion (Majer 1972, Greenslade 1976a, Leston 1978, Greenslade and Halliday 1983, Fox et al. 1985, Greenslade 1987, Savolainen and Vepsäläinen 1988). This competitive exclusion can involve active defences of territory boundaries, both inter-specifically (Fox et al. 1985, Greenslade 1987, Adams 1994) and intra-specifically (Ettershank and Ettershank 1982).

Despite often despotic behaviour of dominant ants, the functional dominance exerted by them can be highly patchy across the landscape. For example, nests of dominant species may be irregularly distributed through space in association with spatially clustered food resources (Palmer 2003, van Wilgenburg and Elgar 2007), and strength of competitive control is inversely related to distance from the nest (Hölldobler and Wilson 1990). Dominant ant forager density may also be spatially patchy in association with habitat heterogeneity. Open habitats generally favour dominant species at broad scales (Andersen 2003, Arnan et al. 2014). Dominant ants also often increase in response to habitat disturbances resulting in more open habitats (Hoffmann and Andersen 2003), such as construction of roads (Gibb and Hochuli 2003), fire (Vanderwoude et al. 1997, Parr and Andersen 2008) or vegetation clearing or management (Greaves 1971, Arnan et al. 2009). Microhabitat complexity may

also regulate forager success at fine scales, with dominant ants less able to monopolize resources in more complex microhabitats (Gibb 2005), presumably due to the difficulty in recruiting to resources in these more rugose environments (Gibb and Parr 2010).

Fine-scale patchiness in dominant ant abundances has been cited as a potential mechanism facilitating coexistence in ant communities, whereby competitively subordinate species will preferentially exploit these spatial gaps in the activity of dominant ant foragers (Andersen 2008). This ‘interstitial hypothesis’ is a derivation of the aggregation model of species coexistence, in which spatial aggregation of resources leads to aggregation of superior competitors, in turn providing unoccupied space for inferior competitors to exploit (Shorrocks et al. 1979, Atkinson and Shorrocks 1981). Aggregation can occur at multiple spatial scales simultaneously (Inouye 1999), meaning that fine-scale patchiness in dominant ant forager density could potentially promote competitive coexistence even within areas of high overall competitive dominance.

An empirical test of the interstitial hypothesis in an Australian tropical savanna produced results contradictory to predictions (Arnan et al. 2011). Rather than revealing simple negative associations, dominant ants appeared to benefit subordinate ants indirectly through suppressing the abundances of sub-dominant Myrmicine species at fine scales. The observed three-tiered competition ‘cascade’ is analogous to trophic cascades where lower trophic levels are benefited indirectly by apex predators through the suppression of intermediate-level mesopredators (Letnic et al. 2009, Ritchie and Johnson 2009). Although these results seemingly contradict previous studies demonstrating negative responses of subordinate species to dominant ants at fine-scales (Andersen 1992, Andersen and Patel 1994), they do provide an alternative explanation for the observed pattern of high species richness in association with strong competitive dominance at broader scales across much of Australia (Andersen 1995).

Despite the influences of habitat complexity on dominant ant forager densities and the outcomes of competitive interactions at fine scales, heterogeneity in microhabitat complexity has not previously been investigated as a potential driver of fine-scale patchiness in competitive dominance. In this study, we aim to test the interstitial hypothesis and the alternative hypothesis of a three-tiered competition cascade for determining the abundances and species richness of subordinate and sub-dominant ant species at fine scales. Under the interstitial hypothesis, we expect to find negative associations between abundances of dominant species and both sub-dominant and subordinate ant species. Alternatively, positive associations between dominant species and subordinate species (and negative associations between dominant and sub-dominant species) would support the hypothesis of a three-tiered competition hierarchy.

We also investigate the role of fine-scale heterogeneity in microhabitat complexity as a driver of fine-scale patchiness in dominant ant abundances, and examine how fine-scale responses relate to patterns of species richness at coarse spatial scales. Finally, we examine patterns of dominant species distributions across the landscape to identify non-random associations amongst dominant species.

4.2 Methods

Study area

Ants were sampled within two conservation reserves (Big Bush and Ingalba Nature Reserves) and several adjoining private properties near Temora, New South Wales, Australia (lat., long= $-34^{\circ}26'$, $147^{\circ}25'$). The study area occurs within a predominantly cleared agricultural landscape supporting mostly wheat, canola and sheep farming. The vegetation comprises a

mosaic of several plant communities, predominantly Box/Ironbark woodlands characterised by Inland Grey Box (*Eucalyptus microcarpa*) and Mugga Ironbark (*Eucalyptus sideroxylon*), and a shrubby heathland community occurring on shallow soils on shale ridges. Full characterisation of plant communities can be found in Chapter 3.

Sampling

We sampled ants at three levels of spatial hierarchy (see Figure 4.1). Five sites were oriented on a roughly linear north-south transect, over a distance of around 19km. Within each site, we established 16 plots, located at points on a 4x4 grid spaced at 0.02 decimal degrees (approximately 187m on latitudinal and 222m on longitudinal axes). Within each plot ants were sampled in 16 individual pitfall traps (150mL cylindrical plastic vials containing 50mL of 100% Ethylene Glycol) spaced at 5m on a 4x4 grid. For further details of the sampling procedure see Chapter 3.

Traps were buried to ground level then left for a minimum of five days before opening to minimise ‘digging in’ effects (Greenslade 1973). Traps were then opened for an eight day period in February 2012. Following collection, ants were sorted from the traps and transferred to 70% ethanol. Ants were sorted to species groups in the lab, and representatives of each were mounted. Species-level identifications were conducted and/or confirmed by Alan Andersen (CSIRO Tropical Ecosystems Research Centre, Winellie NT).

We recorded variables contributing to the complexity of microhabitat at the ground level within a 2x2m sub-plot centred on each pitfall trap. We recorded the depth and cover of leaf litter, and the cover of monocotyledon and dicotyledon forbs, woody debris in three classes (<2.5cm, 2.5-10cm and >10cm) and moss/lichen.

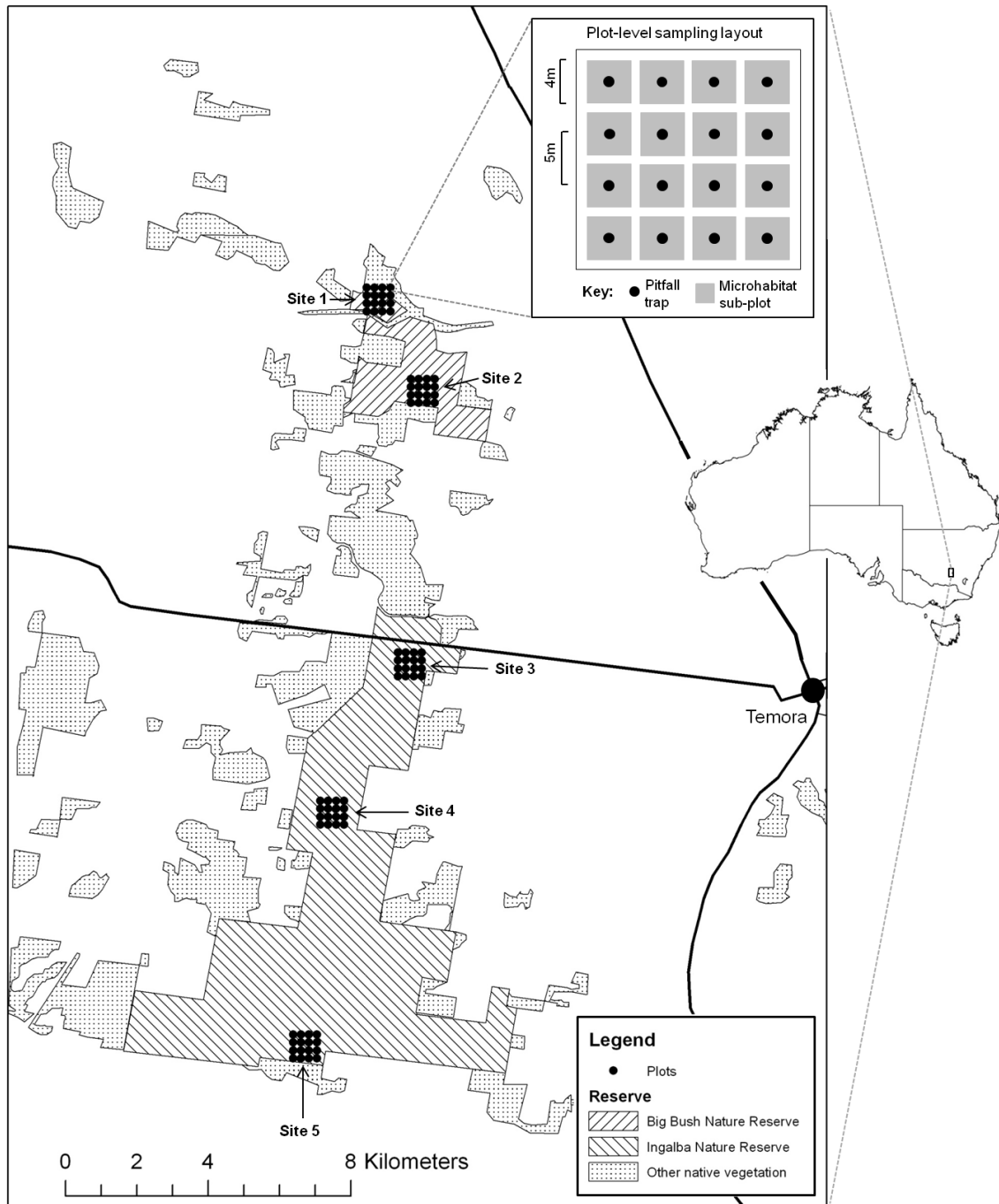


Figure 4.1. Layout of sites and sampling procedure across Big Bush and Ingalba Nature Reserves.

Dominance hierarchy groups

We populated a competitive hierarchy model based on the functional group categorisation of ant species based on continent-wide shared behavioural, physiological and morphological traits (Andersen 1995), as well as shared responses to a range of disturbances (Hoffmann and Andersen 2003). Our hierarchy consisted of three distinct competitive tiers following Arnan (2011): ‘dominant’ species, ‘sub-dominant’ species and ‘subordinate’ species.

Within our study system, the dominant species group was analogous to the ‘Dominant Dolichoderinae’ functional group, comprising the genera *Iridomyrmex*, *Anonychomyrma*, *Froggattella* and *Papyrius*. These species are usually highly abundant and aggressive, dominating food resources in hot and open environments (see Figure 4.2). They are sensitive to shade and structurally complex habitats. The sub-dominant species group was based on the ‘Generalized Myrmicinae’ functional group, including the genera *Monomorium*, *Pheidole* and *Crematogaster*. These three genera are widely distributed and functionally ubiquitous across the globe. They are often able to successfully defend resources through rapid recruitment and monopolization. The subordinate species group included members of both the ‘Subordinate Camponotini’ (*Camponotus* and *Polyrhachis*) and ‘Opportunists’ (*Doleromyrma*, *Nylanderia*, *Rhytidoponera*, *Paraparatrechina*, *Tapinoma* and *Tetramorium*) functional groups. Opportunist species are typically unspecialised and behaviourally submissive, inhabiting disturbed environments and other areas of low ant diversity. Subordinate Camponotini are similarly submissive species, but often co-occurring with Dominant Dolichoderinae by foraging at times when they are less active, including nocturnally. They can often be highly diverse at fine scales and typically have large body sizes.



Figure 4.2. Direct interference competition between a dominant species (*Iridomyrmex purpureus*) and a larger subordinate species (*Rhytidoponera punctiventris*).

The remaining species trapped were not included in our categorisation due to a lack of interaction with dominant ants. These species were representatives of the Cold-climate Specialists, Hot-climate Specialists, Specialist Predators, and Cryptic Species functional groups (Andersen 1995). These species were however included in the counts of total species richness for trap, plot and site-level species richness counts.

Abundance scores

Following Arnan (2011) we generated six-point abundance scores for each competitive group within each pitfall trap, based on pooled group-level abundances. Abundance scores were based on the scale as per Arnan (2011): 0 (0, 'none'), 1 (1-5, 'very low'), 2 (6-10, 'low'), 3 (11-20, 'medium'), 4 (21-50, 'high') and 5 (>50, 'very high'). We also generated abundance scores for each group based on abundances at the plot-level. Scores were based on a similar six-point abundance scale as per the trap-level abundance scores, though with higher abundance criteria: 0 (0, 'none'), 1 (1-10, 'very low'), 2 (11-30, 'low'), 3 (31-100, 'medium'), 4 (101-1000, 'high') and 5 (>1000, 'very high').

Microhabitat complexity indices

We generated microhabitat complexity indices based on habitat structural variables collected in our 2x2m sub-plots centred on each pitfall trap (Figure 4.3). We first calculated a six-point score based on the percentage cover of each recorded variable (leaf litter, monocotyledon and dicotyledon forbs, woody debris in three size classes, and moss/lichen cover): 0 (0%), 1 (>0-20%), 2 (>20-40%), 3 (>40-60%), 4 (>60-80%) and 5 (>80-100%). We also calculated a score based on the depth of litter, with values: 0 (absent), 1 (>0-0.5cm), 2 (>0.5-1cm), 3 (>1-1.5cm), 4 (>1.5-2cm) and 5 (>2cm). Our microhabitat complexity index was calculated as the sum of each component score.

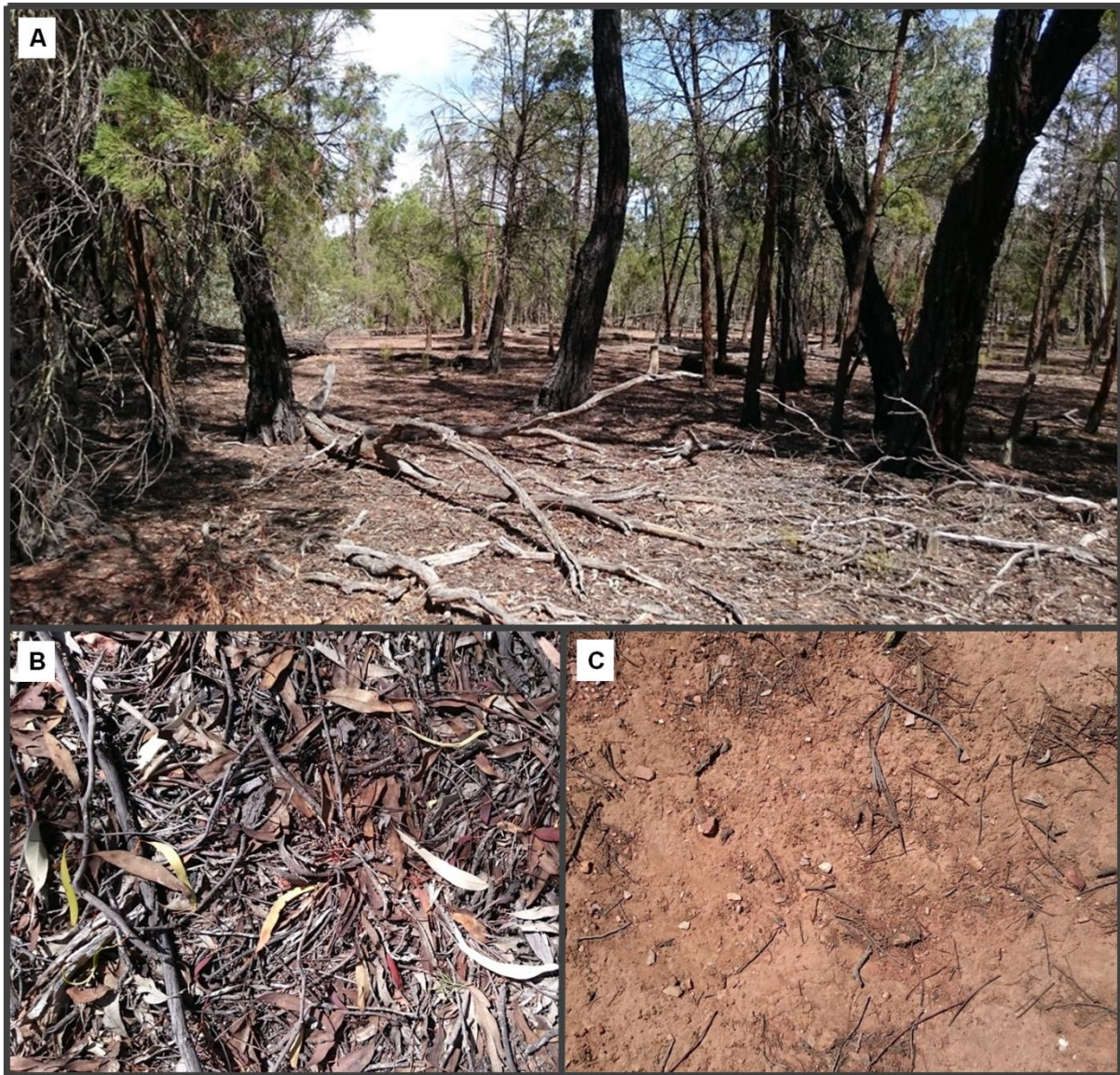


Figure 4.3. Examples of: (A) an open woodland habitat within the study area; (B) high fine-scale habitat complexity; and (C) low fine-scale habitat complexity.

Species richness estimations

During the sampling period, 184 of the 1280 traps were removed from the ground, most likely by foxes or dogs. We therefore estimated species richness at plot-level by extrapolating to 16 pitfall samples using the EstimateS program (Colwell and Elsensohn 2014). We generated species richness estimates for total species richness, total non-dominant species (all species besides ants in the Dominants hierarchy group) and Subordinate species groups. We used uncorrected Chao2 estimations based on 1000 permutations. Only plots sampled with eight or more traps (out of 16) were used for plot-level species richness estimations, reducing our effective sample size to 1030 individual traps in 71 plots. As our plot-level sample size was reduced for some sites, we also calculated species richness estimates at site-level using the above methods. We extrapolated to 16 plot samples for each site, for total, sub-dominant and subordinate groups.

Dominance hierarchy and microhabitat complexity effects on abundance and species richness

We first used simple correlations to identify patterns of association amongst the abundances of dominant, sub-dominant and subordinate abundance scores, and microhabitat complexity, at trap-level. We used Kendall's rank correlations due to the large number of tied observations, which prevented significance testing using Spearman's rank correlations.

Generalized Linear Mixed-effect Models (GLMM) were then used to test for between-group dominance interactions and microhabitat complexity effects on abundances and species richness of each hierarchy group, at trap and plot-level. Abundances of each group were based on trap and plot-level abundance scores. Species richness was based on the trap-level observed richness, and estimated species richness for plot-level analyses. Extrapolated species richness estimates were rounded to the nearest integer for GLMM analysis.

Microhabitat complexity values were based on mean trap-level indices for plot-level analyses. The standard deviation of trap-level microhabitat complexity indices was also calculated for plot-level models. All models were run based on Poisson distributions using the ‘lme4’ package in R (Bates 2010).

We tested for site-level patterns of association between microhabitat complexity, dominant ant abundance, subordinate ant abundance and subordinate species richness using simple linear regression based on Pearson correlation. Microhabitat values were site-level means based on trap-level microhabitat indices. Abundance values for dominant and subordinate species were based on the means of plot-level abundance scores. We used estimated site-level species richness of subordinate species (see above).

Co-occurrence patterns amongst dominant species

We compared the abundances of our dominant ant species to identify pairs of species showing strong competitive interactions. We used a probabilistic model of species co-occurrences to compare observed patterns of co-occurrence against those expected under a null model of random distribution of occurrences amongst sampled plots for each species (Veech 2013). We calculated expected and observed co-occurrence for both trap-level and plot-level data, using the R package “cooccur” (Griffith et al. 2015). We included only dominant species with total abundances of greater than 100 individuals, and that were present in greater than 20 traps and 10 plots. We first identified pairs of species showing either positive or negative patterns of occurrence at the plot level, then compared these plot-level responses to within-plot responses within individual traps. For trap-level comparisons we restricted our analyses to plots where both species were present. We based our analyses on the total dataset, including traps from plots sampled by fewer than eight traps (these were

excluded from other analyses, see above). Species pairs with expected co-occurrences of <1 were removed from the analyses.

We also recorded rudimentary morphometric data on ant species for descriptive purposes (mass, head width and hind femur length) on our six most abundant dominant species. Mean mass was calculated by weighting a sample of between 25 to 90 individuals from three or more colonies. Head width and hind femur length were based on means from three or more individuals, and were recorded using a Leica M165 C stereo microscope with DFC295 camera attachment (Leica Microsystems GmbH, Germany).

4.4 Results

Dominance hierarchy groups

We recorded 109622 individual ants from 142 species across all sites. Our three dominance hierarchy groups represented 86.9% of captured individuals (95265 individuals). The dominants group consisted of eleven species in four genera. The most abundant species was *Iridomyrmex chasei*, contributing $>50\%$ of all captured ants (55151 individuals). Other abundant species were *I. purpureus*, *Anonychomyrma* sp. A (*nitidiceps* group), *I.* sp. A (*mjobergi* group) and *I. bruneus*. The sub-dominants group comprised *Crematogaster* (four species), *Monomorium* (13 species) and *Pheidole* (seven species). The subordinates group comprised 18 species from the Opportunists functional group and 19 species from the Subordinate Camponotini functional group. The most abundant species were *Rhytidoponera metallica* (12337 individuals) and *Rhytidoponera punctiventris* (3958 individuals). These two species were also the only two species recorded in all plots sampled. Our reduced

dataset (excluding plots sampled with fewer than eight traps) included 104924 individuals in 71 plots.

Dominance hierarchy abundance patterns

Dominant ants had a strong negative association with the abundances of Subordinate species, at both trap and plot level (Figure 4.4, Table 4.1). Dominant ants however showed no association with the abundances of sub-dominant species based on simple correlation (Figure 4.4). There was however a mutual positive association between the abundances of dominant species and sub-dominant species at trap-level (Table 4.1).

Microhabitat complexity significantly reduced the abundances of dominant species at trap level (Figure 4.4, Table 4.1). A negative correlation was also seen at plot-level, however this relationship is not supported by our GLM model (Table 4.1). There were however no associations between microhabitat complexity and abundances of either sub-dominant or subordinate species. Similarly, there was no effect of within-plot variation in habitat complexity on abundances of any dominance hierarchy groups at plot-level.

Dominant ant effects on species richness patterns

Abundances of dominant ants reduced the trap-level species richness of subordinate ants (Table 4.2). This fine-scale influence of dominant ants on species richness of subordinate ants did not translate to negative relationships at coarser spatial scales, as no negative relationships were observed at either plot or site level (Table 4.2). Dominant ant abundances had no association with the species richness of non-dominant ants (all species besides the ‘dominants’ group), at trap, plot or site-level. Species richness of both subordinate and non-dominant ants was lower in high-complexity samples at trap-level (Table 4.2). This

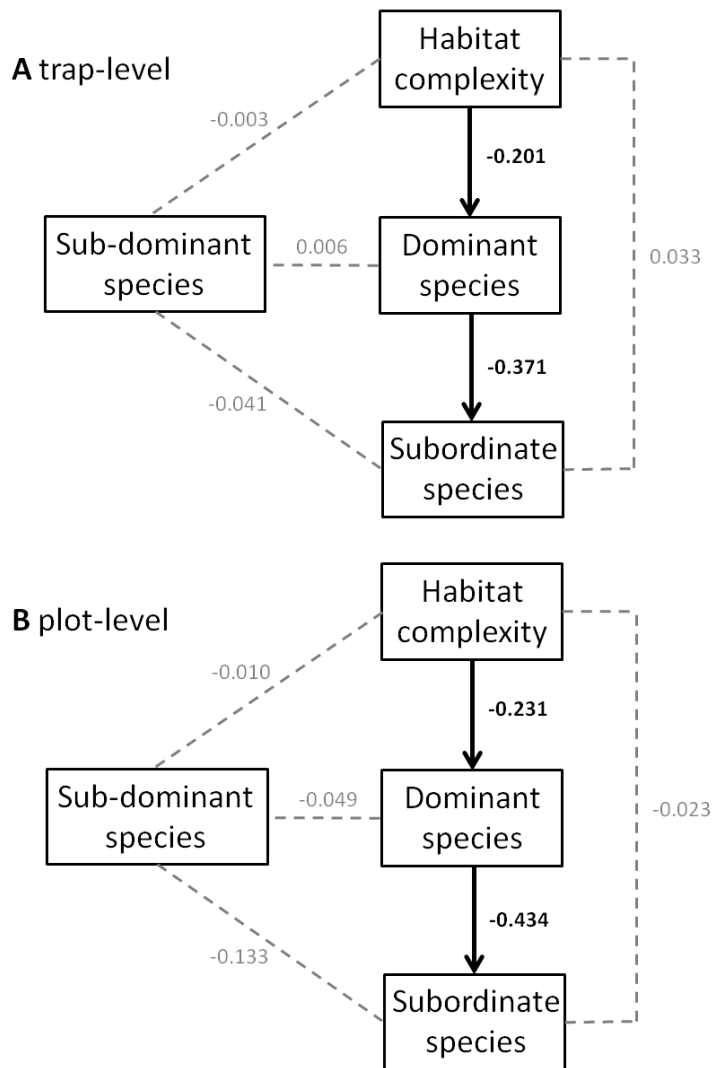


Figure 4.4. Kendall's rank correlations amongst abundance scores of dominance hierarchy groups and habitat complexity at (A) Trap-level and (B) Plot-level. Reported coefficients are Kendall's tau. Solid black arrows indicate statistical significance at the $\alpha=0.05$ level.

Table 4.1. Results of Generalized Linear Mixed-effect Models for dominance hierarchy group abundances across trap and plot-levels. Asterisks denote significance level (*= <0.05 , **= <0.01 , ***= <0.001).

	Dominant species		Sub-dominant species		Subordinate species	
	Estimate +/- S.E.	Z-value	Estimate +/- S.E.	Z-value	Estimate +/- S.E.	Z-value
Trap-level (df =1029)						
Intercept	0.403 +/- 0.51	0.789	0.811 +/- 0.17	4.846***	1.260 +/- 0.13	9.96***
Microhabitat complexity	-0.046 +/- 0.01	-3.96***	-0.012 +/- 0.01	-1.040	-0.011 +/- 0.01	-1.126
Dominants			0.057 +/- 0.02	2.765**	-0.055 +/- 0.02	-3.389***
Sub-dominants	0.056 +/- 0.02	2.75**			-0.020 +/- 0.02	-1.303
Subordinates	-0.024 +/- 0.03	-0.827	-0.032 +/- 0.03	-1.212		
Plot-level (df = 70)						
Intercept	1.312 +/- 1.653	0.794	2.345 +/- 2.045	1.147	1.204 +/- 1.787	0.674
Mean microhabitat complexity	-0.187 +/- 0.161	-1.614	-0.161 +/- 0.209	-0.770	0.009 +/- 0.185	0.046
St.dev. microhabitat complexity	-0.358 +/- 0.740	-0.483	-0.977 +/- 1.088	-0.898	0.358 +/- 0.956	0.374
Mean*St.dev. (mic. hab. complex.)	0.065 +/- 0.076	0.845	0.093 +/- 0.110	0.850	-0.043 +/- 0.099	-0.433
Dominants plot abundance			-0.027 +/- 0.050	-0.545	-0.132 +/- 0.044	-2.988**
Sub-dominants plot abundance	0.098 +/- 0.074	1.339			0.036 +/- 0.052	0.695

association was not observed at coarser scales however, with estimated plot-level species richness being positively associated with microhabitat complexity at plot-level. The within-plot heterogeneity in microhabitat complexity also positively affected estimated non-dominant species richness at plot-level, and a significant interaction between mean and variance in microhabitat complexity was detected.

Coarse-scale relationships between habitat complexity, dominant ants and subordinate ants

We found strong variation amongst sites in dominant ant abundances, despite microhabitat complexity being relatively uniform amongst sites (Figure 4.5). Dominant ant abundances were not significantly associated with microhabitat complexity ($t_3=-1.739$, $P=0.180$, $R^2=0.502$) or subordinate ant estimated species richness at site-level ($t_3=2.351$, $P=0.100$, $R^2=0.648$). However, subordinate ant abundances did show significant negative association with dominant ant abundances at this coarse scale ($t_3=-3.213$, $P=0.049$, $R^2=0.775$).

Surprisingly, we found a significant negative association between subordinate ant abundances and estimated subordinate species richness ($t_3=-4.519$, $P=0.020$, $R^2=0.871$).

Co-occurrence patterns amongst Dominant Dolichoderinae

Only one pair of species showed strong negative co-occurrence at the plot scale (*Iridomyrmex purpureus* with *Iridomyrmex chasei*, see Table 4.3). These two species were our most abundant of the dominants group, with total abundances of 1649 and 55151 and occurrences in 25 and 26 plots respectively. These species co-occurred in only two plots, and at trap level they co-occurred in only one trap. This observed pattern suggests strong competitive exclusion between the two species. Surprisingly, three species pairs showed significant positive association at plot-level (*I. purpureus* with *Iridomyrmex* sp. A (*mjobergi* group), *I. c.f. bicknelli* with *I. sp. A* (*mjobergi* group), and *I. bruneus* with *I. chasei*). These species

Table 4.2. Results of Generalized Linear Mixed-effect Models on species richness of Subordinate ants and total non-dominant ants at trap, plot level and site-level. Asterisks denote significance level (*= <0.05 , **= <0.01 , ***= <0.001).

	df	Subordinate species		Total non-dominant species	
		Estimate +/- S.E.	Z-value	Estimate +/- S.E.	Z-value
Trap-level					
Intercept	1029	1.346 +/- 0.090	14.94***	2.288 +/- 0.072	31.95***
Microhabitat complexity	1029	-0.020 +/- 0.008	-2.357*	-0.026 +/- 0.006	-4.52***
Dominants trap abundance	1029	-0.036 +/- 0.010	-3.56***	0.004 +/- 0.010	-0.42
Plot-level					
Intercept	70	0.204 +/- 1.168	0.175	1.696 +/- 0.528	3.212**
Mean microhabitat complexity	70	0.154 +/- 0.120	1.281	0.805 +/- 0.265	3.043**
St. dev. microhabitat complexity	70	0.709 +/- 0.593	1.197	0.153 +/- 0.054	2.828**
Mean*St. dev. (mic. hab. complex.)	70	-0.072 +/- 0.061	-1.185	-0.077 +/- 0.027	-2.840**
Dominants plot abundance	70	0.012 +/- 0.028	0.411	0.016 +/- 0.016	1.013

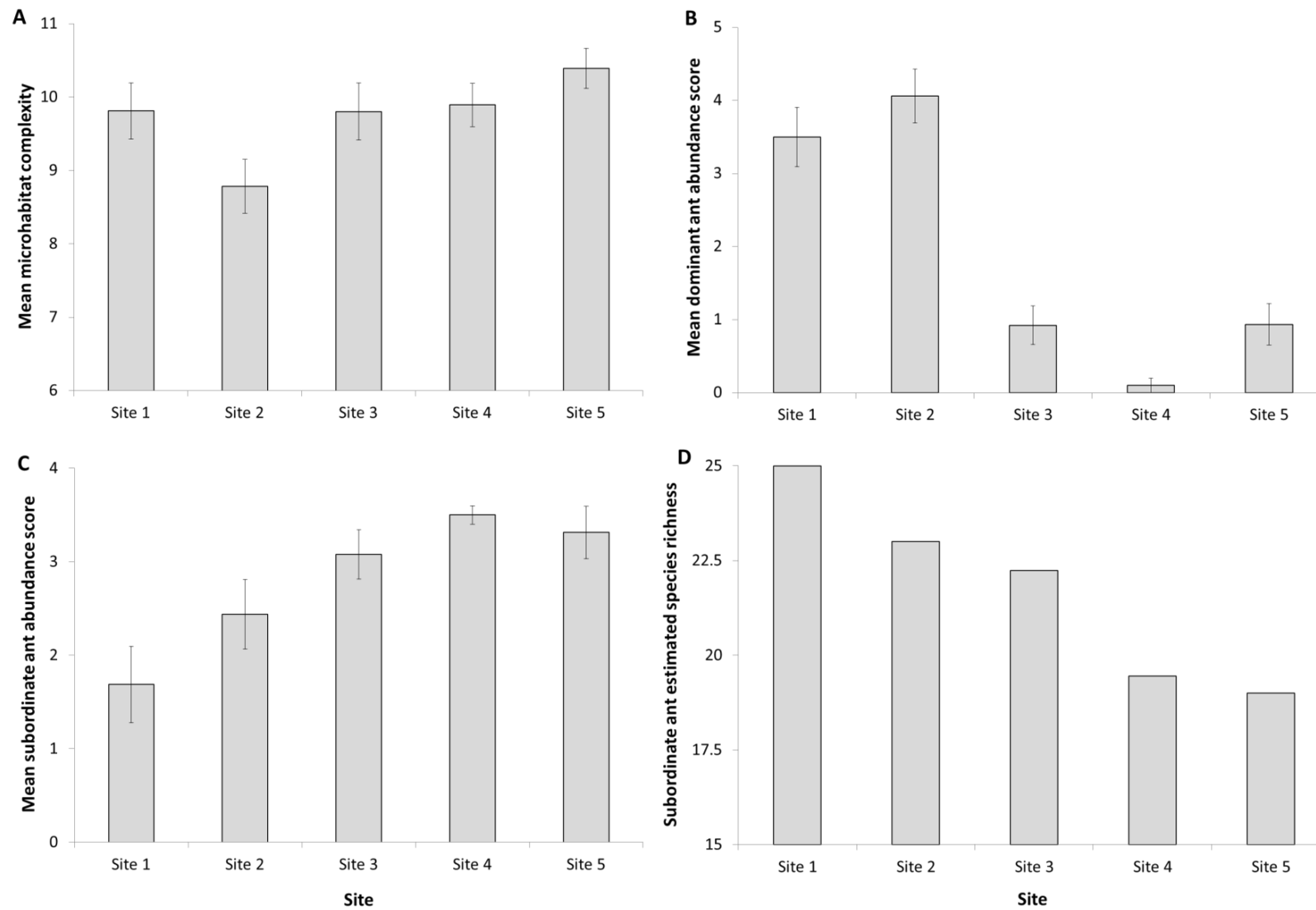


Figure 4.5. Site-level mean microhabitat complexity scores (A), mean dominant ant abundance scores (B), mean subordinate ant abundance scores (C), and estimated site-level species richness of subordinate ants (D). Error bars denote standard error.

Table 4.3. Spatial associations amongst dominant *Iridomyrmex* species based on probabilistic random distribution of co-occurrences.

Level	Sp. 1	Sp. 2	Occurrences		Co-occurrences		Probability	
			Sp. 1	Sp. 2	Observed	Expected	<Observed	>Observed
Plot	<i>I. bruneus</i>	<i>I. chasei</i>	29	26	18	9.4	1	<0.001
Trap			58	231	49	53.4	<0.05	0.994
Plot	<i>I. bicknelli</i>	<i>I. sp. A</i>	33	33	20	13.6	0.999	<0.01
Trap			50	104	21	18.1	0.863	0.219
Plot	<i>I. chasei</i>	<i>I. purpureus</i>	26	25	2	8.1	<0.01	0.999
Trap			17	6	1	3.6	<0.05	0.999
Plot	<i>I. purpureus</i>	<i>I. sp. A</i>	25	33	18	10.3	0.999	<0.001
Trap			147	97	59	58.0	0.658	0.444

pairs however showed either no association or negative association (as for *I. bruneus* with *I. chasei*), at trap-level.

Our dominant species varied greatly in morphological traits, particularly in size. Our largest dominant ant, *I. purpureus* (mean weight = 12.236mg, hind femur length = 2.77mm, head width = 1.59mm) was around 110 times heavier than our smallest dominant species *Iridomyrmex* sp. A (*mjobergi* group) (mean weight = 0.107mg, hind femur length = 0.55mm, head width = 0.43mm). Our four other most abundant dominant species were *I. chasei* (mean weight = 0.462mg, hind femur length = 0.79mm, head width = 0.57mm), *I. bruneus* (mean weight = 1.659mg, hind femur length = 1.37mm, head width = 0.82mm), *I. c.f. bicknelli* (mean weight = 0.506mg, hind femur length = 1.17mm, head width = 0.54mm), and *I. ?septentrionalis* (mean weight = 0.743mg, hind femur length = 1.02mm, head width = 0.70mm).

4.4 Discussion

Effects of microhabitat complexity and dominant ant abundances

Our results demonstrate a clear association between spatial heterogeneity of microhabitat complexity and forager abundances of dominant ants at fine-scales. In turn, fine-scale forager abundances was strongly negatively associated with the abundances and species richness of subordinate ants at these fine scales. As we detected no association of subordinate ant abundances with fine-scale microhabitat complexity, this relationship appears to be related to associations with dominant ants alone. Patterns at broader scales revealed a general negative correlation between microhabitat complexity and dominant ant abundances, however this negative relationship was not evident once the spatial location of samples was controlled for.

While abundances of subordinate species were negatively associated with dominant species at plot level, we found no relationship with species richness. The abundances of dominant ants varied greatly amongst sites, with far greater abundances in the northern two sites (sites one and two) (Figure 4.5). This pattern was not associated with underlying differences in microhabitat complexity amongst sites. Dominant abundances at these broad scales were predictably negatively associated with subordinate ant abundances, however the species richness of subordinate ants was actually positively associated (though not significantly so) with dominant ant abundances (see Figure 4.5). Surprisingly, we found that species richness was negatively associated with abundances in subordinate ants at these coarse scales.

These results suggest that even under strong competitive dominance, subordinate species may be able to exploit fine-scale heterogeneity in dominant ant forager density, and that this patchiness in dominant ant forager density may be driven by microhabitat structure at fine scales. These findings therefore support the interstitial hypothesis as an explanation for the prevalence of high species richness even in the presence of strong competitive pressures from highly aggressive species (Andersen 2008) and contradict findings of assemblage-level control of species richness by dominant ants (Parr 2008). Further, our results suggest a mechanistic explanation for patchiness in the competitive dominance effects of dominant ants.

The interstitial hypothesis is derived from the aggregation model of competitive coexistence (Shorrocks et al. 1979, Atkinson and Shorrocks 1981), in which aggregations of competitively superior species will form due to aggregations of resources. In this particular application of the model, resource aggregations represent those patches in which the payoffs for relative foraging effort are greatest. As fine-scale microhabitat complexity increases the

time needed to locate resources (Fewell 1988, Gibb and Parr 2010) and decreases the ability of dominant ants to successfully monopolize resources (McGlynn and Eben Kirksey 2000, Gibb 2005, Gibb and Parr 2010), complex microhabitats could therefore represent patches of low resource aggregations for competitively superior dominant ant species, through differential responses of competitive ability to microhabitat complexity between dominant and subordinate species (Amarasekare 2003).

If competitively inferior subordinate ants preferentially exploit complex microhabitats representing low resource density patches, we should expect to find greater association with these microhabitats amongst subordinate ants than for other groups of ants. We found no association of subordinate (or sub-dominant) ant abundances with microhabitat complexity at either trap or plot level, despite strong effects on dominant species. Subordinate species richness was significantly negatively associated with microhabitat complexity at trap level but not at plot level. However, this effect was stronger in the total pool of non-dominant species, being significantly associated at both trap and plot levels. These results alone do not provide evidence of any positive associations of subordinate ants with complex microhabitats. However, there is a general trend of greater species richness of ants in more open habitats (Retana and Cerdá 2000, Andersen 2003, Lassau and Hochuli 2004, Arnan et al. 2014, Chapter 2). Our observed weak negative association of ants with microhabitat complexity relative to that of the total assemblage of non-dominant species may therefore reflect a lower sensitivity of subordinate species to detrimental effects of microhabitat complexity such as reduced foraging efficiency (Fewell 1988, Gibb and Parr 2010). Only two ant species were present in all plots in this study, and both were subordinate species (*Rhytidoponera metallica* and *R. punctiventris*). The even distribution and relatively high abundances of these species suggest low sensitivity to microhabitat heterogeneity.

A tendency towards exploitative competition amongst subordinate species predicts that they should be well adapted behaviourally and morphologically to rapidly locate resources (Fellers 1987). Subordinate species in this study are representatives of the Subordinate Camponotini and Opportunist functional groups, which are often characterised by large body sizes (Andersen 1995) (see Figure 4.2). Large body sizes enabling rapid movement across space are generally associated with ability in locating resources (Gibb and Parr 2013), however the relationship between ant body size and foraging efficiency in complex microhabitats is not linear (Kaspari and Weiser 1999). Large body and associated long legs may enable an ant to move more rapidly over complex environments, however small body size may benefit an ant navigating within that same environment (Kaspari and Weiser 2007, Gibb and Parr 2010).

Existence of a three-tiered competition cascade

Abundances of sub-dominant ants (comprising species of *Pheidole*, *Monomorium* and *Crematogaster*) had no association with the abundances or species richness of subordinate ants in this study. Further, we found no evidence of a negative relationship between dominant ants and sub-dominant ants. Although we found no trap or plot-level associations between groups based on raw abundance scores, we found a positive, mutual association between dominant and sub-dominant species once spatial arrangement of samples was accounted for. We therefore find no evidence of the three-tiered competitive cascade in the current study, suggesting that the pattern detected in an Australian tropical savanna (Arnan et al. 2011) is not a consistent phenomenon across Australia. Our findings of a direct negative association between dominant and subordinate ant abundances best match previous results relating abundance patterns at fine scales (Andersen 1992, Andersen and Patel 1994).

Patterns of dominant ant association

Dominant ant occurrences across space revealed two key patterns. Firstly, that pairs of dominant ant species can be negatively correlated at fine scales (trap-level), but positively correlated at intermediate scales (plot-level). We found three species pairs of species showing positive association at plot-level. Observed positive associations may be the result of adaptation for co-existence amongst some species pairs, either through divergence of traits enabling co-occurrence, or through fine-scale partitioning of space. Although our dataset does not contain sufficient numbers of species to enable statistical evaluation of these alternative hypotheses, our results do suggest a possible role of each. For example, the observed positive association between *Iridomyrmex purpureus* and *I. sp. A (mjobergi group)* represent the greatest divergence in size amongst our dominant species, with *I. purpureus* being over two orders of magnitude heavier and with hind femur length over five times longer than *I. sp. A*. This variation in size and leg length is likely to strongly influence the two species' interactions with microhabitat (Kaspari and Weiser 1999) and food resource utilization (Gibb et al. 2015), potentially facilitating coexistence (Brown et al. 2014).

Dominant species pairs may also coexist by partitioning space at fine scales, as suggested by the negative association of *I. chasei* and *I. bruneus* at trap level in our results, despite positive association at plot level. Alternatively, observed positive associations may instead represent shared negative associations with a third dominant species, though we did not detect complimentary negative associations in our analyses.

Our second key finding is that one pair of dominant ants (*Iridomyrmex purpureus* and *I. chasei*) showed evidence of extreme competitive exclusion at both trap-level and plot-level. These two species vary significantly in both body size and abundances in the current study, with *I. purpureus* being around 26 times heavier than *I. chasei*, however abundances of *I. chasei* (n= 55151) are much higher than *I. purpureus* (n=1649), or indeed any other species in

the current study. The meat ants (including *I. purpureus*) are regarded as the most dominant members of Australian ant communities and (Greenslade 1976b, Andersen and Patel 1994, Gibb 2003). Despite *I. chasei* not being regarded as exerting the same degree of aggression, it may still be able to exert significant competitive influences through sheer numerical advantage (Andersen 1992, Cerda et al. 2013).

Competitive exclusion amongst dominant ant species is common in ant communities (Majer 1972, Greenslade 1976a, Greenslade and Halliday 1983, Fox et al. 1985, Greenslade 1987, Savolainen and Vepsäläinen 1988). Competitively dominant species may vary in the strength of competitive exclusion they exert on subordinate species, and different dominant species may even be associated with unique assemblages of non-dominant species (Hölldobler and Wilson 1990). Previous manipulative studies have shown little influence of competitive dominance in shaping assemblage structure and composition (Gibb 2003, Andersen and Majer 2004, Gibb and Hochuli 2004, Gibb and Johansson 2011), however experimentally suppressing the abundances of one species may enable other dominant species to increase in abundances (Gibb and Hochuli 2004) or even to colonise the territory of the suppressed species (Fox et al. 1985). The observed competitive exclusion between *I. chasei* and *I. purpureus* presents an opportunity to study the differential effects of dominant ant species in structuring communities, particularly as these two species vary dramatically in both size and abundances in the study area. This competitive interaction may also provide an ideal study system to evaluate the role of differential food resource utilization as a factor in structuring co-occurrence patterns amongst dominant ant species (Blüthgen 2004).

Conclusions

Our finding of a direct link between fine-scale heterogeneity in microhabitat complexity and fine-scale patchiness in the abundances of dominant species demonstrates a potential

mechanism for enabling coexistence of subordinate species with dominant species at broader scales. This result, along with our findings that strong competitive effects of dominant ants on subordinate ants at fine scales do not result in reductions in species richness of subordinate ants at broader scales, provide strong evidence to support the interstitial hypothesis of competitive coexistence.

Chapter 5

**Competitive displacement of a behaviourally
dominant ant by a numerically dominant ant
reduces species richness in associated ant
communities**

Abstract

Competition for resources drives niche partitioning to enable species coexistence. This is particularly true for ant communities, with competitively subordinate species employing a range of behavioural and physiological adaptations to facilitate coexistence with highly aggressive dominant ant species. Competitive interactions however are often strongest between dominant species, and can include total competitive exclusion between species, and will actively defend territories along boundaries. Dominant species can also vary in their strategies for achieving competitive dominance, and invasion by dominant ants can rapidly alter the composition of ant communities through species loss.

We investigated the differences in competitive pressures exerted on ant assemblages by two abundant dominant ant species occupying mutually exclusive territories and varying in size and abundance, *Iridomyrmex purpureus* and *I. chasei*, to determine whether the type and strength of competitive dominance varies between species. We compared the assemblages of ant species within the territories of the two species and at the boundaries of their ranges where the two species occurred in close proximity. We also contrasted the performance of the dominant ants at monopolising resources within their territories, and the species richness of other ant species recorded at baits. We also re-visited sampling locations along boundaries. We found that interference competition at territory boundaries was asymmetrical, with *I. chasei* consistently outcompeting *I. purpureus* and expanding their range. More baits were monopolized by *I. chasei*, and fewer species were recorded at baiting sites within their territories. The composition of species recorded at baits was also different between species' territories. We found no differences in assemblage composition of affiliate ant species caught in pitfall traps along territory boundaries, however the rapid shifts in territory boundaries indicate that these assemblages likely had insufficient time to respond to changes in dominant

ant identity. These results demonstrate that dominant ant identity can have a structuring influence on ant communities through regulation of species richness and even assemblage composition.

Keywords: Competition, dominant ants, ants, interference competition, ant communities, competitive exclusion, *Iridomyrmex*, Meat Ants

5.1 Introduction

Competition for resources is a fundamental driver of community patterns (HilleRisLambers et al. 2012). Competition is a mainstay of ant community ecology (Hölldobler and Wilson 1990), and a common factor in ant communities is the presence of highly aggressive dominant species controlling resources and inhibiting the local abundances of competitively subordinate species through interference competition (Savolainen and Vepsäläinen 1988, Andersen 1992, Andersen and Patel 1994). Consequently, competitively inferior ant species have developed adaptations for limiting direct competition with dominant species.

Subordinate species can avoid peak times of activity of dominant species through specialised adaptation to foraging at sub-optimal temperatures (Cerdá et al. 1998b, Schultheiss and Nooten 2013). Competitively subordinate species can also exploit fine-scale spatial heterogeneity in the prevalence of dominant species (Albrecht and Gotelli 2001), such as more complex microhabitats where dominant species are less abundant (Chapter 4) or where the abilities of dominant ants to successfully monopolize resources are diminished (Gibb 2005, Gibb and Parr 2010). Additionally, subordinate species may co-occur through specialisation for rapid discovery and exploitation of food resources before more dominant species are able to successfully achieve monopolization, often the cost of ability in defence of resources (Fellers 1987, Adler et al. 2007).

Evidence for the influence of competitively dominant species on ant community structure comes predominantly from diversity of ant species present at provisioned food resources (Savolainen and Vepsäläinen 1988, Andersen 1992) and species richness patterns of species in pitfall traps (Parr 2008, Chapter 4). Experimental manipulation of dominant ant abundances has failed to replicate predicted community-level response (Andersen and Patel 1994, Gibb and Hochuli 2004, Gibb and Johansson 2011). However where multiple

dominant ant species are present in a community, the experimental removal of one can result in increases in another (Gibb and Hochuli 2004), and even facilitate colonisation of previously occupied territory by other dominant species (Fox et al. 1985). Because ant colonies are generally long-lived and persistent even in the presence of strong competition (Wiernasz and Cole 1995, Gordon and Kulig 1996), the relatively short durations of some manipulative studies (Andersen and Patel 1994, Gibb and Hochuli 2004) may not reflect sufficient time for community-level changes to occur.

Competitive exclusion can also structure ant communities by limiting co-occurrence amongst dominant species, resulting in non-random spatial distribution patterns (Savolainen et al. 1989, Gotelli and McCabe 2002). In extreme cases, competition can result in patterns of total exclusion between species pairs across the landscape (Greenslade 1976a, Greenslade and Halliday 1983, Fox et al. 1985, Greenslade 1987, Savolainen and Vepsäläinen 1988).

Mutually-exclusive territories amongst dominant ants with associated non-random assemblages of non-dominant affiliate ant species have long been observed in tropical arboreal systems (Majer 1972, Leston 1973, 1978, Jackson 1984). These checkerboard patterns of dominant ant distributions, termed 'mosaics', are thought to be structured primarily through competitive interactions amongst species, and are maintained through active territorial defence (Adams 1994). These mosaics appear to form almost exclusively in highly structured and defensible tropical arboreal habitats, particularly in highly modified landscapes with depauperate ant assemblages (Götzke and Linsenmair 1996), however they do provide evidence of the role of dominant ants in structuring the composition of assemblages.

Further evidence for compositional regulation of ant communities by dominant species lies in studies of invasive ants. Invasion by the numerically dominant and aggressive Argentine ant

Linepithema humile) results in compositional shifts in native ant assemblages (Sanders et al. 2003), primarily through reductions in local species richness (Holway 1998, Suarez et al. 1998). Similar responses of native ant assemblages are observed for invasions of the red imported fire ant (Gotelli and Arnett 2000), yellow crazy ant (Hoffmann and Saul 2010) and big-headed ant (Hoffmann et al. 1999). The loss of species richness in native ant communities following invasion by a novel dominant species highlights the potential role of species-specific adaptations to avoid competition. For example, the Argentine ant preferentially forages at lower temperatures than the native dominant species *Iridomyrmex bicknelli* in Western Australia (Thomas and Holway 2005). Native ants adapted for avoiding competition by foraging at suboptimal temperatures below that of *I. bicknelli* would likely be poorly adapted to competing with this novel dominant species. Species loss from ant communities following invasion by novel dominant species therefore highlight a potential role for species-specific adaptation in avoiding competitively dominant species.

Dominant members of Australian ant communities belong primarily to the Dolichoderinae subfamily, particularly the genus *Iridomyrmex*. These species are characterised as the ‘Dominant Dolichoderinae’ within a well-supported functional group classification system for Australian ant species (Andersen 1995, Hoffmann and Andersen 2003). While virtually all *Iridomyrmex* species display some aggressive behaviour (Heterick and Shattuck 2011), the meat ants (*Iridomyrmex purpureus* and allied species) have long been regarded as exerting the greatest competitive dominance of all members of Australian ant communities (Greenslade 1976b, Andersen and Patel 1994). The meat ant group is represented broadly by *Iridomyrmex purpureus* over much of Southern and Eastern Australia, and by *Iridomyrmex sanguineus* in Northern Australia (though this group also includes several other morphologically-similar species including *I. reburrus*, *I. viridianeus*, *I. lividus* and *I. spadius*) (Heterick and Shattuck 2011). Despite the widespread distribution and consistent aggressive

behaviour of meat ants, they are often most abundant in open habitats and are often patchily-distributed across at fine scales (Gibb and Hochuli 2003). Other *Iridomyrmex* species may also be highly aggressive and exert strong competitive dominance at fine scales (Fox et al. 1985). We previously found strong checkerboard distributions suggesting competitive exclusion between two dominant *Iridomyrmex* species in a study of ant assemblages in dry-sclerophyll Eucalypt woodlands in Eastern Australia (Chapter 4). These two species, *Iridomyrmex purpureus* and *Iridomyrmex chasei*, have a near total checkerboard distribution at both fine and coarse scales, despite being highly abundant across the study area. These two species have broadly different traits in terms of size, abundance and colony structure (see Methods). While aggressive behaviour in *I. chasei* has previously been noted (Heterick and Shattuck 2011), it has not been recognised to exert strong community-level dominance behaviour to the same extent as *I. purpureus*. This species however is hyper-abundant in the study area, constituting over 50% of total captures in our previous study (Chapter 4).

The natural checkerboard pattern of distributions between two dominant species varying in size, abundance and colony structure provides an ideal study system for investigation of the differential effects of dominant ant species on the species richness and composition of ant assemblages. Because competitively subordinate species may be better adapted for co-existence with dominant ants displaying a specific set of traits, specific dominant ant species may have a filtering effect on assemblage composition at fine scales. While this effect has been demonstrated in arboreal ant communities (Dejean and Corbara 2003), there is little direct evidence to confirm this process within established ground-dwelling ant communities. To investigate this, we compared the differential influences of our two focal dominant ant species (*I. purpureus* and *I. chasei*) on the abundances, species richness, assemblage composition and competitive performance at food resources of all co-occurring ant species (hereafter termed ‘affiliate’ species).

5.2 Methods

This study was carried out in Big Bush and Ingalba Nature Reserves and adjacent private property near the town of Temora, New South Wales, Australia (Lat., Long=-34°26', 147°25'). The study area comprises remnant dry sclerophyll vegetation, mostly Inland Grey Box (*Eucalyptus macrocarpa*) - Mugga Ironbark (*Eucalyptus sideroxylon*) woodlands and shrubby heathlands, within a predominantly agricultural landscape (Chapter 3).

Focal dominant ant species

The two focal dominant species, *I. purpureus* and *I. chasei*, are very divergent in size with the former being heavier (12.236mg cf. 0.462mg) and having longer hind femur (2.77mm cf. 0.79mm) (see Chapter 4). This difference in size is offset by far higher abundances of *I. chasei* (n= 55151) compared to *I. purpureus* (n=1649) in the previous study (Chapter 4). The distribution of nests across the landscape also differs, with polydomous (colonies consisting of multiple associated nests) colonies of *I. chasei* developing complex networks of densely-packed nests across space. In contrast, nests of *I. purpureus* are broadly spaced, though the species is often polydomal with nests interconnected by well-developed trail networks (Greenslade 1975, Greenslade 1976b, van Wilgenburg et al. 2006a). Many other Dominant Dolichoderinae species occur throughout the study area, including several *Iridomyrmex*, and species of *Anonychomyrma*, *Froggattella* and *Prolasius*. While these species may be highly abundant locally, they however are more sparsely distributed across the landscape, show lower overall abundances, and often co-occur with other dominant species at fine scales (Chapter 4).

Determination of dominant ant territories and boundaries

We investigated potential boundaries of dominant ant distributions through investigation of locations known to support both species in close proximity (see Chapter 4). Potential boundaries of territories were determined by traversing the area with a handheld GPS device (Garmin Oregon 450t) and recording the presence or absence of our focal dominant species and any other Dominant Dolichoerinae species along random walk transects. The presence of *I. chasei* was readily detectable due to its higher abundance, rapid activity and presence of nest entrances at regular intervals (spaced at around 2 metres) throughout their territories. Presence of *I. purpureus* required greater effort to verify due to a patchiness of foraging workers beyond the immediate vicinity of nests. Specimens of each species were collected for later identification, however both species were readily identifiable in the field through size and morphology for *I. purpureus*, or abundance and behaviour for *I. chasei*. When the two species were encountered nearby to each other, the area was searched intensively and GPS locations were recorded to mark distributions along the boundary. Each derived territory was also searched to verify the absence of the alternate species. Over 800 GPS points were recorded over a two week period to demarcate boundaries and mark the locations of *I. purpureus* nests.

We also documented fighting between *I. chasei* and *I. purpureus* along boundaries in the study area, and where abandoned nests of *I. purpureus* were occupied by *I. chasei*. These observations were largely opportunistic during the two week period determining boundary locations and during subsequent sampling.

Dominant ant effects on affiliate ant species

We sampled ant assemblages along transects perpendicular to territory boundaries to compare the effects of dominant ant identity on assemblage composition, species richness and

abundances of affiliate ants (all ant species besides our two focal dominant species). We established 17 transects, each consisting of three samples spaced at 50m; one sample along the immediate boundary between dominant ant species territories, and one sample within the territories of each focal dominant ant species (Figure 5.1). Transects were located where a distinct edge of an *I. chasei* territory could be readily identified, and *I. purpureus* could be identified as occurring nearby outside of that territory.

We sampled ants at each plot along using pitfall traps (150mL plastic vials of 45mm diameter filled with 50mL Ethylene Glycol), on a 2x3 grid with traps spaced at 5m. Pitfalls were buried to ground level then left for at least five days to minimise ‘digging in’ effects (Greenslade 1973). Traps were then opened for an eight day period in March 2013.

Following collection, ants were sorted from the traps and transferred to 70% ethanol. Ants were sorted to species groups in the lab, and representatives of each were mounted. Species-level identifications were conducted by Alan Andersen (CSIRO Tropical Ecosystems Research Centre, Winnellie NT).

We generated habitat complexity indices for each sub-plot following our previous study (Chapter 4) to account for structural variation amongst plots. Structural attributes of vegetation contributing to habitat complexity at the ground level were sampled within 2x2m sub-plots centred on each pitfall trap. Each recorded variable (cover and depth of leaf litter, and the cover of monocotyledon and dicotyledon forbs, woody debris in three classes (<2.5cm, 2.5-10cm and >10cm) and moss/lichen) was allocated a score on a six-point scale (0-5), with percentage cover given: 0 (0%), 1 (>0-20%), 2 (>20-40%), 3 (>40-60%), 4 (>60-80%) and 5 (>80-100%). Depth of litter was allocated a score based on: 0 (absent), 1 (>0-0.5cm), 2 (>0.5-1cm), 3 (>1-1.5cm), 4 (>1.5-2cm) and 5 (>2cm). Scores for each variable were then summed to calculate the trap-level habitat complexity index. Trap-level indexes

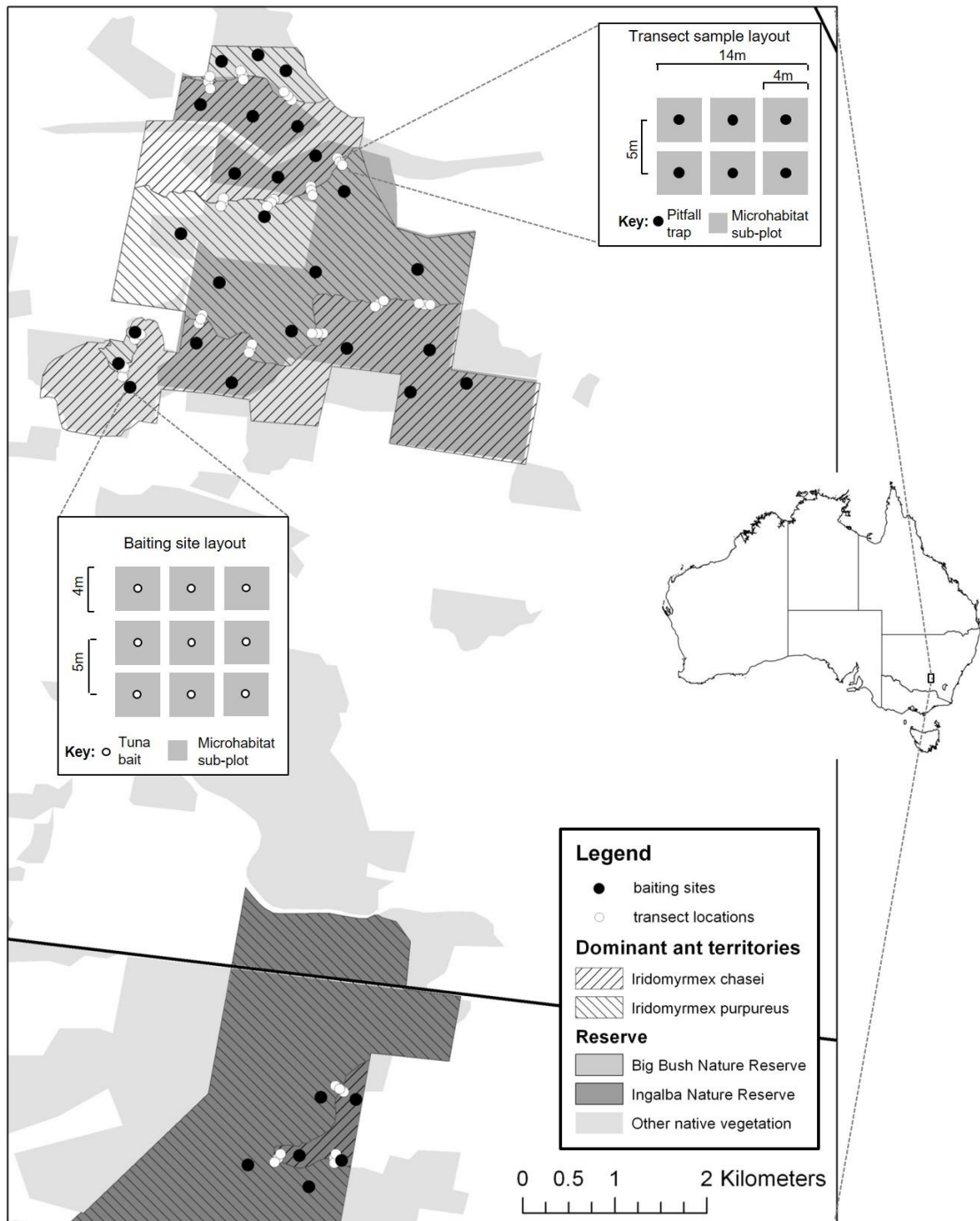


Figure 5.1. Location of territory boundaries, transect samples and within-territory baiting sites within the study area.

were averaged for plot-level habitat complexity values. To determine whether dominant species boundaries were related to underlying structural variation habitat, we compared our derived plot-level habitat complexity values across transect samples using an Analysis of Variance (ANOVA).

Statistical analyses

We compared the composition of affiliate ant species across transect samples ('*I. chasei*', 'boundary' and '*I. purpureus*') using Non-metric Multidimensional Scaling ordination (nMDS). Ordination was based on Bray-Curtis dissimilarity on fourth-root transformed abundance data to reduce the influence of abundant species on pairwise dissimilarities, using Primer v.6 (Clarke and Gorley 2006). Statistical significance of relationships amongst samples was tested using multivariate Generalised Linear Modelling in the MVABUND package in R (Wang et al. 2012), based on a negative binomial distribution. We controlled for spatial autocorrelation by including both the transect (n=14) and boundary (n=5) that each sample was taken from as variables in the model. We also controlled for structural variation amongst samples by including plot-level habitat complexity in our model.

Species richness and abundance of subordinate ants at plot-level were compared amongst samples using multiple analysis of covariance (MANCOVA). We used sample, transect, mean habitat complexity, and abundance of Dominant Dolichoderinae species (ln+1 transformed) as factors in the model. We used the R package for this analysis (R Core Team 2013).

Competition for food resources

We compared the spatial uniformity of competitive pressures between dominant ant species at territory boundaries by comparing rates of dominance of food resources at each trap

location. Food resources were small tuna baits (~1.5cm diameter, Woolworths brand tuna in spring water, Woolworths Limited, Bella Vista, Australia) placed directly on the soil surface. Baits were checked at 5, 10, 20 and 40 minute intervals, and the species and number of ants on or within 2cm of the bait were recorded. Where necessary, representative specimens were sampled using soft forceps from nearby the bait, avoiding behavioural interference. Baiting was completed during March 2013 between 9am and 6pm, with air temperatures at 10cm from the ground between 18-34°C. We determined that a bait was ‘won’ if at or before the 40 minute interval greater than ten workers of one species were present on the bait, and other species were either absent or in low numbers (<5) at the bait. A bait was ‘lost’ if a species present at the bait was later excluded or abundances were significantly reduced through competitive interactions with a winning species. A ‘stalemate’ was reached if no species achieved abundances of greater than ten at the bait during the 40 minute monitoring period.

A further baiting experiment was conducted at sites within the territories of our two focal dominant species in March 2014 to compare the strength and spatial uniformity of competitive dominance effects of the two species within territories. Sites (n=15 for *I. purpureus* and n=16 for *I. chasei*) consisted of nine baits arranged on a 3x3 grid spaced at 5m. Baiting site locations were chosen to maximise spatial representation of each territory (see Figure 5.1). As per our transect plot samples, we recorded habitat variables in a 2x2m sub-plot centred on each bait, and calculated habitat complexity indices for each following our previous methodology (see above). Bait-level complexity indices were then averaged for site-level complexity values. Baits were monitored at 5, 10, 20, 40 and also at 80 minutes (cf. our previous transect experiment, as it was found that some baits took longer than 40 minutes to be detected in the previous experiment).

We used Generalized Linear Mixed-effect Modelling (GLMM) to compare the proportion of baits won by the focal dominant species at (i) transect samples (excluding transect mid-point sample), and (ii) between species at within-territory baiting sites. For the model for transect samples, we included dominant ant species and mean plot-level habitat complexity as fixed-effect factors, and the transect and boundary of each sample as random-effect factors. For the within-territory baiting sites we included the identity of dominant species and site-level habitat complexity as fixed factors, and the discrete territory within which sites were located as a random factor in the model. We also compared the species richness of affiliate ants recorded at baits using GLMM, for both transect samples and within-territory baiting sites. We included dominant species identity, habitat complexity and proportion of baits won by the dominant species as fixed factors in both models. We included territory as a random factor in the within-territory comparison, and both transect and boundary as random factors in the transect sample comparison. All models were run based on a Poisson distribution using the lme4 package in R (Bates 2010).

We also compared the composition of affiliate ant assemblages at baits between dominant ants. We used Non-metric Multidimensional Scaling (nMDS) to represent patterns of assemblage similarity amongst sites. We used the number of baits that each species was recorded at (0 to 9) as a measure of abundance, and generated dissimilarity matrices using Bray-Curtis dissimilarity. The multivariate dispersion of sites based on dominant species was also compared using PERMDISP (Anderson 2006) in Primer v.6. We used multivariate GLM to assess the statistical significance of assemblage patterns. We included dominant ant identity, habitat complexity, territory and the number of baits dominated by the dominant species as factors in the model. We ran the model based on a negative binomial distribution in the MVABUND package (Wang et al. 2012). We then obtained uncorrected p-values for

univariate comparisons to identify species contributing to any observed assemblage-level differences between dominant species.

Monitoring of territory boundaries

We re-visited ant territory boundaries in March 2015, approximately 24 months following initial sampling. We revisited each transect and located the current location of the boundary relative to the identified boundary sampled in the 2013 survey. We extended the original 100m transect line in a straight line and recorded the location of the furthest detected individual in the direction of any detected boundary movement. Where necessary, we used tuna baits to verify species occurrences, however in most cases the presence of *I. chasei* was readily detected by visual inspection of the ground. Species occurrences, including the locations of nests, were recorded using handheld GPS.

5.3 Results

Dominant ant territories and boundaries

We identified seven discrete territories of our focal dominant ant species in the study area; four for *I. chasei* and three for *I. purpureus* (Figure 5.1). The fine-scale definition of boundaries between territories varied, with some areas showing only indistinct boundaries with gradual transition of species abundances. Many areas however showed very distinct boundaries on the scale of less than one metre, with interspecific conflict observable.

Conflict was most apparent near nests of *I. purpureus* where worker density of that species was greatest. Inter-specific fighting at boundaries resulting in death (see Figure 5.2) was observed on six occasions (at spatially independent locations) during January and February 2013. Inter-specific fights at boundaries often involved hundreds or even thousands of

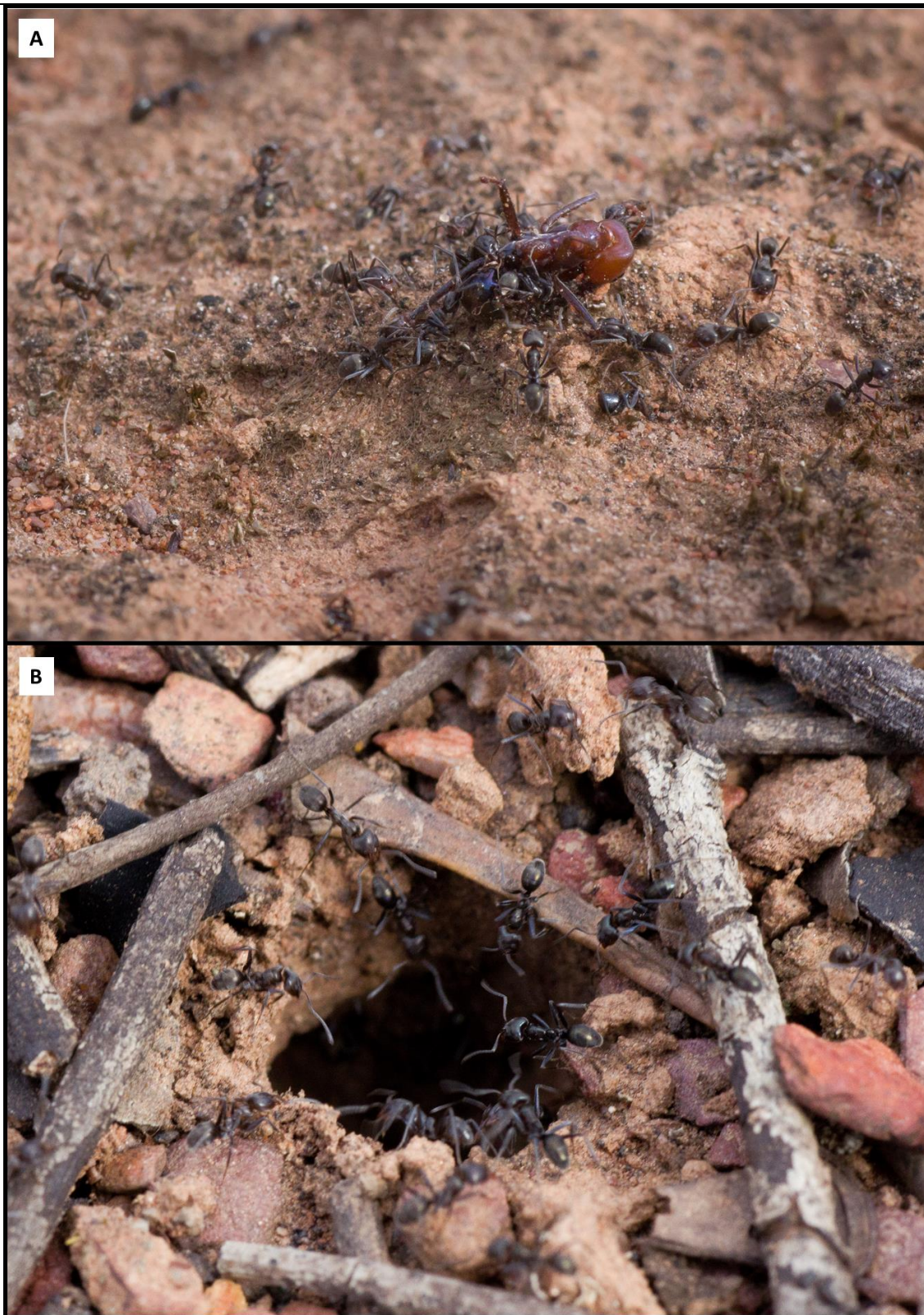


Figure 5.2. Inter-specific competition between *I. chasei* and *I. purpureus*: (A) lethal conflict at territory boundaries; and (B) a former *I. purpureus* nest occupied by *I. chasei*.

workers of each species (though typically far greater numbers of *I. chasei*), and in one case spanning up to 65m. Additionally, we recorded evidence of territory shifts in the form of disused *I. purpureus* nests (n=49) within the current territory of *I. chasei* during January and February 2013. Many of these nests appeared to be actively used by *I. chasei*. One nest located near a transect boundary sample was overtaken in a 12 day period between setting pitfall traps and opening them.

Transect samples

We recorded 43,460 individual ants in 121 species along transect samples, representing 38 genera in eight subfamilies. The most abundant species recorded was *Iridomyrmex chasei* (30,819 individuals), followed by *Rhytidoponera metallica* (1770 individuals) and *I. purpureus* (1659 individuals). Most recorded species were much less abundant, with 59 species (49%) being represented by ten or fewer individuals and 23 species being represented by a single individual. We recorded 11 species in the Dominant Dolichoderinae functional group, belonging to the genera *Iridomyrmex*, *Anonychomyrma*, *Froggattella* and *Papyrius*. Dominant ants recorded in transect plots conformed to expected catches of *I. purpureus* and *I. chasei* based on sample locations in most cases. However, on some transects individuals were recorded in the home territory of the opposing species. This was mainly due to workers of *I. chasei* being recorded within the territories of *I. purpureus*, due to the very high abundances of *I. chasei* (comprising over 70% of all individuals captured). In other cases, only *I. chasei* was recorded along a transect, meaning *I. purpureus* was functionally absent even if their occurrence was detected prior to establishing the transect. We therefore generated decision rules to determine which of the 17 transects to exclude from analyses. We determined that in order to include a transect, (a) both species must be present somewhere on the transect, (b) each dominant species must be present in their purported home territory

sample, and (c) each dominant ant must be most abundant in their home territory sample.

Three transects (T02, T16 and T17) were excluded from all further statistical analyses. Our reduced subset of transects (n=14) showed functional dominance (in terms of proportion of baits dominated) consistent with our experimental design (see Figure 5.3).

Habitat complexity was not significantly different between samples ($F_{2,38} = 0.812$, $p=0.455$) or transects ($F_{13,38} = 0.993$, $p=0.485$). Assemblage composition of affiliate ant species was not different between samples (see Figure 5.4), or the boundary transects were located along (Table 5.1). Assemblages however were affected by plot-level habitat complexity, and were more similar to other plots taken from the same transect (Table 5.1).

The abundances and species richness of Subordinate ant species were not different between plots based on sample, transect or habitat complexity (see Figure 5.5 and Table 5.2). The abundance of Subordinate species was significantly affected by the abundances of Dominant Dolichoderinae species, however there was no effect of dominant ant abundance on species richness of Subordinate ants (Table 5.2).

Competition for food resources

We recorded 42 affiliate ant species at baits on our territory boundaries along transect samples, and 48 species at baits in our within-territory comparison. We found significantly more baits were dominated by *I. chasei* than by *I. purpureus* at both within-territory samples and transect samples at territory boundaries, and this difference was not due to habitat complexity at samples (Table 5.3). The magnitude of differences was however greater within territories than at territory boundaries (Figure 5.6). The mean proportion of traps per site dominated by *I. purpureus* was around 63% lower than the proportion dominated by *I. chasei* at within-territory sites (Figure 5.6). This more uniform monopolisation of resources by *I. chasei* translated into much lower species richness of affiliate ant species at baits, with mean

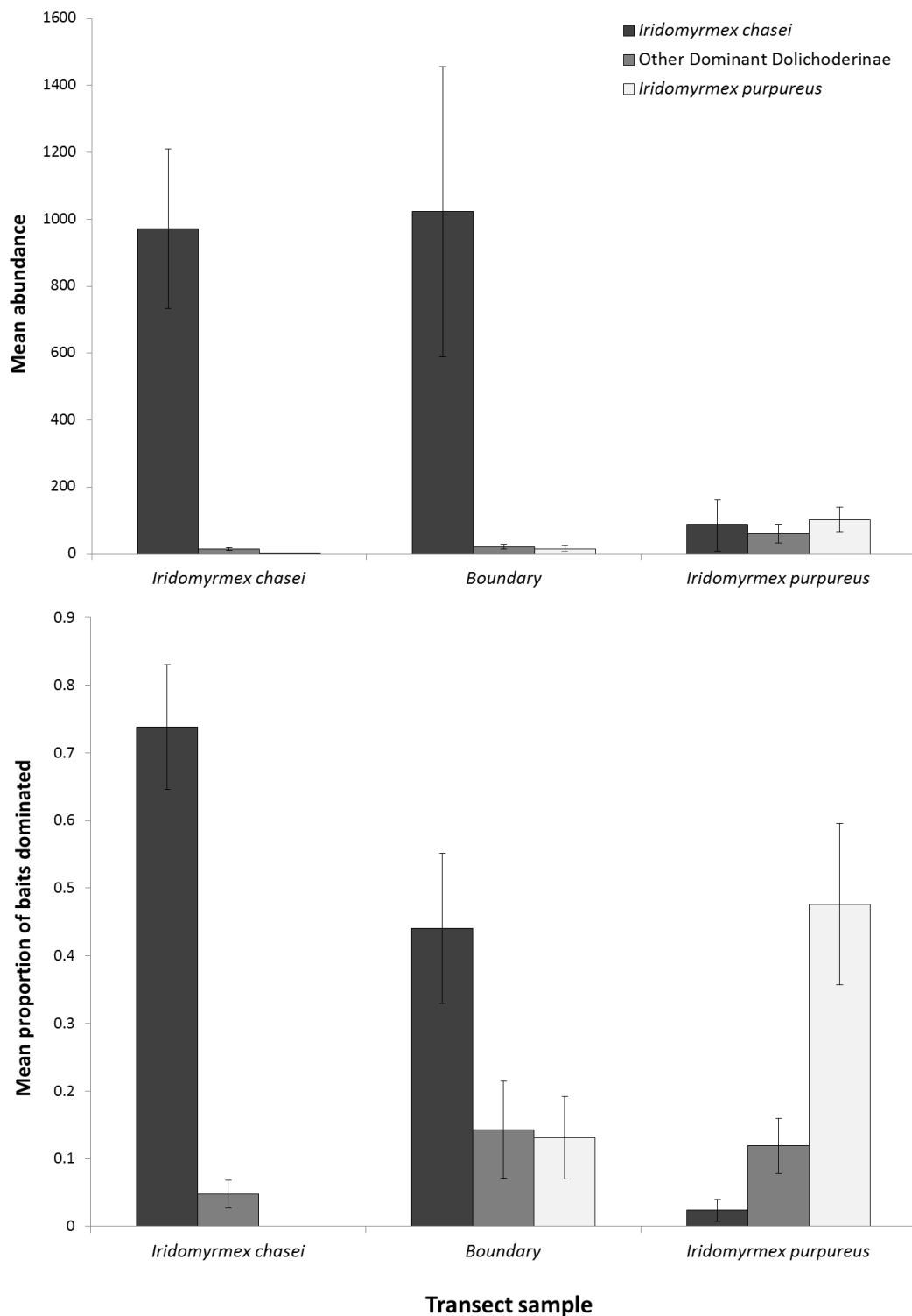


Figure 5.3. Mean plot-level abundances of dominant ants (top) and mean proportion of baits dominated ('won') per plot by dominant ants (bottom) along transect samples (within *I. chasei* territory, at the boundary, and within *I. purpureus* territories), based on our reduced subset of transects (n=14). Error bars denote standard error.

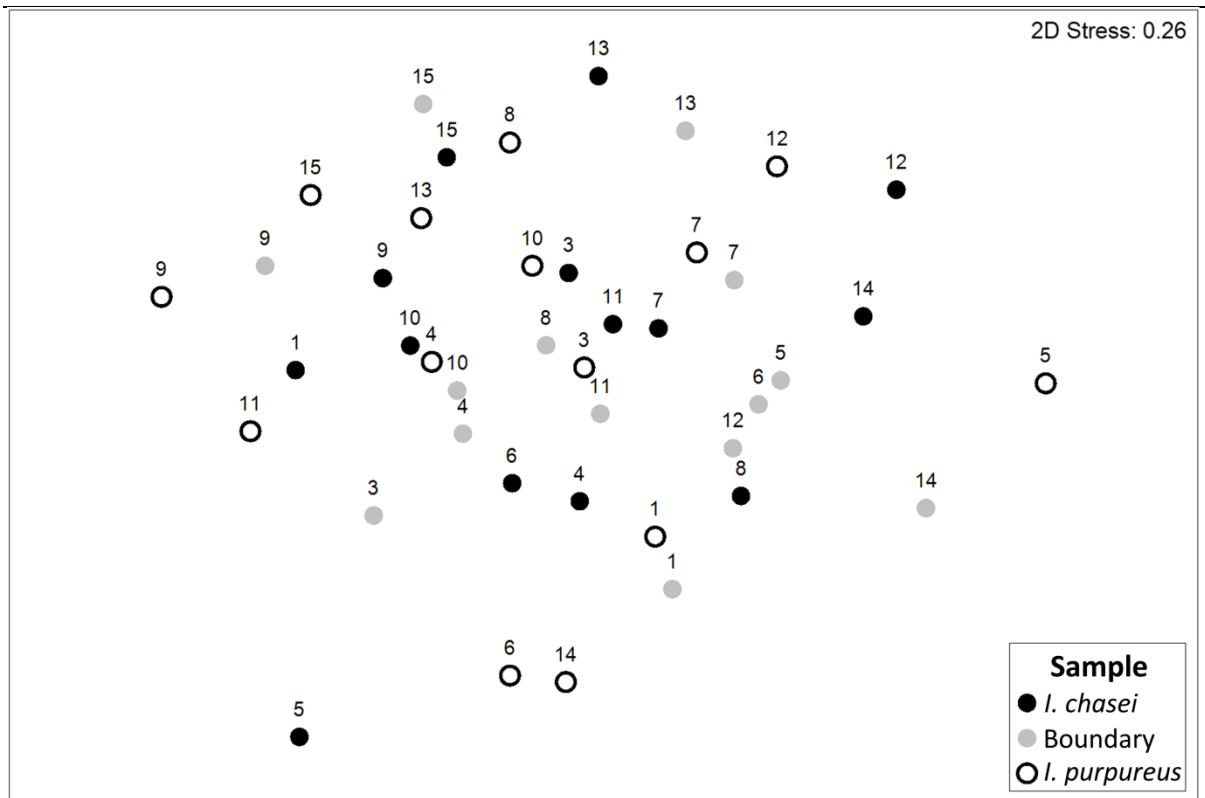


Figure 5.4. Non-metric multidimensional scaling (nMDS) ordination of affiliate ant assemblage composition across each of the three samples (within *I. chasei* territory, at the boundary, and within *I. purpureus* territories) along transect samples. Resemblance based on Bray-Curtis dissimilarity on fourth-root transformed abundance data. Labels represent transect number.

Table 5.1. Results of multivariate Generalized Linear Model (GLM) comparing assemblage composition of affiliate ant species across transect samples.

	Resid. d.f.	Diff. d.f.	Deviance	P-value
Intercept	41			
Sample	39	2	288.4	0.170
Transect	26	13	1976.7	<0.001
Boundary	23	3	0.0	0.472
Habitat complexity	25	1	314.1	<0.001

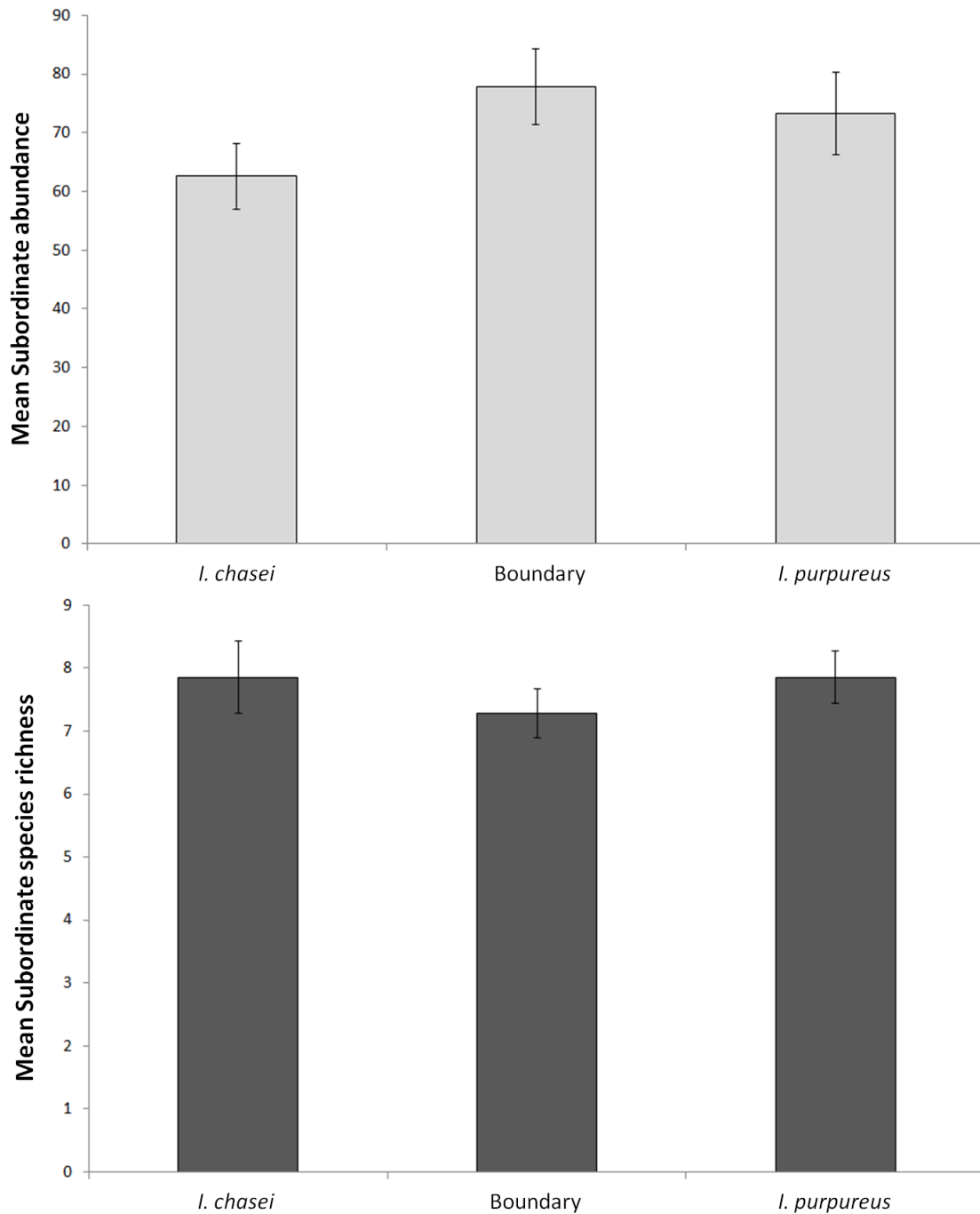


Figure 5.5. Abundances (top) and species richness (bottom) of Subordinate species (all species excluding the focal dominant species) along transect samples (within *I. chasei* territory, at the boundary, and within *I. purpureus* territories), based on data pooled for each plot (6 pitfall traps). Error bars denote standard error.

Table 5.2. Results of multiple analysis of covariance (MANCOVA) comparing abundance and species richness of subordinate ant species in pitfall traps across transect samples.

	Df	Abundances			Species richness		
		Mean square	F-value	P-value	Mean square	F-value	P-value
Dominant ant abundance	1	2568.110	6.795	<0.05	0.239	0.080	0.780
Sample	2	1026.810	2.717	0.086	1.592	0.530	0.595
Habitat complexity	1	94.600	0.250	0.621	4.543	1.512	0.231
Transect	13	804.510	2.129	0.053	3.329	1.108	0.398
Residuals	24	377.940			3.004		

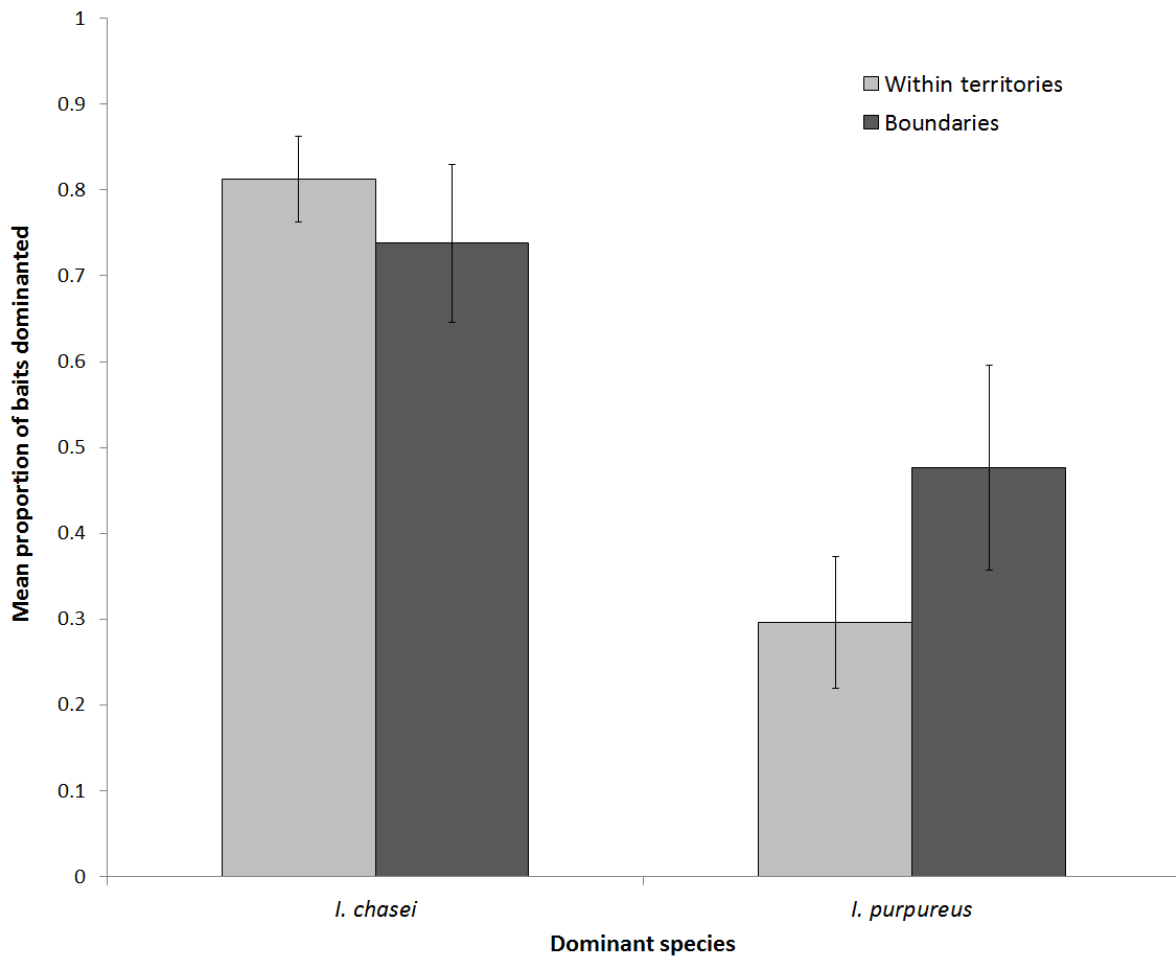


Figure 5.6. Proportion of baits dominated ('won') by the two dominant ant species, at baiting sites within the species' territories (n=9 baits) and baiting sites at territory boundary transects (n=6 baits). Error bars denote standard error.

Table 5.3. Results of Generalized Linear Mixed-effect Model comparing proportion of baits won by the focal dominant ant species, for transect samples at territory boundaries and within-territory baiting sites.

	Boundaries			Within-territories		
	Estimate +/- Std. Error	Z-value	P-value	Estimate +/- Std. Error	Z-value	P-value
Intercept	1.251 +/- 0.751	1.666	0.098	2.876 +/- 0.630	4.567	<0.001
Dominant species	-0.426 +/- 0.207	-2.061	<0.05	-0.938 +/- 0.421	-2.225	<0.05
Habitat complexity	-0.021 +/- 0.069	0.298	0.767	-0.094 +/- 0.060	-1.564	0.118

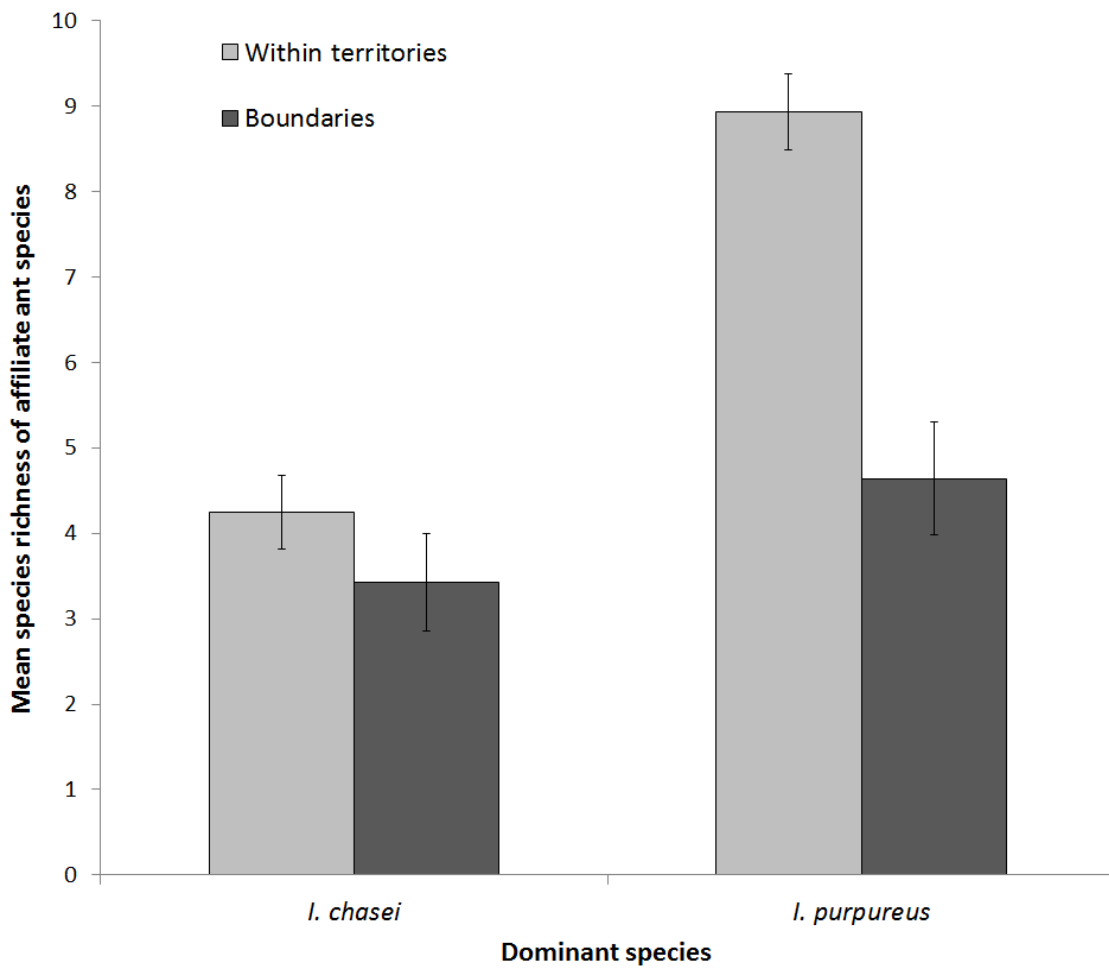


Figure 5.7. Mean site-level species richness of affiliate ant species (all species excluding the focal dominant ant species) at baits in dominant ant territories, for transect samples within-territory baiting sites (n=9 baits per site), and along territory boundary transects (n=6 baits). Error bars denote standard error.

species richness being 52.6% lower in *I. chasei* sites than *I. purpureus* sites within territories (Figure 5.7). This difference in species richness of affiliate ants however was not observed at territory boundaries, though species richness was negatively affected by the proportion of baits dominated (Table 5.4).

Composition of affiliate ant species at baits within territories was significantly different between dominant species (Figure 5.8 and Table 5.5). Assemblage composition was also significantly affected by habitat complexity, the particular territory baits were located in and the number of traps dominated by the focal dominant species at each site (Table 5.5). Eight species were significantly affected by dominant species in our univariate tests, including three *Iridomyrmex* species (*I. bruneus*, *I. c.f. bicknelli* and *I. sp. A (mjobergi group)*), along with *Rhytidoponera metallica* and *R. punctiventris*, *Camponotus* sp. H (*ephippium* group), *Notoncus* sp. C (*enormis* group) and *Pheidole* sp. C. Multivariate dispersion of affiliate ant assemblages at baits was not different between dominant ant species ($F_{1,29}=2.409$, $P_{\text{perm}}=0.176$).

Boundary shifts

Re-surveying of transects revealed widespread range increases by *I. chasei* over 24 months (see Figure 5.9). On average, boundaries had shifted 88.2 metres as measured from the *I. purpureus* sample (50m from the transect boundary midpoint). Distances varied from 0m to 221m, and no transects showed positive territory gain by *I. purpureus*. A number of our transects however appear to dissect the territory boundary at non-perpendicular angles, meaning distances measured may be an overestimation of average distances shifted (Figure 5.9). We also recorded a total of 29 former *I. purpureus* nests that were usurped by *I. chasei* in 2015, within their expanded range. While only four of these nests had previously been recorded as being active during the 2013 surveys, all were within the former territory of *I.*

Table 5.4. Results of Generalized Linear Mixed-effect Model comparing species richness of affiliate species occurring at baits, for transect samples at territory boundaries and within-territory baiting sites.

	Boundaries			Within-territories		
	Estimate +/- Std. Error	Z-value	P-value	Estimate +/- Std. Error	Z-value	P-value
Intercept	1.786 +/- 0.711	2.514	<0.05	1.970 +/- 0.434	4.537	<0.001
Dominant species	0.060 +/- 0.212	0.283	0.777	0.407 +/- 0.198	2.056	<0.05
Habitat complexity	-0.003 +/- 0.063	0.053	0.958	-0.002 +/- 0.040	-0.038	0.970
Number traps dominated	-0.144 +/- 0.040	-3.611	<0.001	-0.067 +/- 0.024	-2.847	<0.01

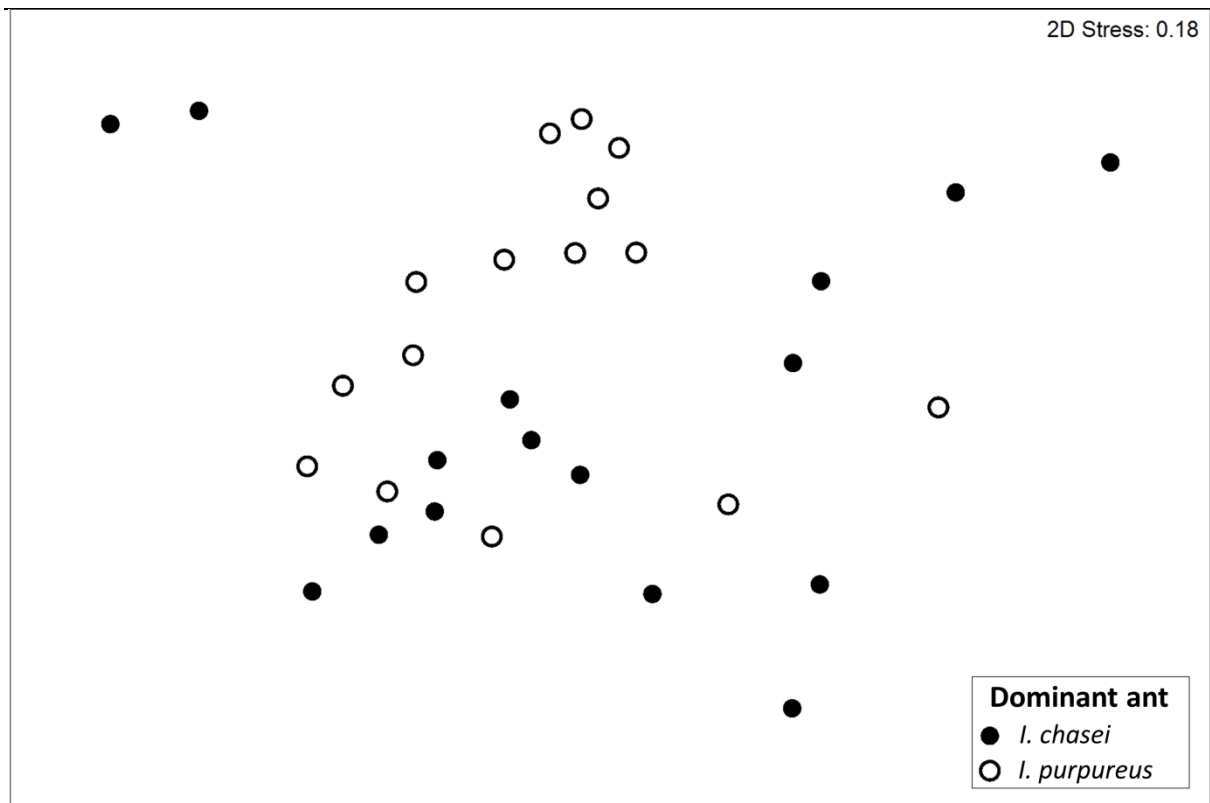


Figure 5.8. Non-metric multidimensional scaling (nMDS) ordination of affiliate ant species assemblages present at baits, between samples taken in *I. chasei* and *I. purpureus* territories. Resemblance based on Bray-Curtis dissimilarity of counts of bait-level occurrences (n=9 baits per site).

Table 5.5. Analysis of deviance table for multivariate Generalized Linear Model (GLM) comparing assemblages of affiliate species occurring at baits between territories of *I. chasei* and *I. purpureus*.

	Resid. d.f.	Diff. d.f.	Deviance	P-value
Intercept	30			
Dominant species	29	1	110.27	<0.001
Habitat complexity	28	1	78.86	<0.01
Territory	22	6	216.76	<0.01
# traps dominated	22	1	94.71	<0.001

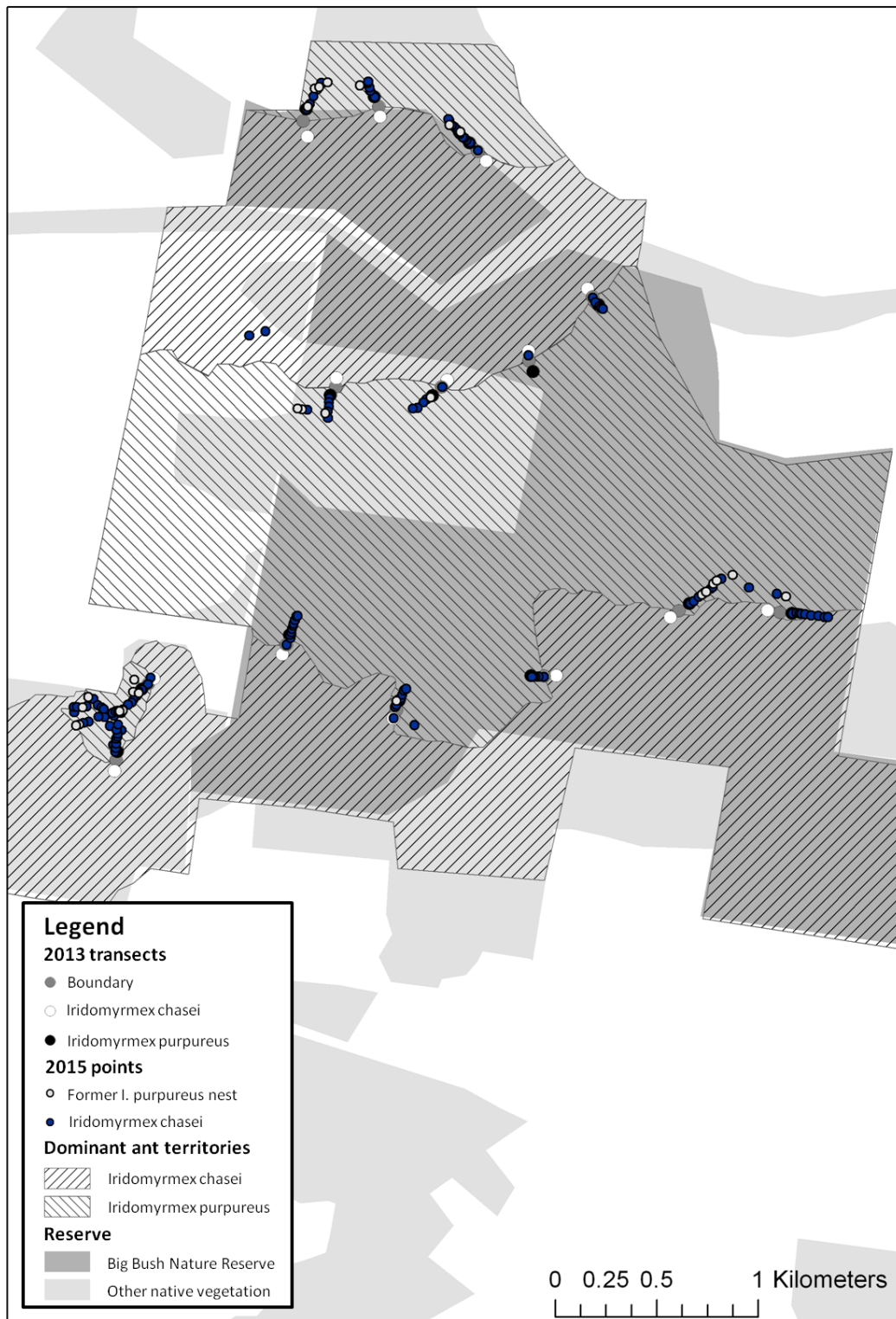


Figure 5.9. Results of re-survey of transects 24 months after initial sampling to assess movement of territory boundaries. Blue circles represent the locations of *I. chasei* in 2015, while open circles represent the locations of *I. purpureus* in 2015.

purpureus and appeared to have been recently maintained. One additional nest was occupied by both species simultaneously.

5.4 Discussion

Our results demonstrate the existence of mutually-exclusive territories of two highly aggressive ant species, maintained by strong active territory defence along boundaries. The boundaries of these territories appear to be highly fluid, contrary to our prior expectations. The primary mechanism for territory boundary shifts appears to be through intense inter-specific competition along boundaries, often involving large-scale lethal conflict involving hundreds or even thousands of workers. The two species however occupy several discrete territories, suggesting a role of dispersal via undirected nuptial flights of mated queens into unoccupied niche space in shaping species distributions.

Both dominant species inhibited affiliate species at baits, however *I. chasei* exerted a much greater competitive dominance of food resources than the notoriously despotic *I. purpureus* (Greenslade 1976b, Andersen and Patel 1994). Despite this, we found no evidence of non-random patterns of affiliate ant assemblage composition between dominant ant species based on samples taken at territory boundaries. However, as territory boundaries were observed to shift rapidly during the study, we conclude that transect samples taken at territory boundaries are likely to represent assemblages only recently exposed to the presence of *I. chasei*. Our finding that species richness of affiliate ants attending baits was not different between dominant species at territory boundaries, but was dramatically lower at *I. chasei* sites within territories suggests that assemblage changes occur gradually over time, and assemblages at boundaries have not yet undergone these changes. The role of dominant ant identity in structuring assemblages of affiliate ants is supported by the observed compositional differences between affiliate ants at within-territory baits. Our baiting experiments however

are likely to reveal only the subset of the community active at moderate temperatures in the temporal periods associated with dominant ants, potentially making detection of the species interactions driving community shifts more likely than through pitfall counts. Additionally, species may be less likely to be detected even when present on baits if resources are rapidly located by dominant species. This is due to our monitoring procedures at discrete time points rather than constant observation.

Short-term exclusion of dominant ants can result in dramatic increases in species richness and abundances of other ant species at baits (Andersen and Patel 1994). Removal or inhibition of one species may also enable increases in foraging activity or even colonisation by another dominant species (Fox et al. 1985, Gibb and Hochuli 2004). However, exclusion may result in only limited effects on abundances and assemblage composition of foraging ants caught in pitfall traps (Andersen and Patel 1994, Gibb and Hochuli 2004, Gibb and Johansson 2011), highlighting the potential disconnect between forager abundances and activity at baits. We previously found both significant negative and positive associations of dominant species abundances in the study area, occurring at both intermediate and fine scales (Chapter 4). Besides the competitive exclusion between our two focal dominant species studied here, relationships were observed amongst the same three *Iridomyrmex* species found to be affected by dominant species identity in this study (*I. bruneus*, *I. c.f. bicknelli* and *I. sp. A (mjobergi group)*). This congruence with our previous findings lends support to the validity of our results from baiting experiments, and further supports our hypothesis that inter-specific competition between dominant species can structure ant communities across space.

While we have no evidence of spatial partitioning based on habitat heterogeneity, the rapid territory gains made by *I. chasei* may be as a result of changes in underlying habitat structure throughout the study area. This study was conducted following a significant La Niña event,

bringing above-average rainfall over much of Eastern Australia. This same event triggered a significant increase in rates of litter fall elsewhere in the state (Travers and Eldridge 2013), and likely caused substantial increases in fine-scale habitat complexity over the study area. Habitat complexity negatively affects the abundances of dominant ants at fine scales (Chapter 4), likely due to the impacts of fine-scale microhabitat on the abilities of dominant ants to locate and successfully monopolize resources (Gibb 2005, Gibb and Parr 2010). Larger ant species may travel more rapidly *over* rugose microhabitats than smaller species (Kaspari and Weiser 1999, Kaspari and Weiser 2007), so we may therefore predict increases in habitat complexity to confer a competitive advantage to the much larger *I. purpureus* in this context. Meat ants however are sensitive to changes in habitat complexity, often being positively affected by disturbance to habitat resulting in structurally less-complex habitats, including through fire (Vanderwoude et al. 1997), land clearing (Greaves 1971) and road construction (Gibb and Hochuli 2003). Alternatively, smaller ants may be better able to forage *within* complex microhabitats, potentially conferring a competitive advantage of small size in foraging success (Gibb and Parr 2010). The greater spatial uniformity of dominance throughout the range of *I. chasei* suggests lower sensitivity to habitat heterogeneity in this species, at least in terms of its foraging success.

Both species are widely distributed over Southern Australia (Heterick and Shattuck 2011), and as such this observed interaction is unlikely to be restricted to this locality, despite not being previously reported in the literature. Polydomy has not previously been recorded in *I. chasei* to our knowledge, at least on the scale of that recorded within the study area.

Although polydomy was observed to be widespread in *I. chasei*, the genetic relationships amongst nests of this species within the study area are unknown. We observed no evidence of intra-specific competition, and strong integration of nests via trail networks, suggesting an absence of polygyny (van Wilgenburg et al. 2006b). We found inter-colony aggression by *I.*

purpureus at two locations, including extensive ritualised fighting at territory boundaries (Ettershank and Ettershank 1982), indicating several distinct colonies occur within the study area (van Wilgenburg et al. 2006a).

The benefits of polydomy in *I. purpureus* may be in enabling greater exploitation of highly temporally consistent food resources such as honeydew (van Wilgenburg and Elgar 2007). However, polydomy may also enable greater exploitation of space through dispersing foraging activity over a greater area (Cerdá et al. 2002), hence enabling greater uniformity of competitive influence across space (Savolainen and Vepsäläinen 1989) and faster discovery of resources (Schmolke 2009, Cook et al. 2013). Polydomy may also enable better resistance to attacks from predators or competitors (Cerdá and Retana 1998). The highly invasive Argentine ant (*Linepithema humile*) has a similar polydomous colony structure to that of *I. chasei* in the study area (Heller 2004). This colony structure has been cited as a key trait enabling invasion success (Holway and Case 2000), along with numerical dominance, however polygyny is also likely to contribute to the species' success (Holway 1999). Particularly, polydomy may enable species to be proficient at both discovery and exploitation of resources, in contrast with native species in which performance at each are negatively correlated (Holway 1999).

The dramatic contrasts in both body size and abundances between our two dominant species highlight the two alternative strategies employed to achieve ecological dominance; behavioural dominance in *I. purpureus*, and numerical dominance in *I. chasei* (Davidson 1998). Although numerical and behavioural dominance are often positively correlated (Savolainen and Vepsäläinen 1988), these two species appear to occupy two extremes along a continuum of a body size versus abundance trade-off. This trade-off is evident in the total biomass of the two species caught in pitfalls within this study, with 19.20g for *I. purpureus*

and 14.24g for *I. chasei*. The combined total biomass of trapped individuals of each species over this study and our previous study (Chapters 3 and 4) was very close, with 39.38g for *I. purpureus* and 39.72g for *I. chasei*.

Although both of our focal dominant species were highly successful at achieving ecological dominance within their own respective territories, we here present evidence of *I. chasei* achieving greater ecological dominance than the meat ant *I. purpureus*. The combination of small body size, numerical dominance, highly aggressive behaviour and polydomic colony structure seen in *I. chasei* mimic the traits thought to enable ecological dominance by the Argentine ant (Holway 1999), and here appears to be enabling a rapid expansion of territory similar to that seen in invasions by the Argentine ant and other invasive ant species (Hoffmann et al. 1999, Hoffmann and Saul 2010). As *I. chasei* occurs as a highly morphologically variable species distributed over much of Australia, including within heavily urbanised areas (Heterick and Shattuck 2011), it provides an ideal species for further comparative study of behavioural traits and competitive dominance.

Conclusions

Our results provide some limited evidence for the role of assemblage-level filtering of species based on specific dominant ant species, with unique assemblages of species occurring at baits between territories of the two dominant species. Although no differences were detected in our assemblages at territory boundaries, our transect samples were in close proximity with rapidly shifting territory boundaries and assemblages are likely to have had insufficient time to respond to changes in the competitive dominances associated with different ant species. Our results do however demonstrate that meat ants are not necessarily the most dominant members of Australian ant communities where they occur, and that numerical dominance and polydomous colony structure may be implicated in the success of *I. chasei* in this context.

The observed rapidly shifting territory boundaries driven by strong inter-specific competitive interactions also demonstrate that competitive influences of dominant ants can be temporally variable.

Chapter 6

General discussion

Summary of findings

Plant community composition, structure of vegetation, inter-specific competitive interactions and spatial relationships all play a significant role in shaping ant assemblage patterns across the landscape. The relative strengths of each, and interactions between these drivers of assemblage composition is directly related to the effectiveness of community-based conservation strategies, and also provides important insights into the role of niche versus stochastic processes in shaping ant communities. Although plant community classifications can represent structurally distinct habitats (Chapter 2), the composition of ant assemblages is only weakly associated with these plant communities, and only when they are spatially distinct and represent broadly different structural habitats (Chapter 2). The observed patterns of association between plant community composition and ant assemblage patterns can be partially explained by structural attributes of vegetation (Chapters 2 and 3), and ant assemblages also responded to structural variation within plant communities (Chapter 3). Ant assemblage composition patterns were strongly associated with spatial relationships amongst sites within structurally homogenous plant communities (Chapter 2) and across the landscape when habitat is structurally homogenous (Chapter 3). Plant communities are at best only weakly associated with underlying assemblages of ants (Chapter 2) or at worst not associated with ant assemblage composition at all once spatial and structural assemblage drivers are taken into account (Chapter 3).

Competitively dominant ant species abundances had a strong negative relationship with microhabitat complexity at fine scales (Chapter 4). In turn, the abundances of competitively subordinate ants were negatively associated with abundances of dominant ants (Chapter 4). The effects of dominant ants on the abundances of subordinate ant species were consistent across three spatial scales, ranging from within single pitfall traps to collections of plots spaced over hundreds of metres (Chapter 4). This effect on abundances did not however

translate to differences in species richness of subordinate ants, with no effect observed at plot level and even a (non-significant) positive association with dominant ant abundances at broad scales (Chapter 4). These results demonstrate a strong influence of fine-scale microhabitat in moderating the influences of dominant ants at fine scales, enabling competitive coexistence of competitively subordinate species across broader levels of organisation, consistent with the interstitial hypothesis for explaining high levels of local species richness in the presence of strong competitive dominance (Andersen 2008). The abundances of competitively subordinate ants were not negatively affected by dominant ants, and had no effect on subordinate ants (Chapter 4), indicating that three-tiered competition cascades (Arnan et al. 2011) are not a consistent phenomenon in Australian ant communities.

Dominant ants showed patterns of non-random pairwise association across space, and that this association could be both positive at intermediate scales and negative at fine scales (Chapter 4). In addition, two species of dominant ants (*Iridomyrmex purpureus* and *I. chasei*) showed almost total checkerboard distributions across space at both fine and intermediate scales (Chapter 4). This pattern was due to total competitive exclusion across the landscape, with each species controlling discrete territories maintained by active territorial defence (Chapter 5). This active territorial defence was asymmetrical, with *I. chasei* consistently usurping the territory and nests of *I. purpureus* across multiple territory boundaries (Chapter 5). More baits were monopolized by *I. chasei* than *I. purpureus* within their respective territories, and fewer affiliate ant species were recorded at baits at sites within the territories of *I. chasei* (Chapter 5). Similarly, the composition of affiliate ants recorded at baits was also different between dominant ant territories (Chapter 5), indicating that dominant ant species may have a filtering effect on ant assemblages similar to ant mosaics observed in tropical arboreal systems (Majer 1972, Leston 1978). Although the composition of affiliate ants recorded in pitfall traps was not different between samples taken near territory boundaries

(Chapter 5), the observed rapid shifts in territory boundaries (Chapter 5) indicate that assemblages sampled may have not had sufficient time to respond to changes in dominant ant identity.

Plant species composition and structural attributes of vegetation are inherently interrelated, though plant communities supporting very different plant species assemblages can provide similar structural habitats, and structural variation within plant community classifications can also be substantial (Chapter 3). Similarly, plant community composition across the landscape can be strongly spatially structured, with plant communities often restricted in extent (Chapters 2 and 3). This represents the first attempt to partition the influences of all three assemblage drivers for ants, and demonstrate independent contributions of plant community composition (Chapter 2), structural attributes of vegetation (Chapters 2 and 3) and geographical distances between sites (Chapters 2 and 3) on the composition of ant assemblages across the landscape. Inter-specific competition between competitively dominant and competitively subordinate species had a role in shaping fine-scale assemblage patterns, and an influence of fine-scale habitat structure in mediating this interaction (Chapter 4). Interspecific competition between dominant and subordinate species can also be strongly spatially structured, as dominant species, divergent in both traits and strength of competitive dominance they exert on ant communities, can occupy discrete territories across the landscape (Chapter 5).

6.1 Drivers of ant assemblage composition

Strength of spatial versus environmental drivers

It is clear that multiple processes are interacting to drive ant community composition, however the relative strengths of each driver, and the conditions under which they act, are important in answering ecological questions such as mine. Community assemblage patterns

are now recognised to be a result of both stochastic and environmental drivers (Condit et al. 2002, Tuomisto et al. 2003, Gravel et al. 2006, Steinitz et al. 2006, Thompson and Townsend 2006, Smith and Lundholm 2010). The relative strengths of spatial and environmental drivers (incorporating both plant community composition and structural composition of vegetation) were highly context-dependent. When comparing across broadly divergent plant communities over a maximum spatial extent of around 63km, plant community composition was the strongest driver of ant assemblage composition, however prediction based all three components combined was weak (Chapter 2). Examination of spatial turnover patterns within plant communities however revealed highly variable patterns (Chapter 2). One community (Cumberland Plain Woodland) showed very strong spatial assemblage patterns, while others showed either weak or absent patterns. Examination of stochastic versus environmental drivers of ant assemblage at finer spatial scales revealed an overall weak contribution of environmental drivers and strong spatial turnover patterns in assemblages (Chapter 3).

Spatial turnover and dispersal limitation

Pure spatial turnover patterns (independent of associations with underlying environmental drivers) are attributed to stochastic assembly processes, primarily dispersal limitation (Hubbell 2001). Dispersal abilities of taxa are inherently related to species traits (Thompson and Townsend 2006). Highly mobile species capable of dispersal by flight are expected to show lower dispersal limitation than species lacking flight, which presumably explains the observed dramatically higher turnover rates in ground-dwelling invertebrates than birds (Ferrier et al. 1999).

Sexual reproduction and colony establishment in ants involves dispersal of winged queens and reproductive males potentially capable of long-distance dispersal in most species

(Hölldobler and Wilson 1990). Lower rates of spatial turnover would be predicted in ants than in taxonomic groups lacking this mobile dispersal stage, however aspects of the morphology of queens suggest a trade-off between dispersal abilities and colony founding. For example, claustral species (in which the queen will enclose herself in the founded nest and raise new workers from her own resource provisions) have higher resource masses per body size, and lower flight muscle ratio (FMR) than non-claustral species, indicating poor flying ability and hence shorter dispersal distances (Helms and Kaspari 2015). Empirical studies of ant dispersal distances under natural conditions are logistically near-impossible, and dispersal abilities are instead estimated indirectly based on physiological capacities (Vogt et al. 2000) and distributions of colonies across the landscape (Johnson 2001), and are likely confounded by density of suitable mates (Noordijk et al. 2008). Assumptions of long distance dispersal capabilities in ants may therefore be unjustified.

Inter-specific competition as an assemblage driver

Despite strong negative influences of dominant ant abundances on abundances of subordinate ant species, species richness of subordinate species was not affected at intermediate or broad scales (Chapter 4). Assemblage composition of ants however was influenced by patterns of association amongst dominant ant species across the landscape (Chapters 4 and 5). These findings suggest a role of competitive interactions in driving patterns of spatial turnover (Chapter 3).

Competitive exclusions amongst dominant ants are likely to be related to the observed patterns of spatial turnover and pairwise saturation (the percentage of plot pairs sharing no species from that group) amongst the Dominant Dolichoderinae functional group (Andersen 1995) in my *Temora* dataset (Chapter 3). I found high levels of saturation (46.64%) despite that group having the highest overall abundances of all groups. By comparison, the next

three most abundant functional groups, the Opportunists, Generalized Myrmecines and Hot Climate Specialists had saturation levels of 0%, 1.05% and 0.28%, respectively. Competitive exclusions between *Iridomyrmex chasei* and *I. purpureus* (Chapters 4 and 5) are likely the primary drivers of this pattern. *I. chasei* was restricted to sites 1, 2 and a single plot in site 3, and contributed the greatest amount of all species to observed site-level assemblage patterns (Chapter 3). My data also indicate a role of dominant ant species identity in filtering assemblages of affiliate ants (Chapter 5). While further studies tracking the long-term responses of assemblages to changes in dominant ant identity and abundances is required to verify these associations due to the rapidly shifting territory boundaries observed, these results present the additional mechanisms of competitive exclusion and assemblage filtering for explaining spatial turnover in ant assemblage composition.

6.2 Stochastic assemblage processes and community assembly

Neutral theory and ant community assembly

Niche and neutral community theories present competing explanations for the composition of local species assemblages. Under niche theory predictions, local assemblages are strictly the result of both species' adaptations to the abiotic environment and adaptations for coexistence with other species (Chase and Leibold 2003, Soberón 2007), and that coexisting species cannot occupy the same niche (Chesson 2000). Neutral theory however treats species occupying the same trophic levels as functionally and competitively equivalent, with local assemblages instead determined through predominantly stochastic processes such as dispersal limitation resulting in strong spatial structures (Hubbell 2001). Practical application of this theory however is limited to landscapes displaying homogeneity in underlying abiotic conditions over great distances such as lowland tropical rainforests (Hubbell 2001, Condit et al. 2002, Volkov et al. 2005).

Local species richness in Australian ant communities is very high, particularly in arid regions (Andersen 2007). This local richness appears to exceed that which can be explained through traditional niche partitioning facilitating species coexistence (Andersen 2008). For example, up to 15 species of *Monomorium* occupying roughly equivalent niche space can be found within a 10x10m plot in northern Australia's wet/dry tropics (Andersen et al. 2012).

Numerous interacting mechanisms have been proposed to account for this high species richness, particularly under conditions of strong competitive dominance from behaviourally aggressive dominant species (Andersen 2008). Chief amongst these is high longevity and persistence of colonies even under strong competition (Gordon and Kulig 1996), enabled through modularity of colonies. Strong persistence may enable equivalence amongst co-occurring species (Andersen 2008). Under these conditions local species richness would be restricted by the size of regional species pools (Ricklefs 1987), the availability of mated queens and suitable colony establishment sites.

My results provide further support for neutral dynamics in ant communities through strong pure spatial turnover of assemblage patterns within structurally homogenous communities (Chapter 2), and across the landscape when structural composition of vegetation is largely homogenous (Chapter 3). These findings, in combination with observed weak contribution of environmental drivers (plant community composition and structural attributes combined), indicate that stochastic assembly processes are the primary driver of ant assemblages in this context. However, the role of inter-specific competition resulting in mutually exclusive territories of dominant ant species across the landscape should not be discounted as a potentially contributing to observed turnover patterns.

6.3 Plant community surrogacy and conservation

Community-level patterns

The basis for utilizing plant community surrogates to represent total biodiversity across the landscape involves an assumption of strong cross-taxon congruence between all taxonomic groups. This assumption evokes the near century-old debate contrasting the Individualistic theory of plant communities as a tightly-integrated association of species analogous to individual organisms (Clements 1916, Clements 1936), compared to the Continuum theory of communities as collections of species each distributed based on their own unique responses to their environment (Gleason 1926, Goodall 1963). While both theories present simplistic and outdated concepts of plant associations each falsified by subsequent developments in the field of community assembly (Biondi et al. 2004), the logical basis for plant community surrogacy appears to be an extension of the Individualistic theory to cover all taxonomic components of ecological communities.

There was only a weak association between plant community associations, driven predominantly by associations with structural attributes and shared spatial turnover patterns (Chapters 2 and 3). Specifically, threatened plant communities within the Sydney region were characteristically poor predictors of plant ant assemblages, with co-occurring plant communities supporting largely homogenous ant assemblages (Chapter 2). Plant community composition also had no direct influence on ant assemblage composition after spatial and structural assemblage drivers were accounted for (Chapter 3). These results support previous findings that plant community surrogacy, along with a range of other surrogacy methods are poor predictors of invertebrate assemblage patterns (Ferrier 1997, Mac Nally et al. 2002, Rodrigues and Brooks 2007, Santi et al. 2010). Broader-scale habitat based surrogates such as land systems however do provide reasonable representation of invertebrates (Oliver et al.

2004). Indeed our results do support the use of broadly divergent plant community forms as a basis for representing ants, for example the tall wet-sclerophyll forest community Blue Gum High Forest supported distinct assemblages from dry-sclerophyll plant communities occurring on the significantly drier Cumberland Plain (Chapter 2).

Spatial turnover and effectiveness of plant community surrogates

The degree to which plant communities represent assemblages of underlying taxonomic groups depends largely upon the specific drivers of β -diversity across the landscape of each group. Groups showing associations with the same set of environmental and bioclimatic drivers as plant communities, or associated directly with plant community composition through direct effects on habitat structure should be well represented by plant community surrogacy. In contrast, taxonomic groups showing weak environmental assemblage patterns and strong pure spatial turnover are unlikely to be represented under plant community surrogacy strategies. My results demonstrate a weak representation of ant assemblages based on a practical application of plant community surrogacy.

Plant communities (and underlying patterns of plant species composition) however can be spatially clustered across the landscape due to associations with similarly clustered abiotic and climatic factors (Ferrier et al. 2002, Ferrier and Guisan 2006). Consequently, even in the absence of strong direct causal association plant community surrogacy could provide adequate representation of underlying assemblages of ants or other invertebrate species through shared spatial turnover patterns across the landscape. Indeed, congruence between plant community composition and assemblages of a variety of invertebrate taxa can be strong relative to structural attributes of vegetation when spatial patterns of association are not accounted for (Schaffers et al. 2008). However when spatial patterns are taken into account the strength of invertebrate association with plant-based surrogates is low (Oliver et al. 1998).

Variation between taxonomic groups in surrogate efficacy

The comparative strengths of strength of spatial and environmental assemblage drivers, and also the specific environmental variables driving patterns of β -diversity vary amongst taxonomic groups (Chase and Myers 2011). Empirical support for the use of plant community surrogates comes predominantly from associations with vertebrate taxa (Ferrier 1997, Oliver et al. 1998). Vertebrate taxa however show lower spatial turnover than invertebrate taxa when directly compared within studies (Oliver et al. 1998, Ferrier et al. 1999, Mac Nally et al. 2004). Additionally, invertebrate groups also vary in spatial turnover patterns across the landscape, with ant assemblages showing comparatively lower turnover rates than flies (Oliver et al. 2004) and ground dwelling spiders and beetles (Ferrier et al. 1999). This suggests that the demonstrated poor representation of ant assemblages by plant community surrogacy is likely to be common amongst invertebrate taxa, particularly those with poor dispersal abilities.

Implications for plant community surrogacy and biodiversity offsetting strategies

While regional species pools may be adequately represented across the landscape when large areas of native vegetation are conserved, my results emphasise the importance of conserving vegetation across the entire landscape, particularly in highly fragmented landscapes. While my results show that broad plant community forms are useful predictors of assemblage composition of underlying species assemblages, the degree of spatial isolation is likely to be a better predictor of local conservation significance of remnant vegetation. Specifically, this means that spatially isolated remnants are more likely to support unique and poorly represented components of regional biodiversity than remnants clustered with other remnant vegetation.

Consideration of ecological integrity of remnant vegetation is central to applied conservation ecology. Small isolated fragments are considered to have relative lower value than larger, connected remnants due to lower long-term viability as a result of disproportionate edge effects, weed invasion and other detrimental processes (Fischer and Lindenmayer 2007). My results however demonstrate that despite the associated negative effects of fragmentation, isolated native vegetation is important in local conservation. Based on my findings, optimal representation of ant communities in regional conservation strategies would be achieved through maximising representation of not just floristic diversity across the landscape, but also both the structural forms of vegetation and maximising the geographical spread of conserved vegetation across the landscape. Further, the incorporation of other biotic components and processes into community definitions (Ferrier et al. 2004, Ferrier and Guisan 2006) could enhance representation of species in conservation strategies. Recently, the IUCN Redlist criteria were expanded to incorporate listing of ecosystems under existing hierarchies of threat to extinction (Keith et al. 2013). While this action is likely to advance the recognition of ecological communities as important components of biodiversity, implementation of this should aim to represent all taxonomic components of communities.

The specific aim of biodiversity offsetting strategies is to ensure that no biodiversity is lost through impacts of development (DEC 2006). For this reason, it is critical that the composition of species supported in compensatory habitat is as close as possible to that lost through development actions. The similarity of assemblage composition between sites is negatively related to the geographical distance between them. Therefore, best practice for selection of suitable offset sites should incorporate strict criteria for spatial fidelity, along with existing criteria for floristic composition and/or broad community types.

Although there is merit to conservation using plant community surrogate approaches, the consideration of spatial assemblage patterns in these strategies is of critical importance.

Incorporating biotic drivers such as competition may also complement these coarse-scale approaches. Competitive pressures from dominant ant species can play an important role in influencing assemblage patterns, and these competitive pressures can vary dramatically over spatial and temporal scales due to dominant ant identity and shifts in territory boundaries. For example, spatial patterns of dominant ant distributions due to mutually-exclusive territories may in fact be contributing to spatial turnover, meaning both stochastic and competition-based assemblage drivers are contributing to observed turnover patterns. Although these drivers complement habitat-based processes, building the stochastic processes and competitive interactions into habitat-based models of surrogacy will enhance the predictive value of the models assessing landscapes for conservation.

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