

Effect of fragmentation, habitat loss and within-patch habitat characteristics on ant assemblages in semi-arid woodlands of eastern Australia

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Abstract The reliability of ants as bioindicators of ecosystem condition is dependent on the consistency of their response to localised habitat characteristics, which may be modified by larger-scale effects of habitat fragmentation and loss. We assessed the relative contribution of habitat fragmentation, habitat loss and within-patch habitat characteristics in determining ant assemblages in semi-arid woodland in Queensland, Australia. Species and functional group abundance were recorded using pitfall traps across 20 woodland

patches in landscapes that exhibited a range of fragmentation states. Of fragmentation measures, changes in patch area and patch edge contrast exerted the greatest influence on species assemblages, after accounting for differences in habitat loss. However, 35% of fragmentation effects on species were confounded by the effects of habitat characteristics and habitat loss. Within-patch habitat characteristics explained more than twice the amount of species variation attributable to fragmentation and four times the variation explained by habitat loss. The study indicates that within-patch habitat characteristics are the predominant drivers of ant composition. We suggest that caution should be exercised in interpreting the independent effects of habitat fragmentation and loss on ant assemblages without jointly considering localised habitat attributes and associated joint effects.

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Introduction

Habitat fragmentation and loss are critical processes influencing species distribution across a landscape. The commonly recognised consequences of increased fragmentation on landscape structure are increased isolation among similar patch types and reduction in patch size

(MacArthur and Wilson 1967; Andrén 1994). Classically, patch area reduction and increased isolation should have detrimental effects on species abundance and richness since patches are less likely to be colonised after a local extinction (Brown and Kodric-Brown 1977; Hanski 1999), and should hold smaller populations that are more vulnerable to environmental and demographic stochasticity (Fahrig 1997; Foley 1997). These deleterious effects may be exacerbated by an associated increase in edge environments that influences species movement patterns across patch boundaries (Bhar and Fahrig 1998).

While patch area and isolation are the most commonly tested measures of fragmentation (Laurance and Bierregaard 1997; Fahrig 2003), they are unable to consistently predict species richness patterns in manipulative fragmentation studies (Debinski and Holt 2000). The conceptual shift from island biogeography theory (MacArthur and Wilson 1967) to models that consider the landscape matrix to be heterogeneous and not necessarily hostile to native species (e.g. habitat variegation concept, McIntyre and Barrett 1992), has led to alternative landscape features such as landscape heterogeneity and contrast between adjacent land types being increasingly incorporated into fragmentation studies (McGarigal and Marks 1995; Wiens 1997; Fahrig 2003). Such features are important drivers of population dynamics in some species (Niemelä 2001; Jules and Shahani 2003), which may override the effects of area and isolation. Inconsistent effects of area and isolation among fragmentation studies also result from confounding effects of habitat loss (Andrén 1994; Fahrig 2003); once the effects of fragmentation and loss are separated, habitat loss may exert a stronger and, in some cases, opposite effect on species dynamics to fragmentation (Fahrig 2003). Differences in patch isolation have been shown to reflect changes in habitat loss more closely than changes in fragmentation *per se* (defined as the breaking apart of habitat independent of habitat loss; Fahrig 2003). Thus, it is important to account for the relationship between the amount of habitat in the landscape and fragmentation characteristics to ensure that

habitat loss impacts are not misinterpreted as fragmentation effects (Fahrig 2003).

The consistency of species responses to fragmentation may be further modified by within-patch habitat conditions. Indeed, the degree of natural and anthropogenic disturbance may influence species dynamics to an equal or greater extent than larger scale landscape structure (Ross et al. 2002; Jellinek et al. 2004; Pharo et al. 2004). Disturbances such as grazing and fire in woodland habitats have major impacts on vegetation structure (Russell-Smith and Stanton 2002; Bowman and Prior 2004), plant cover (Hobbs 2001), soil nutrition (Guinto et al. 1999) and soil–water infiltration (Hobbs 2001), thereby altering habitat suitability for a range of fauna (Martin and Green 2002). Localised habitat effects should be particularly influential on populations of smaller, less vagile species such as many ground-dwelling insects, for which dispersal distances are too low for larger-scale landscape structure to exert a strong influence (Abensperg-Traun et al. 1996).

Ants are the most commonly used insect bioindicators of habitat condition in Australia, owing to their abundance, diversity, sensitivity to disturbance and close relationship with soil structure and nutrient cycling (Hoffmann and Andersen 2003; Andersen and Majer 2004). Functional groupings of ants that are based primarily on competitive dynamics and inter-taxa differences in habitat requirements (Andersen 1995) have been applied successfully to assess post-disturbance recovery from fire, mining and grazing (Vanderwoude et al. 1997; Hoffmann and Andersen 2003). However, the importance of habitat differences as determinants of ant composition, and thus the reliability of ants as habitat bioindicators, has not been quantified against the independent (pure) effects of habitat loss and fragmentation and joint (confounded) effects that are simultaneously explained by aspects of habitat fragmentation, loss and within-patch characteristics (Cushman and McGarigal 2002). To determine this, we devised a simple conceptual model that emphasised three major influences (habitat fragmentation, habitat loss, within-patch habitat characteristics) and associated joint effects on ant species assemblages in fragmented landscapes (Fig. 1).

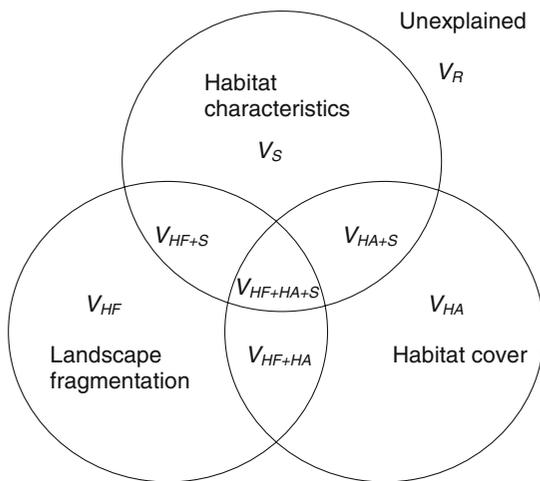


Fig. 1 Conceptual model of major determinants that influence ant assemblages in fragmented landscapes divided into the independent effects of landscape fragmentation (V_{HF}), habitat cover (V_{HA}) and within-patch habitat characteristics (V_S), corresponding joint effects (V_{HF+HA} , V_{HF+S} , V_{HA+S} , $V_{HF+HA+S}$) and unexplained effects (V_R)

We formulated two hypotheses. First, we predicted that differences in habitat loss would account for a greater proportion of variation in ant species assemblages among patches than the effects of habitat fragmentation. This hypothesis tested Fahrig's (2003) theory that habitat loss exerts a greater influence on species dynamics than fragmentation once both effects are separated. Second, we predicted that ant composition should be more strongly influenced by within-patch habitat characteristics than by fragmentation or habitat loss. In particular, we would expect those habitat characteristics that increase or reduce low temperature stress, where stress is defined as any factor limiting productivity (Andersen 1995), would show strong correlations to ant species abundance. This prediction is based on findings from other invertebrate studies in eucalypt woodlands (Abensperg-Traun et al. 1996; Hoffmann and Andersen 2003) and reflects the importance of temperature as a key determinant of ant community structure (Andersen 1995).

We tested our predictions in semi-arid poplar box (*Eucalyptus populnea*) woodlands, a major vegetation type in the Brigalow Belt South bioregion in southern Queensland, Australia (Sattler and Williams 1999). The 27.2 million ha

bioregion has been extensively modified for agricultural development since approximately 1850. In the western region, where we conducted our study, approximately 36% of native vegetation remained in 2003 (Queensland Department of Natural Resources and Water 2003). Vegetation clearing has had a major impact on distribution and abundance of poplar box woodlands, and the condition of remaining poplar box remnants is largely unknown. By understanding the relative importance of habitat loss, fragmentation and within-patch habitat characteristics, we can determine whether ants are viable bioindicators of poplar box woodland condition, or whether ant communities are being driven more strongly by landscape structure.

Methods

The study was conducted from March–August 2003 in southern Queensland, Australia. Ants were sampled in poplar box remnants across an area of approximately 4.5 million ha, extending west from Miles (150.11 E 26.39 S) to Morven (147.6 E 26.25 S) and north from Surat (149.4 E 27.9 S) to Injune (148.33 E 25.50 S). Using 1:100,000 ecosystem mapping, 20 patches were selected that were mapped either as poplar box woodland on alluvial plains or as poplar box dominant or co-dominant ecosystems. Within the bioregion, all patches were located within one sub-region to reduce biogeographical variability and represented a broad range of fragmentation states, particularly maximising differences in poplar box patch area, degree of contrast between patches (patch edge contrast) and isolation between poplar box patches (Euclidean nearest neighbour). One 100 × 10 m plot was located as far as possible from patch boundaries to reduce edge effects and where access was allowed by the landholder. Plots were also sited in positions to minimise the number of idiosyncratic landscape features (e.g. dams).

Environmental predictors

Three sets of environmental predictors that we anticipated may influence ant assemblages were

derived: (1) fragmentation characteristics (2) habitat loss and (3) within-patch habitat characteristics. Fragmentation measures (Table 1) were calculated for a 500 ha landscape surrounding each plot, which represented a circular area of 1.3 km radius centred on each plot. The 1.3 km radius landscape was an appropriate scale for dominant ant species such as *Iridomyrmex* spp. (Greenslade and Halliday 1983; Hölldobler and Wilson 1990), by representing a scale larger than its home range but smaller than its regional distribution. However, some poplar box patches were isolated such that they were the only one within the 1.3 km radius; thus, Euclidean nearest neighbour distance metrics were calculated within a 5 km radius (8,000 ha). Habitat loss (also referred to as habitat cover) was measured as total area of native vegetation cover remaining in each 500 ha landscape in 2003 (Table 1).

Eight measures of fragmentation were calculated using FRAGSTATS 3.0 (McGarigal and Marks 1995; Table 1). These metrics described individual poplar box patch features (patch area, patch shape, land use contrast of adjacent patches), characteristics of all poplar box patches in each 500 ha landscape (disjunct core area density, mean nearest neighbour distance, density of edge habitats weighted by land type contrast, interspersion and juxtaposition of poplar box patches) and characteristics of all patch types in the 500 ha landscape (land type diversity). Weightings were assigned to each land type according to the similarity to poplar box; smaller values were assigned to land types that showed greater similarity to poplar box (e.g. other native vegetation). Core areas were defined as poplar box patch areas excluding an edge width of 100 m. The selected metrics did not exhibit unpredictable or inconsistent responses to changes in grain size (e.g. patch richness, patch richness density, Shannon's diversity index) or extent (e.g. patch density, edge density, landscape shape index, mean shape index; Wu et al. 2002) and did not include metrics that provide unreliable estimates where the frequency of relevant patch types in the landscape was low (e.g. double log fractal dimension; McGarigal and Marks 1995).

The eight selected fragmentation metrics and one measure of habitat cover were combined with

seven habitat variables representing annual rainfall, soil properties, vegetation attributes and patch disturbance (Table 1). Percentage soil clay content was assessed from the soil particle size distribution, and measured using 20 × 10-cm deep soil cores per patch, which were bulked together and sub-sampled. Samples were air-dried, passed through a sieve to remove roots and rocks and ground to < 2 mm for particle size analysis. The percentages of coarse sand (0.2–2.0 mm), fine sand (0.02–0.2 mm), silt (0.002–0.02 mm) and clay particles (< 0.002 mm) were separated gravimetrically and assessed using a hydrometer. Projected foliage cover was measured using a gimbal ring sighting tube at 1 m intervals along a 100 m transect. Annual rainfall data was calculated for each plot from Bureau of Meteorology observational data over 35 years (1968–2003), which were spatially interpolated to assess rainfall at plots sited between stations. The severity of patch disturbance from a range of sources (Table 1) was measured on a scale of 0 (no evidence of disturbance) to 5 (severe disturbance) for each disturbance type, and was determined by on-site visual assessments and information from land managers. Given that ants often respond to low temperature stress at ground level (Hoffmann and Andersen 2003; Andersen 1995), sources of disturbance were collated into two groups: those associated with increasing plant cover (weed occurrence), and hence decreased ground-level insolation, and those associated with decreasing plant cover (all others; Table 1). Scores were then summed to produce a disturbance index for each group. Density of shrub-layer (mid-stratum) vegetation 1–4 m in height and/or less than 5 cm diameter at breast height was measured within one 50 × 10 m subplot per plot.

Ant sampling

Each 100 × 10 m sampling plot ($n = 20$) contained two grids of nine pitfall traps that were spaced 5 m apart in a 3 × 3 configuration. Each plot was sampled in March and August 2003 to incorporate seasonal variation in community structure. Individual traps consisted of 120 ml jars (40 mm diameter) containing 60 ml of 70%

Table 1 Definitions and mean, standard deviation (SD), maximum and minimum values for eight measures of fragmentation (1–8), one measure of habitat cover (9) and seven measures of within-patch habitat characteristics (10–16)

Predictor	Units	Mean	SD	Max	Min	Definition
1. Patch area	ha	158.4	160.7	497.3	1.1	Focal patch area.
2. Patch shape	–	1.9	0.6	3.1	1.0	Focal patch perimeter divided by the minimum perimeter possible for a maximally compact patch. Greater values indicate more irregularly shaped patches.
3. Patch edge contrast	%	29.0	12.4	47.2	0.0	The sum of the focal poplar box patch perimeter segment lengths (m) multiplied by corresponding land use contrast weights, divided by total patch perimeter (m), and multiplied by 100. Value of 100 represents a poplar box patch for which the entire perimeter is adjacent to a land type of maximum contrast.
4. Disjunct core area density	no. 100 ha ⁻¹	0.4	0.4	1.6	0.0	The number of disjunct core areas within poplar box patches per 100 ha.
5. Mean Euclidean nearest neighbour	m	433.6	364.8	1782.5	143.6	The mean shortest straight-line distance between a poplar box patch and nearest poplar box patch within an 8000 ha landscape.
6. Contrast weighted edge density	m ha ⁻¹	6.5	3.3	12.5	0.0	Sum of the lengths (m) of each edge segment of all poplar box patches, multiplied by the corresponding contrast weight, divided by the total landscape area (m ²) and multiplied by 10,000. Larger values indicate greater edge density of poplar box patches in the landscape and/or greater contrast between poplar box patches and neighbouring land types.
7. Interspersion and juxtaposition index	%	68.1	27.6	100.0	0.0	The observed intermixing of all poplar box patches with other land types divided by the maximum interspersion for all, multiplied by 100. Greater values indicate greater fragmentation of poplar box in the landscape.
8. Simpson's diversity index	–	0.4	0.2	0.7	0.0	One minus the sum, across all patch types, of the proportional abundance of each patch type squared. Greater values indicate greater number of land types and/or greater evenness of different land types in the landscape.
9. Habitat cover	ha	255.4	147.1	497.3	26.6	Area of total native vegetation cover within a 500 ha landscape.
10. Shrub layer density	plants ha ⁻¹	638.0	849.5	2780.0	0.0	Density of mid-stratum vegetation.
11. Projected foliage cover	%	37.6	7.8	49.0	22.0	Percentage of ground area occupied by the vertical projection of foliage and branches of live tallest and mid-stratum stems.
12. Disturbance (weed)	–	1.3	0.7	3.0	0.0	Score of weed infestation, where higher scores indicate greater disturbance.
13. Disturbance (plant biomass removal)	–	3.1	1.2	5.5	1.0	Sum of scores for each source of patch disturbance that are likely to remove plant biomass (erosion, grazing, logging, prescribed burning, wildfire, woody treatment), where higher scores indicate greater disturbance.
14. Mean long-term rainfall	mm	556.2	29.2	613.8	505.2	Average annual rainfall recorded from 1968 to 2003.
15. Bare ground	%	25.1	15.5	64.0	6.6	Percentage cover of bare ground.
16. Soil clay content	%	20.9	9.0	40.0	8.0	Percentage clay content (< 0.002 mm particle size) from 0–10 cm soil layer.

ethyl alcohol and a few drops of glycerol to reduce evaporation. The traps were sunk into the ground so that the jar rims were flush with the soil surface and disturbed soil and litter were replaced around the mouth of the trap after insertion. Traps were opened for a 4-day period, following sampling methods previously adopted in Australia and South Africa (Jackson and Fox 1996; Samways et al. 1997; Vanderwoude 1999). Heavy rain and hot sun during sampling periods severely affected trap contents in six plots, resulting in traps being filled with water and/or silt and drying out due to excessive evaporation, respectively. Prior to sealing, the contents of rain-affected traps were allowed to settle, excess rainwater was decanted off and replaced by 70% ethyl alcohol or methylated spirits. Where possible, we identified ants to species/morphospecies level using a combination of keys, determined specimens and expert assistance, and assigned them to the nine functional groups (Dominant Dolichoderinae, Subordinate Camponotini, Hot Climate Specialists, Cold Climate Specialists, Tropical Climate Specialists, Cryptic Species, Opportunists, Generalized Myrmicinae, Specialist Predators). We refer to morphospecies as “species” throughout this paper for simplicity. Species prevalence in each trap was recorded using an abundance scale (1 = 1 individual, 2 = 2–5 individuals, 3 = 6–20 individuals, 4 = 21–50 individuals and 5 = 50 + individuals).

Analysis

After combining sampling months, species abundance ratings were averaged over all traps at each plot rather than summed, to reduce the impact of differences in the numbers of traps that were rain or sun-affected among plots (see previous paragraph). Given the logarithmic nature of the abundance scale, further transformation of species data was not required to meet the assumptions of normality prior to multivariate analyses. A species accumulation curve on combined sampling month data (maximum permutations = 5000) determined the efficiency of the sampling methods to capture total species richness. Multivariate analyses were carried out on species that

were present at five sites or greater ($n = 31$) to further improve statistical robustness.

We used a series of partial redundancy analysis (RDA) runs to partition among-patch variation in species assemblages among landscape fragmentation, habitat cover and within-patch habitat characteristics. Prior to analysis, preliminary detrended correspondence analysis (DCA) was undertaken to confirm that species responses to environmental predictors were more linear than Gaussian ($< 3SD$; ter Braak and Šmilauer 2002). The RDA also accounts for potential confounded effects between sets of environmental predictors assuming linear inter-relationships. However, one of the eight fragmentation variables, diversity of land types, showed a strong quadratic response to habitat cover. Thus, we derived residuals from linear and quadratic regressions between fragmentation variables and habitat cover, and used the residuals as fragmentation measures. Where non-linear relationships are present, this approach provides a more accurate method of separating the effects of fragmentation and habitat cover than using covariates, while still being able to calculate the independent effects of both factors. Nevertheless, the joint effects of habitat cover and fragmentation (V_{HF+HA} ; Fig. 1) are negligible using this method and thus not interpretable. Mean Euclidean nearest neighbour and shrub-layer density (Table 1) were transformed prior to regression analysis to meet the assumptions of normality and variance homogeneity. Collinearity was checked using correlation analysis on fragmentation and habitat variables, but there were no highly correlated relationships among variables (fragmentation: $r < 0.66$; habitat: $r < 0.44$).

Based on Borcard et al. (1992), we calculated eight individual variance components. These were the proportion of variance attributable to: independent effects of habitat fragmentation (V_{HF}), habitat cover (V_{HA}) and within-patch habitat characteristics (V_S); joint effects of fragmentation and habitat cover (V_{HF+HA}), fragmentation and within-patch habitat characteristics (V_{HF+S}), habitat cover and within-patch habitat characteristics (V_{HA+S}) and fragmentation, habitat cover and within-patch habitat characteristics ($V_{HF+HA+S}$); and none of the above (residual variation; V_R).

The eight variance components were derived from the proportion of total variance (ce_x) explained by each of a series of RDA runs. Firstly, two RDA runs selected fragmentation and within-patch habitat measures that significantly contributed to explained variation (ce_1, ce_2). To derive these, we assigned eight fragmentation residuals (first RDA) or seven within-patch habitat characteristics (second RDA) as independent variables. A forward selection procedure then excluded variables that did not significantly contribute to explained variation in each run. We tested significance at a 5% level ($P \leq 0.05$), which was assessed by Monte Carlo permutation tests ($n = 5000$) that do not require multivariate normality (Manly 1991). An RDA run to select significant measures of habitat cover was unnecessary, since habitat cover was represented by one variable. Secondly, we calculated V_{HF} , V_{HA} and V_S from three additional RDA runs. The third, fourth and fifth RDA runs assigned significant fragmentation measures, within-patch habitat variables and habitat cover as independent variables, respectively, while treating significant variables from the other two groups as covariates. For example, independent fragmentation effects (V_{HF}) were calculated by assigning significant fragmentation measures as independent variables and significant within-patch habitat characteristics and habitat cover as covariates.

Thirdly, we undertook a further three RDA runs to calculate joint effects of significant variables from any two of the three groups of environmental predictors (V_{HF+HA} , V_{HF+S} , V_{HA+S}). The sixth RDA run allocated significant fragmentation variables and habitat cover as independent variables, and treated significant within-patch habitat characteristics as covariates. The proportion of variance derived from the RDA (ce_3) represented the proportion $V_{HF} + V_{HA} + V_{HF+HA}$, from which the variation component of joint effects of fragmentation and habitat cover (V_{HF+HA}) was derived by:

$$V_{HF+HA} = ce_3 - (V_{HF} + V_{HA})$$

Using the same approach, the seventh RDA run assigned significant fragmentation measures and within-patch habitat characteristics as independent variables, while controlling for

habitat cover, to produce the proportion ce_4 ($V_{HF} + V_S + V_{HF+S}$). The variation component of joint effects of fragmentation and within-patch habitat was calculated as:

$$V_{HF+S} = ce_4 - (V_{HF} + V_S)$$

Joint effects of habitat cover and within-patch habitat were calculated by an eighth RDA in the same fashion (ce_5), and were derived by:

$$V_{HA+S} = ce_5 - (V_{HA} + V_S)$$

From results of previous RDA runs, we then calculated the joint effects of the three sets of variables ($V_{HF+HA+S}$) using the following equation:

$$V_{HF+HA+S} = (ce_1 - V_{HF}) - V_{HF+S} - V_{HF+HA}$$

Finally, selected measures of fragmentation, habitat cover and within-habitat characteristics were assigned as independent variables in a ninth RDA run that determined total variation explained by fragmentation, loss and within-patch habitat effects. V_R was calculated as one minus the sum of all other variance components. For each RDA run, the significance of the sum of all canonical variates (trace) was calculated using a Monte Carlo permutation test ($n = 5000$). This statistical approach was also used to examine variation in ant functional group assemblages but showed qualitatively similar results to the species analysis.

Results

A total of 116 ant species from 26 genera was sampled in March and August 2003 (Appendix 1). Average species richness per plot was 21 after pooling both months, and genus and species richness tended to be greater in March than in August. The lack of asymptote in the species accumulation curve (Fig. 2) suggests that the sampling methodology did not capture total species richness across the study area.

Patch area was the only significant measure of fragmentation that explained variation in ant species assemblages across patches, after account-

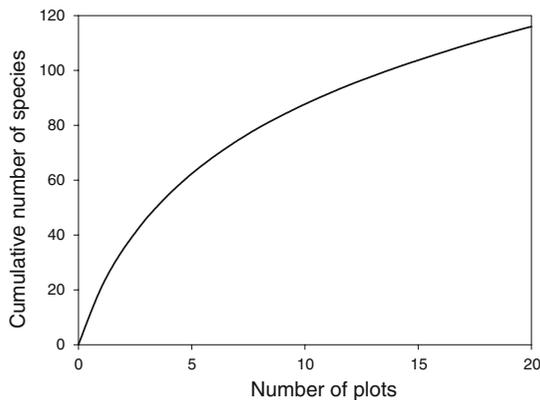


Fig. 2 Species accumulation curve showing cumulative number of ant species sampled across 20 plots for March and August combined

ing for habitat cover (Table 2). There was also a tendency for the degree of edge contrast of the neighbouring patch to be related to variation in ant species assemblages (Table 2). There were three significant within-patch habitat condition predictors: percentage of clay content in the soil,

average annual precipitation for each patch from 1968–2003 and habitat disturbance severity from erosion, grazing, tree and shrub removal, prescribed burning and wildfire. Variation in species assemblages also tended to be influenced by bare ground cover (Table 2). Given high data variability and small sample size, we included the degree of edge contrast and bare ground cover in our final model. The six variables and habitat cover exhibited significant linear relationships with species assemblages (Monte Carlo permutation test: $F = 1.5$, $P = 0.001$) and accounted for 46.1% of the total variation. Of this, the independent effects of within-patch habitat characteristics explained the largest proportion of variation, compared to the pure effects of fragmentation and habitat cover (Fig. 3a).

Joint effects of fragmentation and within-patch habitat characteristics and the combined effects of fragmentation, habitat cover and within-patch habitat characteristics accounted for most of the joint effects (Fig. 3a). Within-patch habitat characteristics and habitat cover confounded 35%

Table 2 Nine RDA model runs on species assemblages, indicating covariates used, predictors selected by a forward stepwise procedure and total variance explained by each model run after accounting for the effects of the covariates (trace)

Model	Covariates	Selected Predictors			Trace ^b
		Predictor	Eigenvalue ^a	P-Value	
1. Fragmentation		Patch area	0.11	0.001	0.182
		Patch edge contrast	0.07	0.066	
2. Within-patch habitat		% soil clay content	0.09	0.009	0.304
		Rainfall	0.08	0.037	
		Disturbance (plant biomass removal)	0.07	0.048	
		% bare ground	0.06	0.080	
3. Fragmentation	Within-patch habitat + habitat cover				0.118
4. Habitat cover	Fragmentation + within-patch habitat				0.054
5. Within-patch habitat	Fragmentation + habitat cover				0.245
6. Fragmentation + within patch habitat	Habitat cover				0.396
7. Habitat cover + within-patch habitat	Fragmentation				0.309
8. Fragmentation + habitat cover	Within-patch habitat				0.170
9. Fragmentation + habitat cover + within-patch habitat					0.461

^a Variance explained by each predictor

^b Sum of all canonical eigenvalues, where 1.0 represents a model where all variance in the data is explained by selected predictors

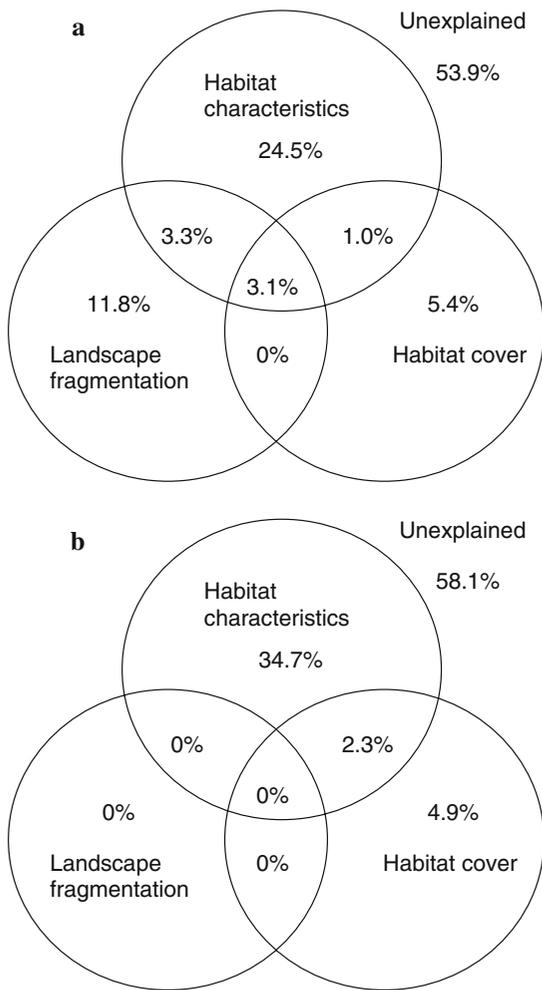


Fig. 3 Percentage variation explained of (a) ant species and (b) functional group assemblages among 20 patches as a result of variance partitioning. Variance components represent the independent effects of fragmentation (V_{HF}), habitat cover (V_{HA}) and within-patch habitat characteristics (V_S) and proportion of unexplained variation (V_R). V_{HF+HA} , V_{HF+S} , V_{HA+S} , $V_{HF+HA+S}$ quantify the degree to which fragmentation, habitat loss and localised within-patch habitat effects are confounded

(6.4/18.2 × 100) of the explanatory power of fragmentation, while 43% (4.1/9.5 × 100) of the explanatory power of habitat cover was confounded by the effects of significant variables from the other two categories. In contrast, fragmentation and habitat cover confounded only 23% (7.4/31.9 × 100) of the effects of within-patch habitat characteristics on species assemblages. As expected from the use of residuals, the joint effects of fragmentation and habitat loss

were negligible (Fig. 3a). When examining the corresponding responses on a functional group basis, there were qualitatively similar patterns, with the exception that fragmentation explained no variation in functional group assemblages across patches (Fig. 3b).

Clear responses of species to habitat and landscape variables were limited (Fig. 4). The preference of *Monomorium* 6 for sites with increased patch edge contrast indicates the broad habitat tolerance of Generalised Myrmicinae, and the positive relationship between abundance of *Notoncus* 7 (a Cold Climate Specialist) and habitat cover demonstrates a response to increased shadiness at landscape scale. Other clear responses were to local habitat conditions. A group of species—*Monomorium* 3, *Pheidole* 9 (both Generalised Myrmicinae) and *Leptogenys* 1 (Specialist Predator)—were associated with increasingly lighter soils, while *Camponotus* 11 (Subordinate Camponotini) and *Crematogaster* 3

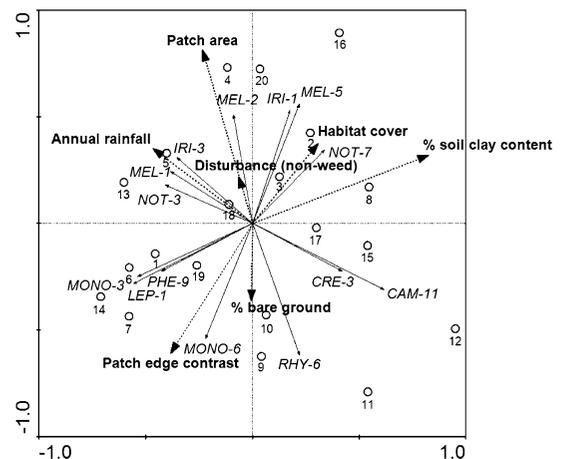


Fig. 4 Biplot based on redundancy analysis of species abundance using significant fragmentation measures, within-patch habitat variables and habitat cover; abbreviations are based on Appendix 1. Only species that show a minimum fit to the model of 20% or more are displayed for simplicity of presentation. Species arrows (solid) pointing in approximately the same direction as the environmental arrows (dotted) indicate a high positive correlation with that environmental predictor, arrows crossing at right angles indicate near-zero correlation and arrows pointing in opposite directions indicate high negative correlation. Longer environmental and species arrows indicate those metrics and species that provide more certainty about the predicted correlations. Site (patch) scores are indicated by numbered open circles

(Generalised Myrmicinae) became more abundant as rainfall decreased. Species of *Monomorium* (Generalised Myrmicinae) and *Rhytidoponera* (Opportunist) were generally more abundant in sites where species of *Iridomyrmex* (Dominant Dolichoderinae) and *Melophorus* (Hot Climate Specialist) were less dominant.

Discussion

Our results demonstrated that habitat fragmentation metrics accounted for greater variation in species assemblages among patches than habitat cover. As expected, within-patch habitat characteristics were identified as stronger drivers of ant species assemblage differences among patches than habitat fragmentation or cover.

Our study suggests that within-patch habitat characteristics are the predominant influence on ant assemblages in Australian semi-arid woodlands. Differences in localised habitat characteristics explained over twice the amount of species variation across patches than did fragmentation measures. This difference, combined with our finding that over one-third of total fragmentation effects on species assemblages were confounded by the influence of within-patch habitat characteristics and habitat loss, suggests that fragmentation effects are considerably weaker than the impact of within-patch habitat. Thus, previously reported fragmentation effects on ant species (e.g. Suarez et al. 1998; Sobrinho et al. 2003; Schoereder et al. 2004) may largely be demonstrating independent and joint effects of within-patch habitat characteristics associated with fragmented states, rather than the sole effects of fragmentation per se. Indeed, our findings support Abensperg-Traun et al.'s (1996) conclusions that habitat characteristics were stronger predictors of arthropod communities than landscape structure in *E. salubris* woodlands in southwestern Australia.

Differences in local habitat structure and complexity are commonly associated with changes in animal communities (reviewed by Tews et al. 2004), including arthropod dynamics (Gardner et al. 1995; Hansen 2000; Lassau and Hochuli 2004). Features such as diversity, spatial distribution and architectural complexity of plant

communities have been suggested as important determinants of animal assemblages (Lawton 1987). While the direct effect of shrub density on ant species assemblages was not detected in this study, the significant effects of disturbance associated with removal of plant biomass (e.g. logging, fire and grazing) are likely to be highly associated with changes in habitat structure among patches (Gardner et al. 1995). Anthropogenic disturbance is a major driver of ant communities, which is mediated largely through associated habitat structure changes leading to low temperature stress (Hoffman and Andersen 2003). Many ant species are thermophilic (Hölldobler and Wilson 1990) and are likely to be attracted by areas of low plant cover, where there is higher ground insolation. Thus, our finding that bare ground cover influences ant assemblages was unsurprising, although several *Melophorus* species (MEL; Fig. 4), a recognised Hot Climate Specialist, responded contrary to expectations by reacting negatively to increasing bare ground cover. The positive responses of *Monomorium 6* (Generalised Myrmicinae) and *Rhytidoponera 6* (Opportunist) to less native vegetation cover and greater bare ground supported previous findings that Opportunists and Generalised Myrmicinae prefer more open habitats (Lassau and Hochuli 2004). *Notoncus* (NOT; Fig. 4) is a Cold Climate Specialist, a group that prefers cooler, more mature forests (Ottonetti et al. 2006). The positive correlation between their abundance and percentage native vegetation cover suggests that *Notoncus 7* may be responding to canopy cover at a landscape scale, rather than to local conditions.

The most important habitat predictor of variation in ant species assemblages was clay content of the soil. Clay and sand content is important for the construction of nest mounds for some ant species (Davis-Carter and Sheppard 1993), changes in which can alter nest building activity (de Bruyn 1993). Soil texture and strength may influence differences in community assemblages in semi-arid landscapes (Bestelmeyer and Wiens 2001), and soil structure is likely to have indirect effects on ant composition through changes in vegetation and drainage (Greenslade and Greenslade 1977). Another significant factor in our study

that has implications for changes in vegetation structure, and hence ant species assemblages, is long-term annual rainfall differences. Long-term rainfall is a major factor influencing woody species recruitment, assuming that density-dependent effects for woody species are relatively weak; indeed, rainfall may have greater effects on woody vegetation structure than management practices such as fire (Fensham et al. 2005). However, not enough information on adult life spans is known to accurately establish the degree to which temporal factors such as rainfall may influence colony persistence.

The principal pattern emerging from species responses to selected environmental predictors was niche separation according to competitive ability. *Iridomyrmex* spp are members of the Dominant Dolichoderinae that are a competitively superior group of species that co-exist with Hot Climate Specialists (*Melophorus* spp.) in similar habitats (Andersen 1995; Fig. 4). The observation that competitively inferior *Monomorium* 6, *Pheidole* 9 (Generalised Myrmicinae) and *Rhytidoponera* spp (Opportunists) exhibited very different habitat preferences to Dominant Dolichoderinae and Hot Climate Specialists confirms that competitive ability is an important determinant of ant assemblage composition (Andersen 1995). Functional group analyses indicated that functional groups generally responded to habitat differences based on expected inter-taxa differences in habitat preferences and competitive ability. This is despite the fact that functional group responses to disturbance are seen to be less reliable in arid and semi-arid environments (Hoffmann and Andersen 2003).

The majority of variation in ant assemblages explained by habitat loss, fragmentation and within-patch habitat characteristics represented independent effects of each group. The low proportion of variation that was simultaneously explained by variables belonging to two or more groups was relatively low, suggesting that there was a low number of redundant variables (Cushman and McGarigal 2002). This is expected given the removal of non-significant variables prior to variance partitioning. Nevertheless, it was interesting to note that habitat fragmentation and loss effects were each confounded by within-patch

habitat characteristics to a greater extent than localised habitat effects were confounded by landscape structure. For example, our results indicate that 43% of variation that would be normally considered as independent effects of habitat loss on ant assemblages represents effects that are unable to be distinguished from the effects of fragmentation or local habitat characteristics. The results highlight the disadvantages of quantifying independent landscape structure effects on animal assemblages without also considering localised patch characteristics. The presence of joint effects also emphasises the inter-relationships between landscape structure, microclimate and intra-patch vegetation characteristics (Saunders et al. 1991; Didham and Lawton 1999).

The high total variation that remained unexplained by species and functional group models is likely to be largely due to the lack-of-fit of data to the model, and less related to unmeasured explanatory variables or random variation (Økland 1999). Thus, while variance partitioning is a useful method to compare the amount of variation explained by the three groups of predictors, the amount of unexplained variation is less useful as a predictor to determine the degree to which all important variables were captured. Nevertheless, we recognise that other habitat characteristics that were not included in this study may have important influences on ant community structure. For example, the severity of habitat disturbance, fragmentation and habitat loss may only be influential on diversity if it has been sustained sufficiently long for the community to adapt (Mac Nally et al. 2000; Davies et al. 2001). Temporal ecological responses to vegetation change have been largely ignored (Lunt and Spooner 2005), and cannot be accounted for in ‘snapshot’ studies such as this. Furthermore, species responses to fragmentation and habitat loss can be also confounded by factors such as pre-fragmentation population size, population variability, species mobility (Davies et al. 2000; Tscharrntke et al. 2002), grain (Chust et al. 2003) and scale (Andersen 1997; Chust et al. 2003). For the latter, regional effects of fragmentation may override more localised fragmentation processes, but measures of ant abundance and diversity are scale-dependent and so cannot be used to determine

ant assemblage differences among landscapes at larger scales (Andersen 1997).

The species accumulation curve suggests that our sampling may not have detected all ant species present. Sampling for arthropods using pitfall traps is associated with multiple sources of bias (e.g. Spence and Niemelä 1994), since the abundance and richness of species collected is a function of the ability of an individual to be trapped as well as the external community structure. While the 4-day period that the traps remained open has been used to collect ants in Queensland and New South Wales (Jackson and Fox 1996; Vanderwoude 1999), we recognise that the heavy rain that fell while some traps were open may have biased differences in intra-patch assemblages. Another potential source of bias may be differences in habitat structure among patches that may alter ant trappability (Melbourne 1999). However, given the high variety of responses to habitat structure within beetle species (Greenslade 1964), results from Melbourne's (1999) study of temperate grassland ants may not be applicable to Northern Australian semi-arid ant communities.

Lack of knowledge of the relationships between indicator species and ecosystem characteristics is a major obstacle to successfully using indicator species to monitor degradation and recovery in forest ecosystems (Lindenmayer et al. 2000). Ant life histories are not well known, making it difficult to fully understand the viability of ants, particularly at the species level, as bioindicators of habitat condition. However, we believe that this study contributes towards a better understanding of the utility of ants as bioindicators for habitat condition by demonstrating the importance of habitat characteristics, over landscape structure, as drivers of ant assemblages.

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Appendix

Appendix 1 Abundance rating of 116 morphospecies/species collected in pitfall traps in March and August 2003

Morphospecies/Species ¹	Abundance
<i>Anochetus rectangularis</i> Mayr	1.0
<i>Anochetus armstrongi</i> McAreavey	3.0
<i>Aphaenogaster</i> sp. 1 nr. <i>longiceps</i>	1.6
<i>Calomyrmex</i> sp. 1	1.0
<i>Calomyrmex</i> sp. 2 <i>ephippium</i> gp	1.5
<i>Camponotus</i> sp. 1	1.0
<i>Camponotus</i> sp. 3	1.0
<i>Camponotus</i> sp. 4	1.0
<i>Camponotus</i> sp. 6 <i>aenopilosus</i> gp	1.0
<i>Camponotus</i> sp. 9	1.0
<i>Camponotus</i> sp. 10	1.0
<i>Camponotus consobrinus</i> (Erichson)	1.4
<i>Camponotus loweryi</i> McArthur & Adams	1.3
<i>Camponotus</i> sp. 14	1.0
<i>Camponotus nigriceps</i> (Smith)	1.2
<i>Camponotus</i> sp. 19	2.0
<i>Camponotus</i> sp. 24 <i>novahollandiae</i> gp	1.0
<i>Camponotus</i> sp. 25	1.0
<i>Camponotus</i> sp. 26	1.0
<i>Camponotus</i> sp. 27	1.0
<i>Cerapachys</i> sp. 2 <i>brevis</i> gp	2.0
<i>Cerapachys</i> sp. 3 <i>fervidus</i> gp	1.0
<i>Crematogaster</i> sp. 1	2.5
<i>Crematogaster</i> sp. 2	2.6
<i>Crematogaster</i> sp. 3	2.1
<i>Crematogaster</i> sp. 4	1.0
<i>Crematogaster</i> sp. 5	2.2
<i>Crematogaster</i> sp. 6	2.4
<i>Crematogaster</i> sp. 7	1.8
<i>Iridomyrmex</i> sp. 1	3.4
<i>Iridomyrmex</i> sp. 2 <i>rufoniger</i> gp	3.9
<i>Iridomyrmex purpureus</i> (Smith)	2.9
<i>Iridomyrmex</i> sp. 4	4.0
<i>Iridomyrmex</i> sp. 5	4.0
<i>Iridomyrmex</i> sp. 6	3.2
<i>Iridomyrmex</i> sp. 7	3.2
<i>Leptogenys</i> sp. 1 <i>conigera</i> gp	1.4
<i>Leptogenys exigua</i> Crawley	1.0
<i>Melophorus</i> sp. 1	2.5
<i>Melophorus</i> sp. 2	2.0
<i>Melophorus</i> sp. 3	1.6
<i>Melophorus</i> sp. 4	2.3
<i>Melophorus</i> sp. 5	2.0
<i>Melophorus</i> sp. 6	1.3
<i>Melophorus</i> sp. 8	1.5
<i>Melophorus</i> sp. 10	1.0
<i>Melophorus</i> sp. 11	1.1
<i>Melophorus</i> sp. 13	2.0
<i>Melophorus</i> sp. 14	2.5
<i>Melophorus</i> sp. 18	2.0
<i>Meranoplus</i> sp. 1 <i>dimidiatus</i> gp	1.7
<i>Meranoplus</i> sp. 2	1.7

Appendix 1 continued

Morphospecies/Species ¹	Abundance
<i>Meranoplus puryi</i> Forel	1.3
<i>Meranoplus</i> sp. 5 gp C sensu Andersen	1.7
<i>Meranoplus</i> sp. 6 <i>diversus</i> gp	1.5
<i>Meranoplus</i> sp. 7 <i>diversus</i> gp	1.4
<i>Meranoplus</i> sp. 8	2.0
<i>Meranoplus</i> sp. 9 <i>dimidiatus</i> gp	2.0
<i>Monomorium</i> sp. 1 <i>nigrius</i> gp	2.6
<i>Monomorium</i> sp. 2 <i>laeve</i> gp	3.0
<i>Monomorium</i> sp. 3 <i>carinatum</i> gp	2.2
<i>Monomorium sculpturatum</i> Clark	2.6
<i>Monomorium sordidum</i> Forel	2.7
<i>Monomorium sydneyense</i> Forel	2.7
<i>Monomorium</i> sp. 9 <i>carinatum</i> gp	2.0
<i>Monomorium rothsteini</i> Forel	3.0
<i>Monomorium</i> sp. 11	2.3
<i>Myrmecia varians</i> Mayr	1.3
<i>Myrmecia gilberti</i> Forel	1.0
<i>Myrmecia</i> sp. 5	1.0
<i>Notoncus</i> sp. 1 <i>enormis</i> gp	2.1
<i>Notoncus</i> sp. 2 <i>enormis</i> gp	2.2
<i>Notoncus ectatommoides</i> (Forel)	2.4
<i>Notoncus</i> sp. 4 <i>enormis</i> gp	2.0
<i>Notoncus</i> sp. 6 <i>ectatommoides</i> gp	2.0
<i>Notoncus</i> sp. 7 <i>ectatommoides</i> gp	2.4
<i>Odontomachus ruficeps</i> Smith	1.3
<i>Opisthopsis</i> sp. 1 <i>rufithorax</i> gp	1.0
<i>Opisthopsis pictus</i> Emery	1.2
<i>Pachycondyla</i> sp. 1 <i>porcata</i> gp	1.0
<i>Pachycondyla</i> sp. 4	1.0
<i>Papyrius</i> sp. 1	3.7
<i>Paratrechina</i> sp.1	1.8
<i>Pheidole</i> sp. 1 gp D sensu Andersen	2.4
<i>Pheidole</i> sp. 3 gp B sensu Andersen	3.5
<i>Pheidole</i> sp. 4 <i>longiceps</i> gp	2.3
<i>Pheidole</i> sp. 5 gp E sensu Andersen	5.0
<i>Pheidole</i> sp. 6 <i>ampla</i> gp	2.4
<i>Pheidole</i> sp. 7 gp B sensu Andersen	2.1
<i>Pheidole</i> sp. 8 <i>variabilis</i> gp	3.0
<i>Pheidole</i> sp. 9 gp E sensu Andersen	2.1
<i>Podomyrma</i> sp. 1	1.0
<i>Polyrachis sidnica</i> Mayr	2.0
<i>Polyrachis</i> sp. 2 <i>chariomyrma</i> gp	1.0
<i>Polyrachis schwiedlandi</i> Forel	1.0
<i>Polyrachis hookeri</i> Lowne	1.0
<i>Polyrachis</i> sp. 6 <i>chariomyrma</i> gp	1.0
<i>Polyrachis prometheus</i> Santschi	1.3
<i>Rhytidoponera</i> sp. 2	1.3
<i>Rhytidoponera</i> sp. 3 <i>metallica</i> gp	1.9
<i>Rhytidoponera convexa</i> (Mayr)	1.6
<i>Rhytidoponera</i> sp. 5	1.0
<i>Rhytidoponera</i> sp. 6 <i>convexa</i> gp	1.7
<i>Rhytidoponera</i> sp. 8 <i>cristata</i> gp	1.4
<i>Rhytidoponera</i> sp. 9	1.3
<i>Rhytidoponera</i> sp. 10 <i>metallica</i> gp	1.3
<i>Stigmacros</i> sp. 1 <i>intacta</i> gp	2.0
<i>Stigmacros</i> sp. 3 <i>aciculata</i> gp	1.9

Appendix 1 continued

Morphospecies/Species ¹	Abundance
<i>Stigmacros</i> sp. 5 <i>aemula</i> gp	2.0
<i>Stigmacros</i> sp. 6 <i>inermis</i> gp	1.3
<i>Tapinoma</i> sp. 1	1.8
<i>Technomyrmex</i> sp.1	2.0
<i>Tetramorium</i> sp. 1	1.8
<i>Tetramorium</i> sp. 2	2.0
<i>Tetramorium</i> sp. 3	2.3
<i>Tetramorium</i> sp. 4	2.0

¹ Missing species numbers (e.g. *Stigmacros* sp. 2) represent species that were collected on a preliminary sampling trip prior to 2003

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