

Do landscape health indices reflect arthropod biodiversity status in the eucalypt woodlands of eastern Australia?

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Abstract Ecosystem or landscape health indices are important tools for land managers. While strong predictable relationships between these indices and biotic diversity are often generalized, they are seldom validated. Here we use data from a semi-arid eastern Australian woodland to examine the relationships between arthropod community structure and two sets of landscape health indicators: landscape function analysis (LFA), and a terrestrial index of ecological integrity based on common vegetation metrics (structure, composition and function; SCF). Hierarchical partitioning revealed that the ability of LFA or SCF to account for variation in arthropod richness was low, with the variable of importance taxon-dependent. Similarly, multivariate analyses indicated relatively weak and inconsistent relationships between LFA and SCF indices and arthropod assemblage structure. Results obtained for additional habitat attributes commonly used in terrestrial vegetation monitoring were similar. Our study indicates that strong predictable relationships are rarely apparent, particularly for arthropods. This indicates that these indices have limited use as surrogates of arthropod biodiversity. These results are contrary to the past literature, highlighting the need for additional research and the development of a conceptual and empirical framework linking health indices and arthropod biodiversity. This is necessary to further the theoretical and practical application of these measurements in environmental management.

Key words: arthropod, biodiversity assessment, biotic integrity, ecosystem health, indicator, landscape function analysis.

INTRODUCTION

Climate change, overgrazing and overexploitation of natural resources are recognized as major threats to biodiversity worldwide (e.g. Thomas *et al.* 2004; Ehrlich & Pringle 2008). These threats have resulted in predictions of biodiversity decline at unprecedented levels (Pimm & Raven 2000). Consequently, the conservation of biodiversity has become a crucial part of environmental management across all forms of land tenure from private landholdings to national governance. There are still considerable gaps, however, in our understanding of how human practices and anthropogenic disturbances affect basic ecological processes, and consequently, biodiversity (e.g. Stutchbury 2007). Crucial to the management and conservation of biodiversity are rapid, cost-effective and scientifically defensible methods for assessing how anthropogenic practices affect ecosystem health and condition, and the implications for biodiversity (Western 1992).

A number of approaches and methodologies have been developed to assess landscape health. These include direct measurements of the biophysical environment, which are designed to reflect overall landscape health (e.g. vegetation structure and diversity, Gibbons *et al.* 2008), and measures of ecosystem function (Kienast *et al.* 2009; Rowe *et al.* 2009). In particular, indices of biotic integrity (Karr 1991) have been used extensively to monitor change in ecosystem condition because of anthropogenic influences, particularly in aquatic systems (e.g. Karr 1991; Andreasen *et al.* 2001; Klemm *et al.* 2003; Martinez-Crego *et al.* 2010). Terrestrial indices of ecological integrity (TIEI) have also gained increasing popularity based on similar principles. Ecosystem characteristics such as the composition of the biota (including exotic species), the structure of the habitat (e.g. patch characteristics) and measures of ecosystem function (e.g. decomposition, erosion, infiltration etc.) are key inclusions in any TIEI (Noss 1990; Andreasen *et al.* 2001; Oliver 2002). These indices are also useful for broad terrestrial vegetation (Noss 1990; Gibbons & Freudenberger 2006; Oliver *et al.* 2007; Liira & Kohv 2010) and biodiversity

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monitoring (Failing & Gregory 2003; O'Conner & Kuyler 2009). Indices based purely on the biotic attributes (e.g. animal populations) have also been useful as they are highly correlated with ecosystem condition (arthropods, Karr & Kimberling 2003; birds, Bryce 2006).

Substantial developments have also been made over the past two decades in methodologies to assess the health and condition of semi-arid and arid environments ('rangelands', e.g. Pyke *et al.* 2002; Herrick *et al.* 2005; Watson *et al.* 2007). While rangeland 'health' (or condition) has traditionally been viewed in the context of pastoralism, that is, healthier landscapes produce more plant biomass for livestock grazing (Wilson *et al.* 1984), there has been increased acceptance that functional integrity is a more appropriate way to view the health of rangelands. Functional integrity has been defined in many ways, but broadly it is the ability of landscapes to capture, retain and use critical resources such as water and nutrients (Ludwig *et al.* 2004). This concept is also closely tied to the ability of landscapes to resist stress (stability or resistance; Holling 1986) or recover from stress (resilience, *sensu* Mageau *et al.* 1995), both of which are related to resource retention and production.

An increasingly popular field-based monitoring procedure that is used to assess the functional integrity of rangeland ecosystems worldwide is landscape function analysis (LFA; Ludwig *et al.* 2004). Landscape function analysis has been widely adopted in a range of environments including Australasia (Ludwig & Tongway 1993; Watson *et al.* 2007), the Iberian Peninsula (Maestre & Cortina 2004) and the Middle East (e.g. Ata Rezaei *et al.* 2006). The procedure comprises a suite of measurements that quantify the spatial arrangement and characteristics of resource patches in the landscape. These patches (fertile islands, *sensu* Garner & Steinberger 1989) comprise grass tussocks, logs, shrub and tree hummocks that are known to capture resources such as seed, water, nutrients and organic matter, and are sites of maximum resource retention, productivity and biotic diversity. Their characteristics therefore reflect the functional integrity, or more broadly, the health of a site.

The increasingly widespread adoption of ecosystem health monitoring has stimulated research on the relationships between health and biodiversity, as well as the development of indicators and surrogates. While a positive relationship between ecosystem health and biodiversity is theoretically possible, it has not been confirmed nor quantified widely. The LFA methodology was never intended as an index of the biodiversity value of landscapes. Although only limited research to date has identified reasonable relationships between LFA and indicators of biodiversity (e.g. Ludwig *et al.* 1999, 2004), the procedure is used often by a range of agencies to monitor the functional integrity of the

landscape and give a broad indication of potential biodiversity value, particularly in Australia (e.g. <http://www.lmd.cma.nsw.gov.au/>). Similarly, despite the fact that structure–composition–function (SCF) indices are highly regarded as potential biodiversity surrogates (Oliver *et al.* 2007), their relationship to biodiversity has not been validated in rangeland systems, nor has the use of a TIEI. Indeed, a predictable empirical relationship between the two components (health and biodiversity) needs to be established prior to the widespread development or use of a surrogate or indicator (Smyth *et al.* 2009).

Here we describe a study that examines the relationships between arthropod community structure and two sets of landscape health indicators using data from a semi-arid eastern Australian woodland. We used two sets of landscape health indices: LFA and a TIEI based on common structure, composition and function metrics. We investigated arthropods because they are the dominant group of invertebrates in terrestrial ecosystems, are relatively abundant and species-rich in semi-arid environments, and are recognized as useful in monitoring biological systems (Kremen 1992; Andersen *et al.* 2004). Our research described here does not seek to operationalize these indices as surrogates or indicators of biodiversity, but rather is broadly aimed at improving our understanding of the relationships between landscape health and ground-active arthropod assemblages in rangeland systems. To achieve this aim we ask two specific questions: (i) how much variation in richness and composition of arthropod assemblages can be accounted for by indices of landscape health; and (ii) are single habitat attributes able to account for greater variation in arthropod richness and composition than landscape health multimetrics? Overall, our study aims to improve the management of semi-arid rangelands by providing quantitative insights into patterns of arthropod biodiversity and how they relate to landscape health.

METHODS

Study area

Data used in this study were collected from the north-west flood plains of New South Wales within the Darling Riverine Plains ecoregion (Thackway & Creswell 1995), across an area spanning approximately 2500 km². The climate is semi-arid; rainfall is summer-dominant and averages 475 mm per year. Average temperatures are 20–35°C in January and 4–17°C in July. All sampling was conducted in February 2001.

The geology of the area is predominantly Quaternary alluvium comprising major and minor functional and non-functional plains and low-lying drainage depressions. Low dunes and coarse-textured elevated rises with relief to 5 m

are superimposed on the plains. The dominant soils on the plains are coarsely cracking grey and brown clays (Grey and Brown Vertisols, Isbell 1996). The low rises and dunes are dominated by hard-setting, red and brown duplex loams with coarse-textured topsoils that grade to finer texture at depth (Red and Brown Kandosols, Isbell 1996). Native vegetation on the plains is dominated by an overstorey of coolibah (*Eucalyptus coolibah*), black box (*Eucalyptus largiflorens*) and myall (*Acacia pendula*), grading to bumble box (*Eucalyptus populnea*) and white cypress pine (*Callitris glaucophylla*) on the low rises and dunes. Large areas of native grassland, both natural and derived, are also a feature of the landscape.

Data were generated within 43 woodland remnant patches varying in size, shape, isolation and surrounding land use, representing the diversity of remnant types that exist in the area. Thirty-four remnants were on private land and were grazed frequently by domestic stock, and nine were on travelling stock routes and grazed less frequently. The bumble box community was selected for the study because it provided a range of sites of varying condition at the landscape level (i.e. severely degraded patches represented by a few trees, to large expanses of intact native vegetation). Bumble box is the dominant tree species over large areas of eastern Australia, and the community has been extensively modified in the past by overgrazing, fire, clearing, weed proliferation and invasion of exotic plant and animal pests. Today it continues to be threatened by clearing and overgrazing.

Within each remnant, a 50-m fixed transect formed the basis for all arthropod and landscape health sampling, and was located in an area considered representative of the remnant. Transects were placed centrally within small (<10 ha) remnants or at least 100 m from the remnant edge. Transects were orientated from highest to lowest elevation along the maximum slope (generally <1%), consistent with LFA methodology (Tongway 1995).

Landscape health assessment 1: landscape function analysis

Landscape function analysis categorizes two ecosystem components: (i) landscape organization; and (ii) soil surface condition (Tongway 1995) at relatively fine (<10⁴ m² scales). These two components reflect the ability of the landscape to capture and retain resources (i.e. the functional integrity). We acknowledge that 'health' is a highly value-laden and context-dependent concept (Wilson *et al.* 1984; Tongway & Ludwig 1997). We use the term 'health' as a synonym for the functional integrity of the site; thus, the higher the score for the LFA indices, the greater the health of the landscape. These assessments were made at each site as follows:

Landscape organization

Along the 50-m transect, we recorded the number of persistent elements on the soil surface such as perennial grass butts, shrub and tree hummocks and logs that intersected the transect. These elements trap resources (water, soil) moved by overland flow (water movement across the landscapes), and are critical for moderating the effect of run-off water on

plant growth and soil stability. They are therefore critical for the long-term functioning of arid and semi-arid systems (Ludwig *et al.* 2005). Landscape function analysis involves the measurement of three site-level attributes: (i) the number of obstructions to overland flow per unit length of on-ground transect; (ii) the average width of these obstructions along the transect; and (iii) the average distance between obstructions (fetch). Together these measurements characterize the functional integrity of a site (*sensu* Ludwig & Tongway 2000).

Soil surface condition

Within each site we assessed the morphology of the soil surface (soil surface condition) within 10 0.5-m² quadrats. This involved the assessment of 13 surface features (Appendix S1). These measurements were used to derive three indices of soil surface condition: (i) stability, a measure of how the soil withstands erosive forces or reforms after erosion; (ii) infiltration, which indicates the extent to which rainfall infiltrates into the soil; and (iii) nutrients, which provides a measure of how efficiently organic material is recycled in the soil (Tongway 1995).

Landscape health assessment 2: terrestrial index of ecological integrity

In a 20 × 50 m plot bisected by the 50-m transect, we also derived indices of health, which reflected aspects of landscape structure, composition and function (*sensu* Noss 1990). These indices were derived from individual site-level measurements, which were combined into a single TIEI (Andreasen *et al.* 2001). Structure was based on the cover of trees, shrubs, perennial and annual grasses, forbs, bare ground, cryptogams, litter, logs, as well as the number of patches (measured with LFA). Composition was based on tree, shrub and ground-storey plant richness, percentage of plants that were perennial and native, and the degree of woody plant regeneration. Function was based on attributes that provide insights into how a site maintains key ecosystem processes such as the degree of mistletoe infestation, canopy dieback, extent of tree hollows, the extent of erosion and the cover of perennial grass butts, soil organic matter and soil texture. These 24 different attributes are recognized as important elements of biodiversity assessment (Oliver 2002; Gibbons & Freudenberger 2006).

For each site, each of the 24 attributes was measured and assigned a particular score depending on its perceived effect upon structure, composition or function, with a higher score equating with a healthier landscape. Thus, for example, the range of tree cover values encountered in the bumble box community (range: 0 to 49%) was divided into five classes and scored accordingly: 1 = 0–2%, 2 = 2.1–5%, 3 = 5.1–10%, 4 = 10.1–25% and 5 = >25%. The values of each attribute were placed into classes rather than being treated as nominal values. The use of classes is both valid and standard procedure when creating indices of biotic integrity or for the TIEI (Andreasen *et al.* 2001; Gibbons & Freudenberger 2006). At the level of the site, the scores for each attribute were then summed. For example, for composition,

we summed up the values received for tree, shrub and ground-storey plant richness, percentage of perennial and native plants and woody regeneration. This total value was then divided by the maximum possible score for that index to give the final index score for the site (*sensu* Karr 1991). Overall, therefore, we had nine indices associated with two sets of landscape health measures: (i) LFA (six indices); and (ii) SCF (three indices).

Arthropod sampling

All arthropods were sampled by using pitfall traps (250-mL polycarbonate screw cap containers 100 mm high, 67 mm in diameter). Ten traps were located in a two by five grid pattern (traps 10 m apart) centred along the 50-m transect. Traps were buried with the lip of the container flush with the ground surface and contained 125 mL of monoethylene glycol to kill and preserve the specimens. All traps were active for 11 days. Upon removal, containers were capped and transported to the laboratory, where the monoethylene glycol was decanted off (using a 0.5-mm sieve) and replaced with 70% ethanol. Specimens were sorted under a dissecting microscope to major groups by biodiversity technicians. All ants, beetles and spiders recovered from the traps were further identified to species or morphospecies by specialists at the Australian Museum.

Statistical analyses

LFA and SCF indices and variation in arthropod abundance, species richness and diversity

We used both univariate and multivariate analyses to examine trends in the arthropod community metrics in relation to LFA and SCF. Species richness was calculated as the total number of ant, beetle and spider morphospecies recorded from each survey site. For a diversity measure, we used a bias-controlled effective number of species (Jost 2006), which has been shown to be one of the least biased diversity estimates (Beck & Schwanghart 2009). Bias-controlled effective number of species (hereafter 'diversity') was calculated by using the program SPADE (Chao & Shen 2003). We used hierarchical partitioning (HP) (Chevan & Sutherland 1991) to determine the independent and joint capacity of each landscape health variable (or habitat attribute) to explain variation in arthropod abundance, richness or diversity. This technique gives a measure of how much variation can be attributed solely to that of a variable, compared with that which is due to the presence of other variables in the model (Mac Nally 2002).

We also used HP to determine the independent capacity of four specifically selected LFA variables to explain variation in arthropod abundance, richness and diversity when an additional eight habitat attributes were included in the analyses. For LFA, variables that showed moderate to strong statistically significant co-correlations ($\alpha > 0.5$, $P < 0.001$) were removed from these analyses (two variables). In doing so we retained the maximum amount of variables in the model while minimizing the amount of shared variation that could

be explained by multiple variables. Thus, the four LFA variables selected for these analyses were the number of obstructions, width of obstructions, stability and infiltration. Habitat attributes were raw values that are also used to construct structure, composition and function (above), and represent an alternate method to a multimetric. The habitat attributes selected were cover of forbs and herbs (%), tree canopy cover (%), litter cover (%), soil organic matter (%), proportion of plants as perennials, cover of low shrubs (%), cover of annual grasses (%) and the proportion of plant species as perennials. These were selected following correlation analysis that included LFA variables, with highly correlated variables (>0.7) excluded from analyses. For HP analyses, some non-normal variables were appropriately transformed prior to analyses (log, or square root). We evaluated models based on the R^2 goodness of fit statistic, and the statistical significance of independent effects was calculated by using a randomization test with 1000 iterations (Mac Nally 2002). All HP analyses were conducted by using the hier.part package (Walsh & Mac Nally 2003) within the R statistical program (R Development Core Team 2010).

Relationships between LFA and SCF and species composition

Multivariate methods were used to analyse relationships between the species assemblage structure of ants, beetles and spiders, and LFA, SCF, or a combined LFA/habitat attributes variable set. All multivariate analyses were conducted in PRIMER v6 (Clarke & Gorley 2006). Biotic matrices were created by using Bray-Curtis similarity index on $\log(x + 1)$ transformed data. Environmental variable matrices were created by using a Euclidean distance similarity index based on $\log(x + 1)$ data, with all variables normalized (Clarke & Gorley 2006).

Several tests were used to examine the relationship between LFA, SCF and habitat attributes and arthropod species assemblages. RELATE, a multivariate equivalent of a Mantel test was used to examine the correlation between matrices based on LFA or SCF and arthropod species assemblages (Clarke & Gorley 2006). Further, the BEST (specifically BIO-ENV) analysis was used to identify a subset of factors (LFA or SCF indices and/or habitat attributes), which are the 'optimal' match to a second resemblance matrix (i.e. a species matrix), based on the strength of a Spearman rank correlation coefficient. A global permutation test (9999 permutations) was used to assess the statistical significance of the obtained correlations.

RESULTS

We sampled a total of 60 765 arthropods from 457 species across three arthropod groups (Table 1). Ants were the most abundant (96% of all specimens). Stability was the most variable LFA index, while for structure–composition–function the most variable was composition, although all indices showed substantial variation (Table 2).

Table 1. Total abundance and total, median and range of species and higher taxon (Family) richness by site for arthropod groups

Arthropod group	Species richness			Higher taxon richness			Abundance
	Total	Median	Range	Total	Median	Range	
Ants [†]	119	29	13–39	38	16	9–21	57 880
Beetles	173	12	4–27	26	7.5	4–15	1 180
Spiders	165	17	9–29	24	10	6–13	1 705
Total	457			40 [‡]			60 765

[†]Genera-level richness. [‡]Excluding ants.

Table 2. Descriptive statistics of all health variables used

Variable	Mean	Median	Range	SD
Stability (%)	60.6	61.1	43.8–80.1	6.7
Infiltration (%)	30.1	28.6	20.7–48.9	5.9
Nutrients (%)	24.0	24.1	17.0–39.1	4.4
Obstructions per 10 m	7.1	7.3	0.33–15.4	3.5
Obstruction width (m)	2.6	1.7	0.04–7.5	2.1
Fetch length (m)	1.8	1.1	0.55–15.0	2.1
Structure (%)	56.6	55.6	44.4–66.7	5.3
Composition (%)	74.4	75.0	58.3–91.7	8.4
Function (%)	58.4	56.7	46.7–76.7	6.9

LFA, SCF and arthropod abundance, richness and diversity

Hierarchical partitioning indicated that the independent ability of LFA indices to account for variation in the arthropod community varied with both arthropod taxon (ants, beetles, spiders) and diversity measure (abundance, richness, effective number of species) (Fig. 1). In only one case was a single variable (infiltration in relation to effective number of spider species) able to independently explain more than 10% of variation in the arthropod community. Despite this, several variables were statistically significant, varying among taxa. Infiltration was statistically associated with increases in abundance and diversity of spiders (Fig. 1). The number of obstructions was significant associated with increases in ant abundance, but decreases in ant diversity. Additionally, nutrients and stability were associated significantly with ant abundance.

Hierarchical partitioning analyses for the three SCF indices were similar, although the index that independently explained the greatest amount of variation was generally consistent within a taxonomic group (Fig. 2). For ants, structure had the greatest independent explanatory power for abundance, richness and effective number of species. Structure also independently accounted for the most variation in spider

richness and effective number of species, while composition was most important for spider abundance. The total amount of variation explained by the three SCF indices was low for all taxa (generally less than 10% for all measures), with the highest amount of variation explained being 13.7% for the effective number of spider species and 12.3% for ant abundance (Fig. 2). In only one case was a variable statistically significant in explaining variation in the model (structure and ant abundance).

LFA, SCF and arthropod species assemblages

Our BIO-ENV analyses confirmed that LFA and SCF were generally weak in explaining patterns of the arthropod assemblage composition (Table 3). Subsets of LFA indices selected were not statistically significant, with the exception of a relationship with spiders ($\rho = 0.275$, $P < 0.01$; Table 3). Variables commonly included in LFA subsets were stability (four cases) and obstruction width (three cases). Weak but statistically significant relationships ($P < 0.05$) were evident between subsets of SCF and ant functional groups ($\rho = 0.226$), beetles ($\rho = 0.178$) and spiders ($\rho = 0.191$) (Table 3).

LFA, SCF, habitat variables and arthropod abundance, richness and diversity

The HP analyses that included LFA indices together with eight habitat variables revealed that habitat variables were as important as LFA indices for independently explaining variation in arthropod abundance, richness and diversity (Fig. 3). However, no variable consistently explained substantial variation across arthropod taxa, and no single variable was statistically significant in more than two (of a possible nine) cases. No variable independently explained more than 10% of the variation in arthropod richness, abundance or diversity. A substantial amount of the variation explained by habitat attributes was related to the joint

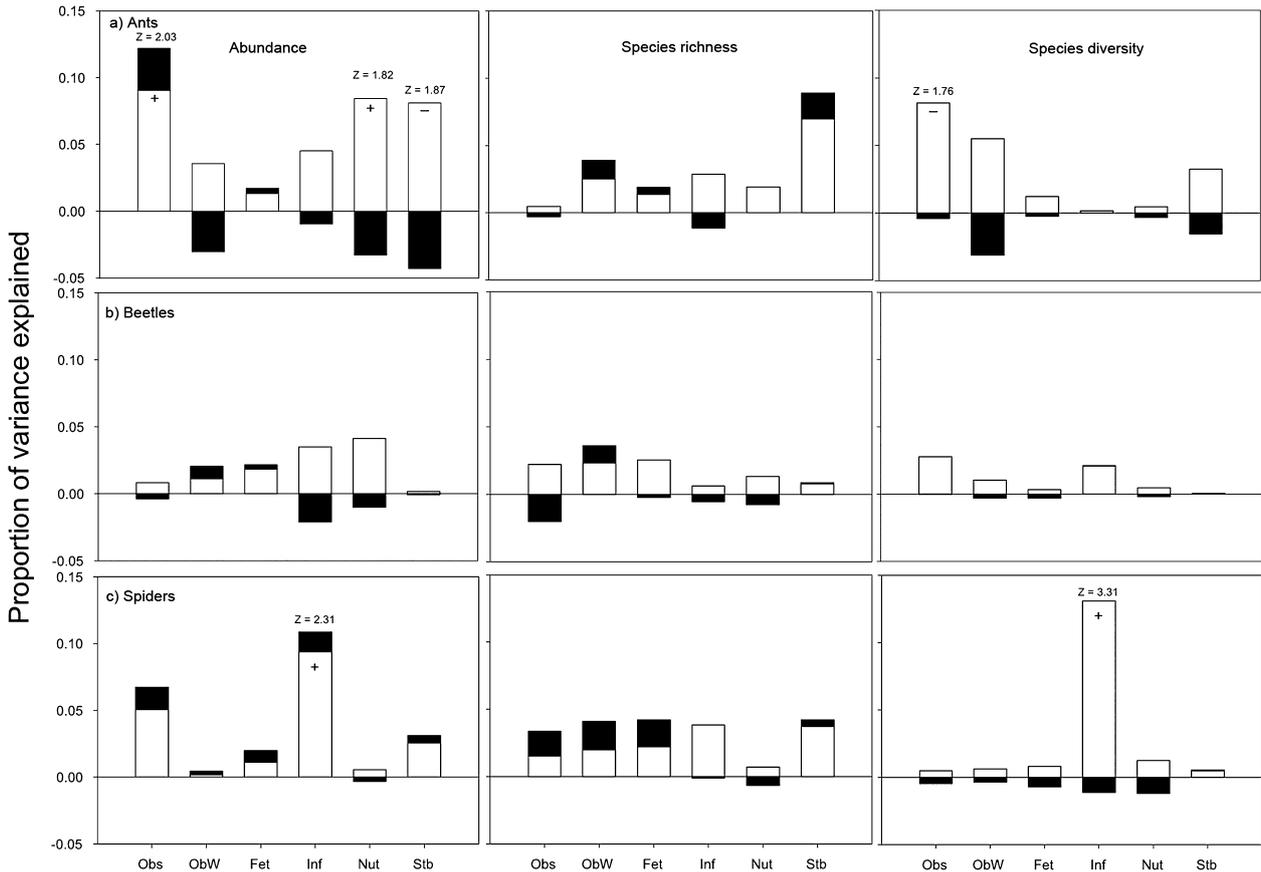


Fig. 1. Proportion of variance explained by independent (white) and joint (black) components of six landscape function analysis indices on (a) ants, (b) beetles and (c) spiders as determined by hierarchical partitioning. Z-score indicates significant effect as determined by randomization tests ($P < 0.05$). Positive or negative relationships are shown by + or - symbols, respectively. Variables: Fet, mean fetch length; Inf, infiltration; Nut, nutrients; Obs, mean number of obstructions; ObW, mean width of obstructions; Stb, stability. Negative joint effects indicate that variable is acting as a suppressor of other variables.

effects of variables (Fig. 3). Furthermore, the independent contributions of habitat variables were often offset by negative joint contributions. The total amount of variation explained by all variables together varied little (approx. 19% and 29%), the exception being for the number of spiders (40%) and the species richness of beetles (8%).

LFA, SCF, habitat variables and arthropod species assemblages

Four-variable BIO-ENV subsets, which included both habitat variables and LFA indices, explained more variation in biotic assemblages than subsets that only included LFA or SCF (Table 4). In the case of ants and beetles, a single habitat variable (tree canopy cover) had a stronger correlation than analyses using LFA variables. For every taxon, with the exception of ant functional groups, tree canopy cover was the single most important variable, and

was included in every pair of variables and subset of four strongest variables (Table 4). Tree canopy cover and stability were selected as the best pair of variables for ants and spiders. For beetles, tree canopy cover and the cover of forbs and herbs were the best pair of variables. For ant functional groups, litter cover was the single most important variable, and with stability, formed the strongest pair. The strongest four-variable subset generally included the strongest pair of variables, but resulted in slight increases in explanatory power with the exception of beetles (Table 4).

DISCUSSION

Recognition of the unprecedented loss of biodiversity because of anthropogenic disturbances has spurred the development and use of surrogates and indicators for biodiversity monitoring (e.g. Churchill 1998; Andersen & Majer 2004). Currently there is a strong

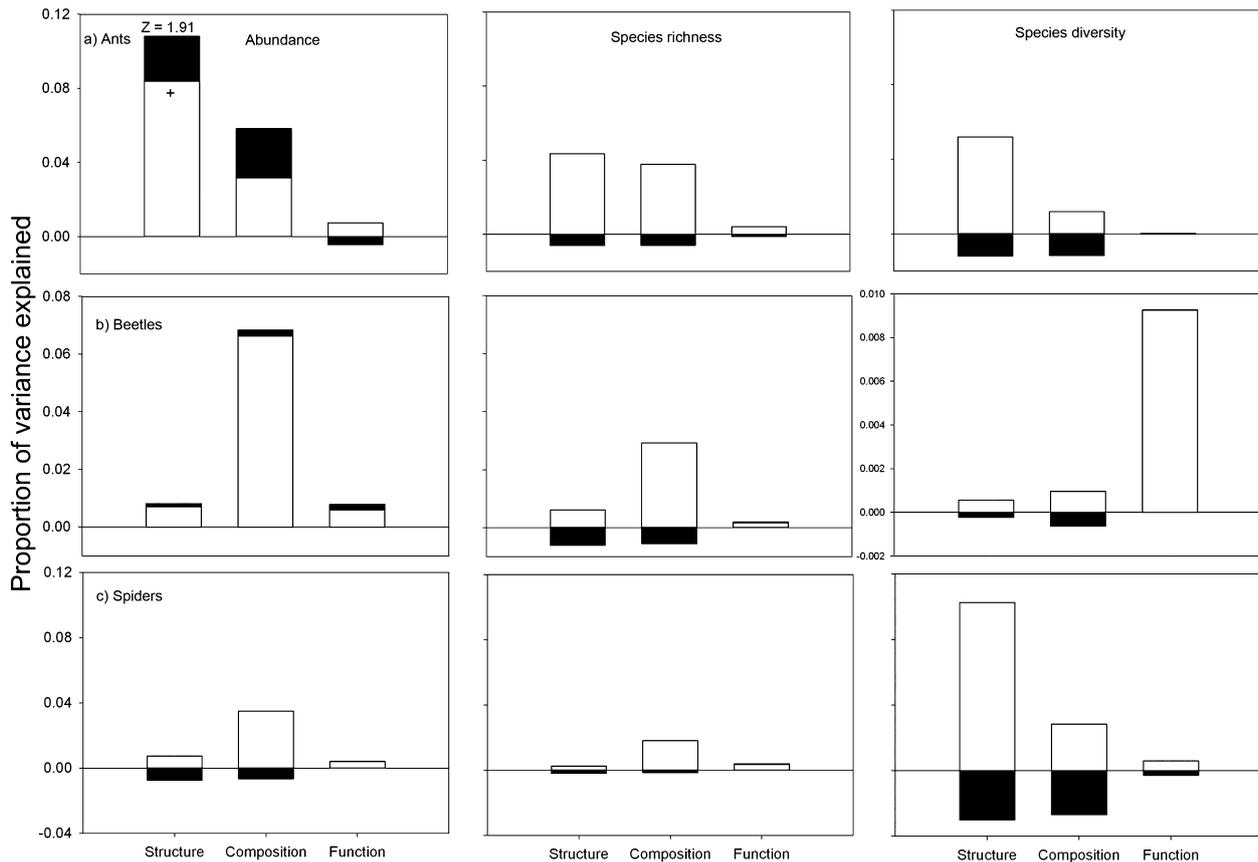


Fig. 2. Proportion of variance explained by independent (white) and joint (black) components of three terrestrial index of ecological integrity (structure–composition–function) indices on (a) ants, (b) beetles and (c) spiders as determined by hierarchical partitioning. Symbols are as in Figure 1.

Table 3. Spearman's rank correlations (ρ) for tests of assemblage similarity between arthropod taxa and LFA or SCF (RELATE), and for subsets of LFA or SCF, which show the strongest relationship to the arthropod taxa (BIO-ENV)

Taxa	BIO-ENV (ρ)	LFA subset	BIO-ENV (ρ)	SCF subset
All taxa	0.180	Obs, ObW, Stb	0.133	All
Ants	0.103	Stb, Ntr	0.12	Str, F
Ants [†]	0.233	ObW, Stb, Ntr	0.226*	All
Beetles	0.079	Fet	0.178*	C, F
Spiders	0.275*	ObW, Stb	0.191*	Str, C

*Statistically significant at $P < 0.05$. [†]Functional groups only. Indices: LFA: Fet, mean fetch length; Inf, infiltration; Ntr, nutrients; Obs, mean number of obstructions; ObW, mean width of obstructions; Stb, stability; and SCF: C, composition; F, function; Str, structure. LFA, landscape function analysis; SCF, structure–composition–function.

emphasis on indicators and surrogates of biotic diversity for regional environmental management (e.g. Munoz-Erickson *et al.* 2007; Smyth *et al.* 2009). For many taxa, however, including ants (Whitford *et al.* 1998; Andersen *et al.* 2004), beetles (Pearce & Venier 2006) and spiders (Pearce & Venier 2006), their reliability as indicators of biotic integrity in relation to rangeland and forestry management has been called into question. Our study shows that there may not be

a predictable and unequivocal relationship between a potential surrogate and biodiversity, despite the fact that the relationship is theoretically sound and supported empirically by earlier research (Ludwig *et al.* 1999, 2004). Such results reinforce our view that surrogates should not be used widely without a clear knowledge of how environmental and ecological factors drive patterns of biodiversity in a given ecosystem.

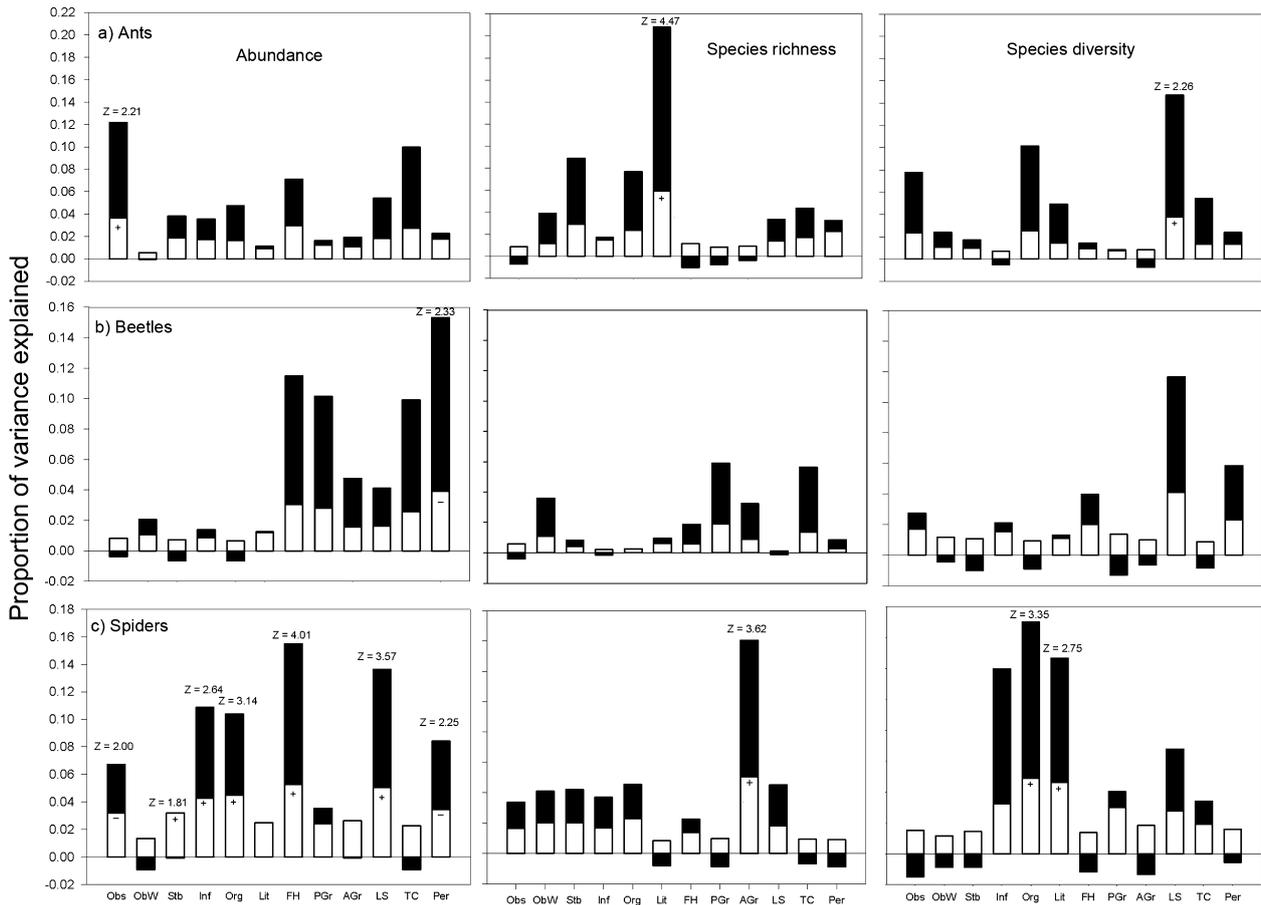


Fig. 3. Proportion of variance explained by independent (white) and joint (black) components of four landscape function analysis indices and seven habitat attributes on (a) ants, (b) beetles and (c) spiders as determined by hierarchical partitioning. All symbols and abbreviations for landscape function analysis are as in Figure 1. Habitat attribute variables: AGr, cover of annual grasses; FH, cover of forbs and herbs; Lit, litter cover; LS, cover of low shrubs; Org, soil organic matter; Per, proportion of plant species that are perennial; PGr, Cover of perennial grasses; TC, cover of tree canopy.

Arthropod biodiversity in relation to LFA and SCF

Few studies have explicitly examined potential relationships between landscape health and biodiversity using LFA. Ludwig *et al.* (1999) showed that with increasing distances from a watering point there were increases in the density and size of perennial vegetation patches (obstructions), as well as plant and grasshopper diversity. Ludwig *et al.* (2004) also showed how changes in plant diversity, plant production and the activity of medium-sized mammals varied in relation to the functional integrity of sites at scales ranging from that of individual plants to whole catchments. Similarly, Dawes-Gromadzki (2005) demonstrated a positive relationship between landscape condition (assessed as the number of permanent plant patches) and the abundance of macro-arthropods, although her study did not use LFA explicitly. The results of our study are therefore somewhat at odds with previous

research that has used LFA, and highlights the inherent variability in relationships between invertebrate communities and measures of landscape function. While there appears to be strong congruence between the LFA attributes and patterns of biotic diversity under some circumstances, we currently do not know why these relationships are so inconsistent. This lack of understanding likely stems from inadequate knowledge of the life history of invertebrate taxa (Redak 2000) and of relationships among invertebrates, soil type, disturbance history and resource retention (Ludwig *et al.* 2004). Indeed, despite the utility of LFA in rangeland monitoring (e.g. Watson *et al.* 2007) and its potential promise as a biodiversity indicator, key questions remain regarding the exact nature of this relationship (Ludwig *et al.* 2004). These questions concern the relationships between resource availability and distribution and species persistence, in particular the spatial and temporal conditions under which resources (e.g. patch obstructions) become important

Table 4. BIO-ENV results using habitat variables and LFA indices

Rank	Taxon	ρ
Ants		
Single variables analysed		
1	Tree cover (%)	0.184**
2	Number of obstructions per 10 m	0.086
3	Stability	0.08
4	Perennial grass cover (%)	0.066
5	Litter cover (%)	0.05
Variables analysed in pairs		
1	Tree cover (%) + stability	0.216**
Four variables analysed		
1	Tree cover (%) + cover of perennial grasses (%) + number of obstructions per 10 m + stability	0.244**
Ant functional groups		
Single variables analysed		
1	Litter cover (%)	0.145*
2	Tree cover (%)	0.101
3	Number of obstructions per 10 m	0.084
4	Stability	0.068
5	Obstruction width	0.052
Variables analysed in pairs		
1	Litter cover (%) + stability	0.192*
Four variables analysed		
1	Tree cover (%) + litter cover (%) + number of obstructions per 10 m + stability	0.259**
Beetles		
Single variables analysed		
1	Tree cover (%)	0.198*
2	Proportion of plants as perennials	0.11
3	Cover of forbs and herbs (%)	0.089
4	Cover of annual grasses (%)	0.043
5	Litter cover (%)	0.04
Variables analysed in pairs		
1	Tree cover (%) + forbs/herb cover (%)	0.21**
Four variables analysed		
1	Tree cover (%) + forb/herb cover (%) + proportion of plants as perennials + annual grass cover (%)	0.199**
Spiders		
Single variables analysed		
1	Tree cover (%)	0.219**
2	Width of obstructions	0.192**
3	Proportion of plants as perennials	0.154**
4	Stability	0.149*
5	Soil organic matter (%)	0.132*
Variables analysed in pairs		
1	Tree cover (%) + stability	0.301**
Four variables analysed		
1	Tree cover (%) + soil organic matter (%) + obstruction width + stability	0.379**

* $P < 0.05$; ** $P < 0.001$. LFA, landscape function analysis.

for the fauna, and how and when this is modified by disturbance such as fire and grazing (Ludwig *et al.* 2004).

Globally there is a wealth of research linking landscape condition (using indices of integrity) to biodiversity values (e.g. Karr & Kimberling 2003; Bryce 2006; Diffendorfer *et al.* 2007). Although indices of ecological integrity are regarded as potential surrogates for biodiversity in forest and woodland systems (e.g. SCF, Oliver *et al.* 2007), such relationships have not been validated in Australia (Fisher & Kutt 2007).

We found very few strong links between SCF and arthropod biodiversity, with these variables unable to explain significant variation in arthropod abundance, richness or diversity. All elements of SCF were however related to the community structure of at least one taxon (ants, beetles or spiders). It is important to note, however, that SCF explained less variation in community structure than many simpler habitat attributes. Contemporary biodiversity management is focused on species assemblages and the structure of biotic communities, rather than richness or diversity

per se (Jennings *et al.* 2008). For this reason we would consider SCF to be of only limited use in biodiversity monitoring, as stronger, more reliable predictors are available for predicting arthropod diversity and community structure.

The use of multimetrics has been criticized as they do not always accurately reflect variation in their individual components (Suter 1993; Andreasen *et al.* 2001). Of specific concern is the loss of information because of the reduction of multiple measurements into a smaller number of indices (e.g. raw habitat attributes into SCF). Here, a low value from one variable can be 'compensated' by increases in several of the other variables (Suter 1993; McCarthy *et al.* 2004), and the exact reason for a given multimetric value is not known. In our case, the final multimetrics of SCF may not capture sufficient variation in fine-scale factors, which may be important for arthropods. This could contribute to the apparent poor relationships between the predictor variable and the measure of diversity. There are several ways to alleviate this problem, including a multiplicative approach (whereby compensation between variables is not linear; McCarthy *et al.* 2004) and the use of 'raw' values (Andreasen *et al.* 2001). In our study, using raw values ('habitat attributes') did reveal a few notably important factors, but this was completely taxon-dependent.

Arthropod biodiversity in relation to additional habitat attributes and LFA

We also investigated whether individual habitat attributes were more closely aligned with arthropod diversity than composite (multiple) metrics. We identified several habitat attributes that were as important as LFA indices in explaining variation in arthropod abundance and richness, and these were primarily measures of vegetative cover (e.g. forb, litter and shrub cover). Tree canopy cover was the variable most strongly related to arthropod assemblage structure, and was important for all taxa (Table 4). Thus, while tree cover is not necessarily a strong predictor of arthropod abundance or diversity, it may be a useful predictor of arthropod community structure. Overall, however, attributes generally had a low explanatory power, indicating few strong, independent relationships between biodiversity and condition. These results are similar to those reported both for LFA and SCF.

Structure and composition of vegetation are considered reliable indicators of animal species diversity (e.g. habitat heterogeneity, see review by Tews *et al.* 2004). Hence, measurement and monitoring of these attributes are an integral part of research (Hughes

et al. 2000; Stoner & Joern 2004; Ferrier & Guisan 2006). They are also widely used by conservation managers (e.g. <http://www.environment.nsw.gov.au>), particularly to assess vegetation condition and habitat quality for vertebrates. However, there remains a paucity of data relating habitat attributes to arthropod diversity (Tews *et al.* 2004). Our results support previous research showing that, though somewhat inconsistent, measures of vegetative cover and structure are related strongly to arthropod diversity (e.g. Gardner *et al.* 1995; Debuse *et al.* 2007; Sanders *et al.* 2008). In particular, other studies have also recognized the importance of trees in structuring arthropod communities (Lassau & Hochuli 2004; Lassau *et al.* 2005; Oliver *et al.* 2006; Barton *et al.* 2009; Gollan *et al.* 2009). Although responses were taxon-specific, it still may be possible to predict broad community structure based on tree cover, particularly within a single vegetation community, and/or where there is little extrinsic environmental variation. However, where a large gradient in environmental variation exists across the study area (e.g. in temperature, soil type, rainfall), changes to plant cover and even species composition may simply be a reflection of these underlying gradients (e.g. Thompson & Eldridge 2005; Tziella *et al.* 2006). In these cases a more effective method would be to use the factor that is driving tree cover as a direct surrogate.

Many authors have stressed the importance of soil characteristics such as soil hardness (Bestelmeyer & Wiens 2001; Gollan *et al.* 2009), soil erodibility (Schell & Lockwood 1997) and soil organic matter content (Lavelle *et al.* 2006) as drivers of arthropod community structure. In our study, soil stability was an important predictor in analyses of arthropod assemblage structure, though mainly in combination with tree cover. Soil organic matter was also important for spiders. Given that the drivers of community structure varied widely across taxa, any study investigating patterns of arthropod distribution in relation to environmental factors should encompass a wide variety of soil and vegetation attributes. Many of the potential drivers identified in this study are part of broad environmental monitoring programmes (McCarthy *et al.* 2004; Gibbons & Freudenberger 2006).

Arthropod communities are structured by fine- and broad-scale environmental variation

Effective indicators must be ecologically relevant at a scale appropriate to the target taxa, either directly or indirectly (Zurlini & Girardin 2008). Arthropod activity can be influenced by environmental variation occurring over fine (centimetre) to broad (kilometre) scales (e.g. beetles, McIntyre 1997; Barton *et al.* 2009; insects in general, Major *et al.* 2003; Lassau & Hochuli

2004). While individual components of LFA such as the number of resource patches are ecologically relevant to fauna and flora across multiple spatial scales (Ludwig *et al.* 2004), LFA typically reflects ecosystem function at the patch–hillslope to catchment scales (e.g. hundreds to thousands of metres). Thus, LFA is expected to be more closely aligned with the diversity of a variety of animals (Ludwig *et al.* 2004) as well as cryptogamic crusts and vascular plants (David Tongway, pers. comm., 2010). However, while arthropods may be responding to variation in landscape function at the patch–hillslope scale, it is possible that finer-scale environmental variation, not directly captured by LFA, plays a greater role in structuring these communities. This is analogous to within-patch characteristics such as vegetation structure being more important in structuring faunal communities than broader, landscape context characteristics such as patch size or connectivity (e.g. Debuse *et al.* 2007; Poyry *et al.* 2009). There is, therefore, a unique scaling issue when using LFA to predict arthropod communities. Theoretically, either LFA data need to be downscaled to consider variation at the scale of individual arthropod movements (e.g. tens of metres) and/or arthropod data need to be upscaled, such as placing a large array of pitfall traps across entire landscapes, to harmonize these two scales (David Tongway, pers. comm. 2010). Currently we lack a standard and empirically tested method for scaling data within a framework of functional integrity that is appropriate for small animals. Without this, generalizations cannot be made among similar studies.

As arthropods respond to such a wide variety of environmental variables across multiple spatial scales, elucidating broad drivers of community structure has been a significant research challenge. Drivers can be taxon-specific (e.g. litter structure is particularly important for spiders, Bultman & Uetz 1984), but there are broad factors that affect a range of taxa (e.g. habitat heterogeneity, Tews *et al.* 2004; climate, Andrew & Hughes 2005). In general, our research highlights the general lack of alignment of LFA and similar measures with most taxa. Many of the factors that drive arthropod communities are specific measures or surrogates of arthropod habitat or the microclimate associated with that habitat (e.g. fine-scale habitat availability, Mazia *et al.* 2006; Nitterus & Gunnarsson 2006; disturbance history, Hoffmann & Andersen 2003). This was confirmed by our study, with all arthropod communities being structured primarily by tree cover, yet affected to a lesser degree by different factors such as litter cover and the number of obstructions (ants), plant composition (beetles) and obstruction width (spiders). Leaf litter is known to structure spider communities and their prey (Bultman & Uetz 1984). Similarly, the selection of nesting sites by ants is often influenced by soil texture (Bestelmeyer

& Wiens 2001). Landscape function analysis indices, however, are constructed specifically to measure the ability of the landscape to capture abiotic resources, that is, ecosystem function (Ludwig *et al.* 2004). This, together with the scale mismatch described above, suggests that LFA indices do not directly measure the components of ecosystems that exert the strongest influence over arthropods. This is a fundamental part of LFA, which will always limit the applicability of LFA as a surrogate of arthropod biodiversity.

Conclusions

The relationships between broader biodiversity values and landscape health deserve greater attention, particularly in environments where the management or conservation of biodiversity is paramount. While the accuracy of LFA (and individual soil surface condition attributes) is continually being validated (McIntyre *et al.* 2003; Maestre & Puche 2009), its potential use in understanding patterns of biodiversity is not. The situation is similar for any index of ecological integrity based on SCF metrics, given their widespread applicability in vegetation monitoring. We found only weak relationships between arthropod biodiversity and LFA and SCF. This could be due to the way multimetrics are derived, although simple habitat attributes showed similar patterns. As arthropods are potentially influenced by fine- to broad-scale environmental variation (centimetres to kilometres), it is possible that LFA and SCF are not reflecting variation at the scale that is driving these communities. A conceptual framework specifically linking landscape health (and associated indices), arthropods and spatial scale is necessary to provide a standard platform upon which to base empirical predictions and testing.

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SUPPORTING INFORMATION

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

Appendix S1. Soil surface features used to calculate soil surface condition (SSC) indices.