Austral Ecology (2003) **28**, 227–236

Patterns of invertebrate biodiversity across a natural edge

J. MARK DANGERFIELD,* ANTHONY J. PIK, DAVID BRITTON, ANDREW HOLMES,
MICHAEL GILLINGS, IAN OLIVER, DAVID BRISCOE AND ANDREW J. BEATTIE
*Key Centre for Biodiversity and Bioresources, Macquarie University, North Ryde, Sydney,
NSW 2109, Australia (Email: mdangerf@rna.bio.mq.edu.au)*

Abstract Most ecologists are comfortable with the notion of habitats as recognizable entities and also with situations where the junction between two adjacent habitats forms a discrete edge. Such edges form naturally because of sharp changes in important edaphic, geomorphological, climatic or chemical properties to which plants, in particular, respond. Less clear is the effect of such edges on assemblages of mobile organisms, especially invertebrates that operate at relatively small spatial scales. The objective of the present study was to sample invertebrate composition across a natural edge between a well-developed riparian habitat on fluvial sands and a saltbush habitat developed on a stony gibber plain in a semi-arid region of New South Wales, Australia. A total of 150 pitfall traps on five 1-km-long transects that straddled the edge produced more than 13 000 adult specimens from 21 ordinal invertebrate taxa. A total of 10 446 beetle, ant, wasp, fly and springtail specimens were further sorted into 426 morphospecies. Comparisons and estimates of trends in abundance and richness were made, along with computation of multivariate dissimilarity and permutation statistics, to determine if the land system edge was coincident with changes in invertebrate abundance and composition. These analyses were unable to detect disjunctions in diversity coincident with the edge. The data suggest that many taxa are either present consistently in both habitats or are mostly found in one habitat but 'leak' several hundred metres across into the other. Few taxa were unique to either habitat. The result is that assemblage composition for invertebrates changes gradually over distances of up to 400 m either side of the edge and that the distance to a recognizable change in composition is taxon dependent. Even sharp habitat edges, as defined by discrete changes in soils and plants, are not edges but broad transition zones for many invertebrate taxa. There are several implications of these results, especially for landscape ecology.

Key words: Australia, boundary, ecotone, invertebrate assemblage, morphospecies, semi-arid, spatial scale.

INTRODUCTION

No two samples of biological diversity are the same. The composition of biological entities is simply too variable in space to make repetition likely. It is also very difficult to obtain sampling precision because most collection methods have inherent variation and bias in their application or cover only a small proportion of a habitat or an organismal assemblage. Despite this, both empirical and theoretical approaches have emerged to describe and predict patterns of biodiversity (Gaston *et al.* 1995). Some researchers, notably those who study plants and vertebrates, have found that determinants of environmental space are reasonable predictors of the occurrence of particular species (Busby 1991) or structural types (Mackey 1993). In this sense the environment might represent a sufficient template to define the local composition of organisms. Most agree, however, that if assemblages or communities exist then they are, to a greater or lesser extent, brought together and maintained by biological interactions that are either self-reinforcing (Perry 1995) or hierarchical (Allen & Starr 1982). Similarly, a discontinuity in abundance of organisms may not be an inherent property of the landscape, but may emerge only from the interplay of species interactions with landscape structure (With & Cirst 1995). The debate over the legitimacy of these emergent constructs has been long and fraught (Palmer & White 1994) and dominated by empirical examples from plant ecology (Hoagland & Collins 1997).

Another conceptual approach to understanding biodiversity has been to consider ecosystems as a series of patches that vary in size and distribution through the landscape (Farnsworth & Ellison 1996). Organisms respond to this heterogeneity in numerous ways and across many scales (Gosz 1993). Similarly, no two organismal groupings would be expected to respond to a significant environmental disjunction in the same way and therefore discontinuity in species abundance should reflect breaks in the grain of this environmental heterogeneity (Shipley & Keddy 1987; Hoagland & Collins 1997).

Breaks in the physical environment are often obvious. Changes in slope, soil or drainage may produce very distinct vegetation patterns with sharp edges.

---

*Corresponding author.

Accepted for publication August 2002.

These edges (van der Maarel 1990) might be distinguished from the more diffuse zones of vegetation change called ecotones (Clements 1905) and then further defined by Leeuwen (1966), that have been the focus of much discussion (Jenik 1992; Backeus 1993; Gosz 1993) and subsequent study (Rivers-Moore & Samways 1996; Turton & Sexton 1996; Breck & Jenkins 1997). Initially, ecotones became a focus because they should be the edges that define the extent of an assemblage, and then later because it became apparent that ecotones may be relatively species rich and so important for conservation. In some cases ecotones, and the effects of underlying environmental gradients producing ecoclines, have become foci for habitat management. This is especially important because human land use practices, especially clearing of native vegetation, tends to increase the proportion of both edges and ecotones in landscapes.

In most cases the extent of an ecotone is considered to be only a few hundred metres. Transect studies rarely extend for more than 300 m across a perceived or real boundary (Kapos *et al.* 1993; Bedford & Usher 1994) and it is often assumed that the environmental gradients that characterize ecotones are relatively severe and short. This is a realistic assumption where soil or moisture effects are the most likely determinants of changes in plant composition and physiognomy or in the case of man-made edges such as those around arable fields. It is also realistic when the focal study organisms are plants or larger animals with known preferences for mixed or transitional habitats (Williams-Linera 1990). The situation is less clear for other organisms, particularly the invertebrates and microorganisms that make up 99% of extant diversity (Pimentel *et al.* 1992; Ponder & Lunney 1999). The objective of the present study was to observe the distribution of invertebrate morphospecies across a natural boundary and to establish whether these distributions result in specific assemblage compositions with a detectable boundary between them.

Invertebrates make irreplaceable contributions to ecosystem processes (Miller 1993) and have direct economic value as pollinators (Janzen 1987), soil engineers (Young *et al.* 1998) and suppressors of pest species (Kogan & Lattin 1993). Invertebrates are also used increasingly in conservation evaluation and environmental monitoring and assessment (Holloway & Stork 1991; Kim 1993; Kremen *et al.* 1993; Oliver & Beattie 1993). One reason that invertebrates are useful as indicators of processes is that, among the many invertebrate species in a given locality, there is an equivalent level of mobility to large animals together with a greater capacity for local habitat or resource specialization. Consequently the range of scales at which heterogeneity might affect assemblage patterns is more likely to be represented among the invertebrates than the vertebrate and plant taxa traditionally studied.

In the present study we focus on ground-active arthropods but also include apterous groups, in particular flies and wasps. We overcome the problem of many invertebrate groups being poorly known, the so-called taxonomic impediment (*sensu* Taylor 1983), by using rapid biodiversity assessment techniques that require only partial taxonomy and the use of morphospecies (Oliver & Beattie 1993, 1996; Beattie & Oliver 1994). We also overcome the time constraints involved with processing the many specimens encountered in samples of invertebrates with the use of information technology solutions including the relational database 'Biota' (Colwell 1996), bar-codes and digital images (Oliver *et al.* 2000) integrated into a system called BioTrack.

We chose to look for patterns in invertebrate biodiversity across a natural edge in an arid system in central Australia. We studied a discrete junction between a stony gibber plain of Cretaceous origin and more recent fluvial sediments. This edge is so discrete as to be observable as a line on the ground. On the one side a treeless gibber plain supports saltbush, bluebush and tussock grasses, while on the other side a braided

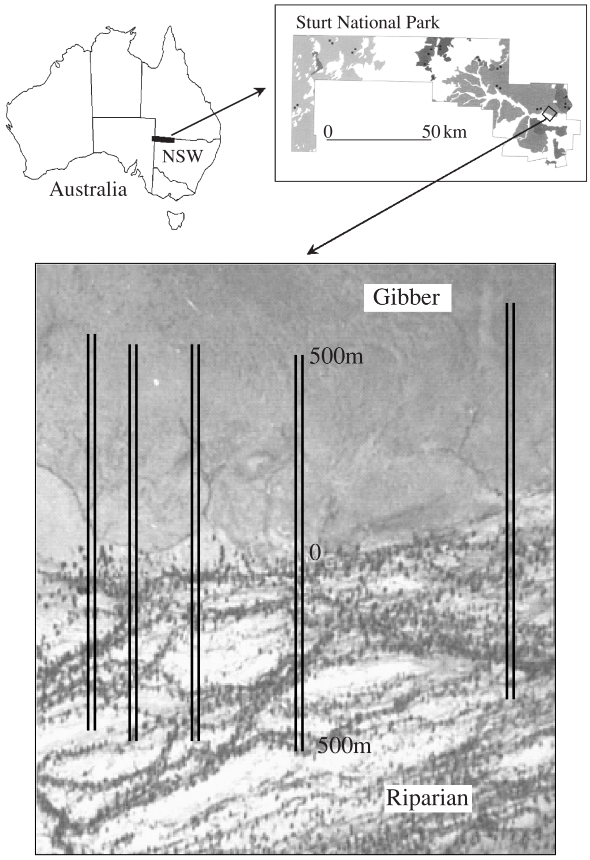

Fig. 1. Location of the study area and aerial photograph to show positions of the paired transects across the natural edge between the riparian habitat and gibber plain habitats, Sturt National Park, New South Wales, Australia.

but ephemeral water course is lined with mature canopy trees and supports a grass-dominated ground layer. Pitfall traps were used to sample invertebrates across this obvious environmental discontinuity for plants. Data generated at a range of taxonomic resolutions enabled us to test the hypothesis that invertebrates show patterns in diversity, abundance and composition that coincide with this soil-mediated boundary. In effect we wanted to establish if the invertebrates responded to an edge or if there was a genuine ecotone and at what scale this effect was apparent.

METHODS

Study area

Sturt National Park in semi-arid north-western New South Wales (NSW), Australia, provided a study area with a known land use history and relatively simple geomorphology. Situated some 1000 km north-west of Sydney, the park occupies approximately 3500 km^2 of mostly rolling downs and sand plain country (Fig. 1). The region is described as warm, arid and characterized by low and unreliable rainfall with an annual average of 227 mm, although the high density of watercourses indicates a wetter climate in the last few thousand years (Milthorpe 1991). Daytime temperatures in summer normally exceed 30°C and at most times of the year the diurnal temperature variation is 20°C.

The eastern half of the park is an undulating landscape on Cretaceous Rolling Downs sediments. A strongly sorted soil is covered with weather-worn pebbles of silcrete and quartz that form bare sections (gibbers) among Mitchell grass (*Astrebla* spp.). Watercourses that drain these plains have deposited pockets of Quarternary colluvials. We selected from 1:50 000 aerial photographs a discrete junction between these Rolling Downs and a major creek line and demarcated a 1-km^2 study area (Fig. 1).

The Rolling Downs country is treeless, apart from stands of gidgee (*Acacia cambagei*) along small creeks and gullies. The dominant perennial community consists of low shrubs of saltbush (*Atriplex* spp.), bluebush (*Maireana* sp.), copperburr (*Sclerolaena* spp.) and tussocks of Mitchell Grass. The watercourse is a complex of channels lined by River Red Gum (*Eucalyptus camuldulensis*) and is well grassed with a range of annual and perennial plant species.

Sampling design

Most studies of ecotones assume that the observable patterns will appear within a few tens of metres from an identified boundary (Rivers-Moore & Samways 1996; Turton & Sexton 1996). Although such a pattern may be true for some plants, we wanted to cover a larger scale for mobile invertebrates and with a design that produced intense sampling both at a boundary and away from it. A series of five paired transects were marked (Fig. 1) with a total of 30 sample points on each pair. On the first transect in the pair we set a pitfall trap at the edge and then 1, 5, 20, 50, 100, 250 and 500 m into the stony gibber plain, hereafter referred to as 'gibber', and this was mirrored in the ephemeral watercourse, hereafter referred to as 'riparian'. The second transect in the pair was set 20 m further along the edge and used the same sample intervals but beginning 500 m into each land system with traps at 500, 499, 495, 450, 250 and 0 m from the edge. This design maintained an equivalent sampling intensity across the edge and within each land system. Transect pairs were separated by 100, 150, 250 and 500 m to cover an area of 1 km^2. The uneven, and somewhat arbitrary, distances between traps within a transect and between transect pairs was chosen to allow comparisons with data from a parallel study looking at the importance of scale for biodiversity assessments and the value of land systems as surrogates for biodiversity (Oliver *et al.* 1999). The restriction to one sampling location, when replication at a large scale was clearly desirable, was a constraint imposed by logistics.

At each sampling point invertebrates were collected in a 6.5-cm-diameter and 10-cm-deep pitfall trap buried flush with the soil surface. Traps contained 250 mL of ethylene glycol and 50 mL of ethanol and were left in place for 10 days in September 1997. After the pitfall traps were recovered the solution was replaced with 80% ethanol to preserve the specimens. All the pitfall traps were sealed and labelled with barcodes following the protocols developed in the BioTrack laboratory (Oliver *et al.* 2000).

Invertebrate sorting

Specimens from all 150 pitfall traps were sorted to ordinal level and abundance was recorded. The five most abundant taxa, Coleoptera, Collembola, Diptera, Formicidae, and non-ant and bee Hymenoptera (wasps), were further sorted to family (ants to genus) and then morphospecies. Morphospecies sorting followed the protocols established by Oliver and Beattie (1993) and efficiency was improved through the use of high-quality digital images of each voucher specimen stored and sorted within the relational database Biota (Colwell 1996). As part of this protocol a series of images are captured that highlight key taxonomic features of the specimen and these are stored alongside ecological, taxonomic and experimental design data (Oliver *et al.* 2000). For each unidentified specimen, taxonomic information was entered into the database and used to reduce the number of potential morphospecies matches, then visual comparisons with the specimen and images were used to make the final identification. Voucher specimens of each morphospecies, together with a series of up to 10 replicates, were retained and have been deposited in the Key Centre for Biodiversity and Bioresources invertebrate collection at Macquarie University, Sydney.

Data analyses

Several statistical techniques are available to search for patterns across ecotones (Ludwig & Cornelius 1987; Fortin & Drapeau 1995). In the present study a series of techniques from visual inspection of abundance patterns to multivariate permutation analyses were used. We avoided analyses that (i) searched for repetitive patterns in one variable (semivariance and spectral analyses); (ii) predicted, interpolated or smoothed the response pattern in two dimensions (kriging); and (iii) detected gradients (e.g. gradient rescaling; Wilson & Mohler 1983). This was because we had a priori defined the expected break point by choosing the discrete soil change between two very different land systems.

We compared relative abundance and richness, and analysed for gradients in abundance and richness away from the edge with standard parametric tests. We also made visual inspections for the distribution of individual morphospecies across the edge and considered assemblage differences with multidimensional scaling and analysis of similarities (ANOSIM) procedures (Clarke & Warwick 1994). This permutation approach takes the assemblage data from a series of samples and computes the likelihood of this group occurring by chance when compared to any other possible grouping in the sample population. In order to locate assemblage changes with respect to distance from the edge we computed ANOSIM comparisons from pairs of positions at different distances along the transects. A priori groupings were allocated by sample position and by using each transect as a replicate. This comparison has low statistical power but provides a visual impression of assemblage changes across the edge for each taxon. Overall the sequence of data interpretation covered individual taxa through to assemblages and represents one possible suite of techniques to assess the patterns of biodiversity across a boundary. Analyses used raw data in all parametric tests and double square-root transformation in the multivariate tests to reduce the dominance of the few abundant taxa.

RESULTS

Patterns in abundance

More than 13 000 invertebrates were sampled from the 150 pitfall traps with abundance highest for ants and wasps (Formicidae, 21%; non-ant Hymenoptera, 9%), springtails (Collembola, 28%), mites (Acarina, 12%) and flies (Diptera, 9%). There was, on average, greater abundance in traps from the riparian habitat than the gibber plain, a pattern that was significant and consistent for all groups except springtails and spiders (Aranea; Table 1). There was a significant increase in total abundance of springtails and flies with distance away from the edge into both riparian and gibber plain habitats (Table 1). Abundance of mites and beetles (Coleoptera) increased with distance into the riparian habitat, and leaf-hoppers (Hemiptera) increased with distance into the gibber plain, while the opposite trends

Table 1. Average abundance per pitfall in each habitat and clines in abundance toward and away from the boundary for nine of the most common invertebrate taxa sampled

	% of total	Mean abundance (± 1 SE)			Abundance clines away from boundary†	
Taxon	abundance	Riparian	Gibber plain	Mann–Whitney	Riparian	Gibber plain
Collembola	28	26.2 ± 2.4	23.9 ± 2.5	–0.9^{NS}	0.31⋆	0.57⋆⋆⋆
Formicidae	21	24.6 ± 3.1	12.0 ± 1.9	–3.8⋆⋆⋆	0.19^{NS}	0.01^{NS}
Acarina	12	18.0 ± 2.1	4.9 ± 0.5	–7.0⋆⋆⋆	0.29⋆	0.20^{NS}
Non-ant Hymenoptera	9	10.6 ± 1.1	4.8 ± 0.4	–5.2⋆⋆⋆	–0.23^{NS}	–0.19^{NS}
Diptera	9	10.1 ± 1.1	6.6 ± 0.6	–2.9⋆⋆	–0.35⋆⋆	–0.26⋆
Coleoptera	7	10.3 ± 1.9	1.8 ± 0.2	–7.0⋆⋆⋆	0.24⋆	–0.02^{NS}
Hemiptera	3	3.5 ± 0.4	2.6 ± 0.3	–2.2⋆	–0.26⋆	0.31⋆⋆
Aranae	3	3.1 ± 0.3	3.0 ± 0.3	0.3^{NS}	0.16^{NS}	–0.05^{NS}
All invertebrates	100	117.0 ± 7.5	68.5 ± 4.4	–5.9⋆⋆⋆	0.25⋆	0.32⋆⋆

†Pearson product-moment correlation coefficients expressed as distance from the boundary such that positive correlations indicate an increase in abundance away from the boundary.

⋆$P < 0.05$; ⋆⋆$P < 0.01$; ⋆⋆⋆$P < 0.001$; $^{NS}P > 0.05$.

were apparent for flies and non-ant Hymenoptera, which tended to be most abundant close to the edge (Table 1).

Spiders, termites (Isoptera) together with grasshoppers and crickets (Orthoptera) were generally infrequent, although the number of grasshoppers increased into the gibber plain. Capture of thrips (Thysanoptera), leaf-hoppers and, to a lesser extent butterflies and moths (Lepidoptera), was patchy mainly because pitfall traps are not the ideal method for sampling these taxa. Patterns in abundance with respect to the edge were difficult to detect for these groups.

Abundance and distribution of morphospecies

A total of 211 wasp, 66 beetle, 64 ant, 61 fly and 24 springtail morphospecies were sorted from a total of 10 446 specimens from these orders. Due to sorting difficulties and the problems of matching males to females the total for wasps is likely to be a significant overestimate of the true number of morphospecies. However, these error rates were internally consistent within the dataset. Overall there were 433 morphospecies recorded in the riparian habitat, of which 40% were represented by one individual. Similarly there were 284 morphospecies in the gibber plain, 47% of which were singletons. Despite the significant richness differences extending the tail of the distribution, the proportional rank–abundance patterns were similar for the two habitats. In the gibber plain there was a slightly higher dominance by the most abundant species and fewer rare species.

The average morphospecies richness per pitfall was greater in the riparian habitat than it was in the gibber plain for wasps, beetles, flies and ants, with a significant increase in richness with distance into the riparian habitat for beetles (Table 2). There was a slight increase in the richness of fly morphospecies towards the edge. There were more species of springtail recorded in the gibber plain than in the riparian habitat, a pattern that had a significant cline (Table 2) and was similar to the trends for the other taxa.

Mantids were recorded only from the riparian habitat and Embioptera and scorpions were recorded at least 450 m into the gibber plain, while all the other higher taxa were recorded in both habitats. The distribution patterns of individual morphospecies across the edge were represented by grouping occurrence data into categories of riparian habitat only, predominantly riparian habitat but also some in the gibber plain, generalists found evenly in both habitats, predominantly gibber plain but also some in the riparian habitat and gibber plain only. Taxa that were recorded in at least three traps were included in the present analysis. There were 10 beetle (29%), 12 wasp (19%), two springtail (18%), five ant (15%) and two fly (6%)

Table 2. Average richness per pitfall in each habitat and clines in richness toward and away from the boundary for six of the most common invertebrate taxa sampled

	Mean richness (± 1 SE)				Richness clines away from boundary[†]	
Taxon	Riparian	Gibber plain	% change	Mann–Whitney	Riparian	Gibber plain
Non-ant Hymenoptera	7.1 ± 0.5	3.7 ± 0.3	–48	–5.2***	-0.13^{NS}	-0.19^{NS}
Diptera	5.2 ± 0.4	3.7 ± 0.3	–29	–2.8**	–0.25*	-0.14^{NS}
Formicidae	4.9 ± 0.3	2.9 ± 0.2	–40	–4.9***	0.05^{NS}	-0.06^{NS}
Coleoptera	4.2 ± 0.3	1.6 ± 0.2	–62	–6.5***	0.32**	0.09^{NS}
Collembola	2.7 ± 0.1	3.2 ± 0.2	18	2.1*	–0.29*	0.40**
Total	24.0 ± 1.1	15.0 ± 0.7	–38	–6.8***	-0.09^{NS}	-0.08^{NS}

[†] As for Table 1.

Table 3. Proportion of invertebrate morphospecies that were sampled during the study only within the riparian habitat, the Gibber plain and within 100 m of only the demarcated boundary[†]

		Riparian specialists		Gibber plain specialists		Present in both habitats		Species sampled within 100 m of boundary	
Taxon	No. species	*n*	%	*n*	%	*n*	%	*n*	%
Non-ant Hymenoptera	105	32	30	5	5	69	66	17	16
Diptera	67	24	36	2	3	41	61	18	27
Coleoptera	50	20	40	7	14	23	46	2	4
Formicidae	49	21	43	2	4	26	53	1	2
Collembola	12	2	16	0	0	10	83	1	8
Total	283	99	35	16	6	169	60	39	14

[†] Only those species that were recorded from a minimum of two pitfall traps were included.

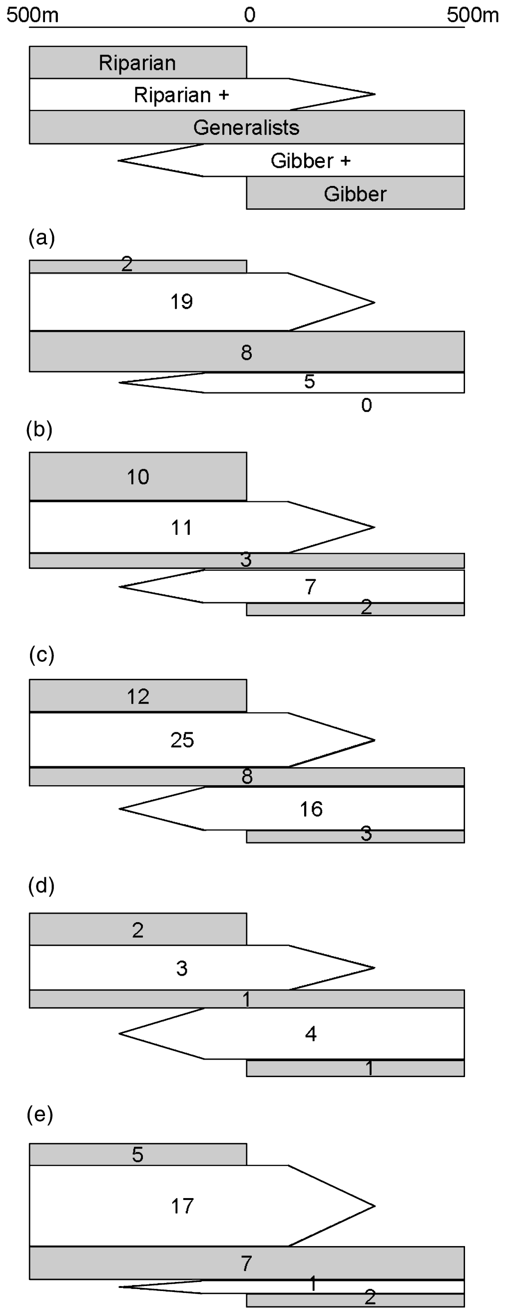

Fig. 2. Numbers of (a) fly (Diptera); (b) beetle (Coleoptera); (c) wasp (Hymenoptera (other than ants)); (d) springtail (Collembola); (e) ant (Formicidae) morphospecies caught in pitfall traps in various zones across the natural edge. The categories are morphospecies that occur only in one of the two land systems (riparian or gibber); those that occur predominantly in one habitat but 'leak' into the other (riparian+ and gibber+); and morphospecies that occur throughout both habitats (generalists). The height of the category bars approximates the percentage of morphospecies in that category as a percentage of the total for that taxon. Data are pooled from each position on the five replicate transects and only morphospecies recorded from at least three separate positions were counted.

morphospecies that were trapped only in the riparian habitat (Fig. 2). Far fewer morphospecies were recorded only from the gibber plain, none in the case of flies (Fig. 2a). The majority of morphospecies were predominantly recorded in one habitat but also crossed over the edge into the adjacent habitat (Table 3).

Families of flies, beetles and wasps and genera of ants were generally distributed across all of these categories. There were, however, two ant genera (*Tetramorium, Meranoplus*), three wasp (*Eyaniidae, Diapriinae, Pompilinae*), two fly (*Ephydridae, Spaheroceridae*) and three beetle families (*Bostrichidae, Melyridae, Tenebrionidae*) unique to the riparian habitat. The *Melyridae* were represented by three morphospecies. There were no genera or families trapped only in the gibber plain. These patterns need to be interpreted with caution, however, given the very short-term duration of the sampling effort. They did, however, contribute to assemblage dissimilarities.

Morphospecies assemblages and changes in composition

Computation of analysis of similarities (ANOSIM) for groups of traps at the same transect position in a pairwise manner for all possible combinations of groups produced a visual estimation of where changes in composition occur in relation to the edge (Fig. 3). If the edge has a strong effect on composition significant ANOSIM estimates should be apparent along the solid lines and in the quadrant defined by these lines. The pattern for 'ordinal' composition was for an increasing proportion of significant differences because the groups were separated by greater distances along transects, but there were also many significant groupings 50 m from the edge and up to 100 m from the edge (Fig. 3a). There were also no significant differences when comparisons were made for trap positions within 50 m of either side of the edge. These results implied that ordinal assemblage composition differed between the habitats but that the change was diffuse across the edge.

Fly, springtail and to a lesser extent wasp morphospecies patterns had fewer significant results as a direct effect of the edge. Trap grouping separated by 900 m, that is at the extreme ends of the transects, were not always different (Fig. 3b,c). The pattern for wasps suggested a significant change at the edge into the gibber plain but less so into the riparian habitat. Composition for these groups was not so strongly influenced by habitat type. Beetle morphospecies composition differences were more closely aligned with the edge and all within habitat comparisons were not significant (Fig. 3d), while ants exhibited strong habitat effects but a diffuse effect across the edge (Fig. 3e).

DISCUSSION

The choice of a natural edge between a stony gibber plain and a riparian habitat was made to maximize the discrete nature of the habitat junction with respect to soils and plant species. The two habitats are classified as different land systems on the basis of their soil and vegetation differences and the junction between them is visible and discrete (Fig. 1). Analyses of invertebrate abundance, richness and composition also suggested differences between the habitats but it was not a simple task to display a discrete junction in these parameters. Although abundance and species richness collectively, and for each taxon, had differences in both absolute amounts, and as trends away from the edge, this did not result in sharp changes in overall composition.

Invertebrates certainly detect landscape features and their perception of habitat heterogeneity, either as grain or extent, is an important process that determines local dispersion of individuals (Johnson *et al.* 1992; With 1994; With & Cirst 1995). A key finding of the present study is that many morphospecies may have only weak responses to sharp changes in the grain and vertical structure of the environment. In the eusocial species, especially ants, a centralized nest and a tactic of central place foraging is very likely to result in foraging across edges. A nest close to a habitat edge would be at a disadvantage if the edge reduced the normal foraging range but may have no effect if constraints on foraging differed to the constraints on nest construction.

At the level of individual organisms, movements across boundaries are a function of both the quality of the local patch and the location of the patch within the landscape mosaic (Wiens 1992). The viscosity of a patch will also affect the way individuals move through a patch and the probability that they will leave (Wiens *et al.* 1997). Each individual will have a unique perception of this grain, extent and patch characters.

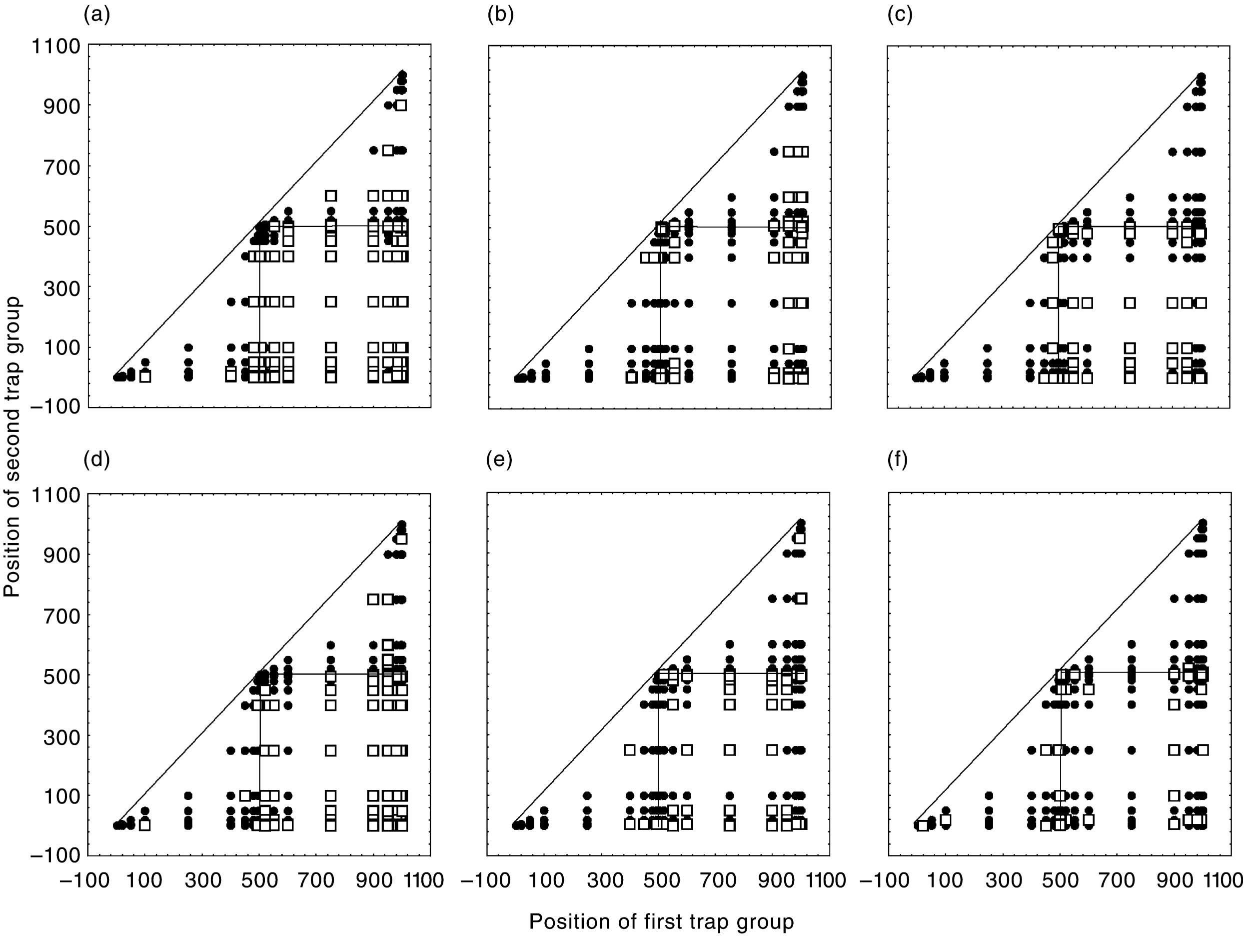

Fig. 3. Summary of multiple pairwise ANOSIM comparisons for (a) ordinal taxa and for morphospecies composition in (b) beetles (c) wasps (d) springtails (e) ants and (f) flies. A priori groups were replicate traps at a given distance along the transects with 0 m being at the extreme in the riparian habitat and 1000 m the gibber plain and the distinct edge at 500 m. Comparisons in the left triangle represent those within the riparian habitat; those in the top triangle represent those within the gibber plain and those in the bottom right quadrat represent comparisons between the habitats. Significant groupings at $P < 0.05$, that is, a significant difference in composition, are represented by a square (□); others are represented by (●).

Consequently, maps of landscape mosaics that are relevant to beetles will not be the same as those for springtails, ants or flies. Thus mapping of landscapes or landscape units in order to understand or classify biodiversity may not be possible if the perceived landscape mosaic differs for each taxon. It also suggests that biodiversity does not behave uniformly across environmental boundaries but that each taxon may have a particular response. This amounts to many responses when we consider the diverse groups, such as arthropods, that make up the bulk of biodiversity.

Perception of edges and landscape mosaics will occur at a range of scales, most likely in hierarchies, yet this does not mean that there will not be interactions between organisms (Wiens *et al.* 1993). The problem becomes how to assess these interactions and especially to establish if they contribute to an assemblage structure or coherence. The evidence here is that, although invertebrate assemblages might be statistically distinct between land systems, there are many members that are common to more than one land system or habitat type. It is also apparent that habitat specialists leak into surrounding habitats for considerable distances. The edge is, in fact, a wide ecotone for invertebrates.

Invertebrate composition will change unevenly and unpredictably across even very discrete habitat edges. In the present study we were able to assess change for distances of up to 500 m on either side of a discrete edge but it is possible that the distributions of individual species or higher taxa may extend even further than this. Our sampling using pitfall traps also restricts our information to a particular subset of the invertebrate assemblage and certainly under-sampled the more mobile flying insects. The more general implication is that each taxon is affected by a different suite of environmental variables, or the same variables but at different scales, so that the assemblage demarcated for plants is not, for example, that for flies or even wasps.

Ants increased in abundance (e.g. *Iridomyrmex*, *Melophorus*, *Monomorium*, *Pheidole*), number of species within genera (e.g. *Iridomyrmex*, *Meranoplus*, *Monomorium*, *Pheidole*) and unique genera (e.g. *Calomyrmex* and *Tetramorium*) in the riparian compared to the gibber plain. This is likely to be the result of increased habitat heterogeneity. Ant richness has been shown to be positively associated with the structural diversity of a habitat (Majer 1978; Andersen 1983) and litter cover (Majer *et al.* 1984), both of which were greater in the riparian habitat. The genera common to both habitats (*Iridomyrmex*, *Melophorus*, *Pheidole, Rhytidoponera*) are abundant and diverse in many arid and semi-arid systems in Australia (Shattuck 1999); have very broad diets; flexible foraging times and a high tolerance of a wide range of physical conditions (Andersen 1991). Some 64% of the morphospecies on the gibber plain were also abundant in the riparian habitat, and at a distance of 500 m there was still a mixture of species that suggests leakage from the riparian habitat. Levels of habitat specialization were as expected but the amount of overlap in individual species distributions and the number of generalist species was considerable.

The primarily soil-dwelling springtails were relatively species poor and almost all morphospecies were found in both habitats. The seven most abundant morphospecies were the same in each habitat and came from four common families (Entomobryidae, Paronellidae, Poduroidea and Smithuridae). This level of overlap in composition explained the lack of a transition across the edge but contradicts other studies in which habitat type (Steinberger 1991) or canopy cover and soil properties produced discrete assemblages of springtails. Perhaps soil conditions were sufficiently similar; or the nature of drainage in these systems (infrequent intense storms creating overland flow and flash flooding) precludes successful colonization by riparian specialists. Floods would also provide a mechanism for rapid dispersal of fauna active on the soil surface.

The beetles were significantly more abundant and speciose in the riparian habitat than in the gibber plain, although only six morphospecies in the gibber plain were represented by more than five individuals. Beetle diversity is affected by abiotic factors, for example soil type (Ayal & Merkl 1994), at large spatial scales but then also by an unpredictable combination of endogenous and external factors (Niemela & Spence 1994). There is evidence from a range of families that beetles can orientate themselves toward habitat features (Parmenter *et al.* 1989), can adjust habitat use at scales of 25 m (Carcamo *et al.* 1995), and that this may be related to levels of herbaceous vegetation cover at scales of 4 m (Niemela & Spence 1994). These intrinsic mechanisms for specific habitat choice might explain why there were, for the most part, riparian habitat specialists or generalists present in all samples. Therefore, the observed differences in abundance and alpha diversity may be the result of small-scale habitat perceptions nested within larger scale responses to environmental factors. Many species are considered as visitors to habitats (Desender 1996), even though some may be able to breed in unusual or transient habitats (Eversham & Telfer 1994). Although there were distinct differences between the habitats for beetle abundance and richness, the transition was diffuse because the majority of morphospecies was trapped up to 400 m from the habitat edge.

The flies and wasps were more diverse in the riparian habitat than the gibber plain. Only five of the abundant flies (29%) and one wasp morphospecies (25%) were sampled only in the gibber plain. There was a tendency for the greatest abundance and diversity of flies, and to a lesser extent bees and wasps, to be coincident with the edge. This suggests that these mobile organisms might use the line of trees as a flight corridor or some may need tree trunks and foliage as platforms for mating displays. For some taxa there are behavioural traits, such as visual cues, that are likely to concentrate abundance and diversity at or around an edge.

In some instances land systems may be reasonable surrogates for biodiversity in that broad assemblage composition differs between samples taken from sites within different land system categories (Oliver *et al.* 1999). Habitats are likely to have a recognizable biological composition that can be distinguished from an adjacent habitat in the same landscape. However, the results of the present study suggest that for the invertebrate taxa the boundaries between systems are diffuse. Even sharp edges are not responded to in the same way by different taxa, with a consequence that habitats 'leak' organisms into adjacent habitats. The extent and intensity of the leak is taxon dependent. Because human land use practices have increased, and continue to increase the proportion of edges in landscapes we might expect the effects of this leakage across edges on assemblage integrity to become more significant. However, it would be important to establish if similar patterns in biodiversity occur across man-made edges.

While we can expect biological composition to change across many scales and levels of organization, it may not always be possible to know, or have the resources to measure, these patterns. It makes some sense to manage landscapes, especially to maintain landscape diversity and heterogeneity in time and space, but this cannot assure that diversity will be maximized or maintained across all taxa. This is especially true if the focus is on the habitats, and organisms they contain, rather than the processes that maintain diversity. One of these processes is the fluidity of movement by individuals within and between habitats and how such movements are affected by the real or apparent barriers that edges represent. Clearly invertebrates do not perceive edges, and by extension the landscape, in the same way that environmental managers do.

ACKNOWLEDGEMENTS

This work was completed as part of a study of land systems as surrogates for biodiversity supported by the Resource and Conservation Assessment Council, Department of Urban Affairs and Planning, NSW State Government. Additional resources were provided by the Key Centre for Biodiversity and Bioresources, Macquarie University. The NSW National Parks and Wildlife Service provided access to Sturt National Park and invaluable logistical support during the fieldwork. Miriam Streulens, Roger Bramble, Rebecca Harris, Graham Osler and Craig Angus also generously gave help in the field. We are grateful for the constructive comments of the referees and editor. This is contribution number 367 of the Commonwealth Key Centre for Biodiversity and Bioresources.

REFERENCES

Allen T. F. H. & Starr T. B. (1982) *Hierarchy: Perspectives for Ecological Complexity*. University of Chicago Press, Chicago.

Andersen A. (1983) Species diversity and temporal distribution of ants in the semi-arid mallee region of northwestern Victoria. *Aust. J. Ecol.* **8**, 127–37.

Andersen A. N. (1991) *The Ants of Southern Australia: A Guide to the Bassian Fauna*. CSIRO Publications, Melbourne.

Ayal Y. & Merkl O. (1994) Spatial and temporal distribution of tenebrionid species (Coleoptera) in the Negev Highlands, Israel. *J. Arid Environ.* **27**, 347–61.

Backeus I. (1993) Ecotone versus ecocline: Vegetation zonation and dynamics around a small reservoir in Tanzania. *J. Biogeogr.* **20**, 209–18.

Beattie A. J. & Oliver I. (1994) Taxonomic minimalism. *Trends Ecol. Evol.* **9**, 448–90.

Bedford S. E. & Usher M. B. (1994) Distribution of arthropod species across the margins of farm woodlands. *Agric. Ecosys. Envir.* **48**, 295–305.

Breck S. W. & Jenkins S. H. (1997) Use of an ecotone to test the effects of soil and desert rodents on the distribution of Indian ricegrass. *Ecography* **20**, 253–63.

Busby J. R. (1991) BIOCLIM: A climate analysis and prediction system. In: *Nature Conservation: Cost Effective Biological Surveys and Data Analysis* (eds C. R. Margules & M. P. Austin) pp. 64–73. CSIRO, Melbourne.

Carcamo H. A., Niemela J. K. & Spence J. R. (1995) Farming and ground beetles: Effects of agronomic practice on populations and community structure. *Can. Entomol.* **127**, 123–40.

Clarke K. R. & Warwick R. M. (1994) *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. Hitchings & Mason, Plymouth.

Clements F. E. (1905) *Research methods in ecology*. University of Nevada, Lincoln.

Colwell R. K. (1996) *Biota. The Biodiversity Database Manager*. Sinauer Associates, Sunderland, MA, USA.

Desender K. R. C. (1996) Diversity and dynamics of coastal dune carabids. *Ann. Zool. Fennica* **33**, 65–75.

Eversham B. C. & Telfer M. G. (1994) Conservation value of roadside verges for stenotopic heathland Carabidae: Corridors or refugia? *Biod. Conserv.* **3**, 538–45.

Farnsworth E. J. & Ellison A. M. (1996) Scale-dependent spatial and temporal variability in biogeography of mangrove root epibiont communities. *Ecol. Monogr.* **66**, 45–66.

Fortin M.-J. & Drapeau P. (1995) Delineation of ecological boundaries: Comparisons of approaches and significance tests. *Oikos* **72**, 323–32.

Gaston K. J., Williams P. H., Eggleton P. & Humphries C. J. (1995) Large scale patterns of biodiversity: Spatial variation in family richness. *Proc. R. Soc. B* **260**, 149–54.

Gosz J. R. (1993) Ecotone hierarchies. *Ecol. Appl.* **3**, 369–76.

Hoagland B. W. & Collins S. L. (1997) Gradient models, gradient analysis, and hierarchical structure in plant communities. *Oikos* **78**, 23–30.

Holloway J. D. & Stork N. E. (1991) The dimensions of biodiversity: The use of invertebrates as indicators of human impact. In: *The Biodiversity of Microorganisms and Invertebrates: Its Role in Sustainable Agriculture* (ed. D. L. Hawkesworth) pp. 37–62. CAB International, Wallingford.

Janzen D. H. (1987) Insect diversity of a Costa Rican dry forest: Why keep it, and how? *Biol. J. Linn. Soc.* **30**, 343–56.

Jenik J. (1992) Ecotone and ecocline: Two questionable concepts in ecology. *Ekologia* **11**, 243–50.

Johnson A. R., Milne B. T. & Wiens J. A. (1992) Diffusion in fractal landscapes: Simulations and experimental studies of tenebrionid beetle movements. *Ecology* **73**, 1968–83.

Kapos V., Ganade G., Matsui E. & Victoria R. L. (1993) Delta ^{13}C as an indicator of edge effects in tropical rainforest reserves. *J. Ecol.* **81**, 425–32.

Kim K. E. C. (1993) Biodiversity, conservation and inventory: Why insects matter. *Biodivers. Conserv.* **2**, 191–214.

Kogan M. & Lattin J. D. (1993) Insect conservation and pest management. *Biodivers. Conserv.* **2**, 242–57.

Kremen C., Colwell R. K., Erwin T. L., Murphy D. D., Noss R. F. & Sanjayan M. A. (1993) Terrestrial arthropod assemblages: Their use in conservation planning. *Conserv. Biol.* **7**, 796–808.

Leeuwen C. G. V. (1966) A relation theoretical approach to pattern and process in vegetation. *Wentia* **15**, 25–46.

Ludwig J. A. & Cornelius J. M. (1987) Locating discontinuities along ecological gradients. *Ecology* **68**, 448–50.

Mackey B. G. (1993) A spatial analysis of the environmental relations of rainforest structural types. *J. Biogeogr.* **20**, 303–36.

Majer J. D. (1978) Preliminary survey of the epigeic invertebrate fauna with particular reference to ants, in areas of different land use at Dwellingup, Western Australia. *For. Ecol. Manage.* **1**, 321–34.

Majer J. D., Day J. E., Kabbay E. D. & Perriman W. S. (1984) Recolonization by ants in bauxite mines rehabilitated by a number of different methods. *J. Appl. Ecol.* **21**, 355–75.

Miller J. C. (1993) Insect natural history, multi-species interactions and biodiversity in ecosystems. *Biodivers. Conserv.* **2**, 233–41.

Milthorpe P. L. (1991) *Lands of the North-West Corner of NSW*. Report no. 12. Soil Conservation Service of NSW, Sydney.

Niemela J. K. & Spence J. R. (1994) Distribution of forest dwelling carabids (Coleoptera): Spatial scale and the concept of communities. *Ecography* **17**, 166–75.

Oliver I. & Beattie A. J. (1993) A possible method for the rapid assessment of biodiversity. *Conserv. Biol.* **7**, 562–8.

Oliver I. & Beattie A. J. (1996) Invertebrate morpho-species as surrogates for species: A case study. *Conserv. Biol.* **10**, 99–109.

Oliver I., Beattie A. J., Holmes A., Dangerfield J. M. & Gillings M. (1999) *Land Systems as Surrogates for Biodiversity*. Key Centre for Biodiversity and Bioresources, Sydney.

Oliver I., Dangerfield J. M. & York A. (1999) When and how to conduct a biodiversity assessment of terrestrial invertebrates. In: *The Other 99%. The Conservation and Biodiversity of Invertebrates* (eds W. Ponder & D. Lunney) pp. 8–18. Transactions of the Royal Zoological Society of New South Wales, Sydney, Australia.

Oliver I., Pik A., Britton D., Dangerfield J. M., Beattie A. J. & Colwell R. K. (2000) Virtual biodiversity assessment systems: The application of bioinformatics technologies to the accelerated accumulation of biodiversity information. *Bioscience* **50**, 441–50.

Palmer M. J. & White P. S. (1994) On the existence of ecological communities. *J. Veg. Sci.* **5**, 279–82.

Parmenter R. R., Parmenter C. A. & Cheney C. D. (1989) Factors influencing microhabitat partitioning among coexisting species of arid-land darkling beetles (Tenebrionidae): Behavioural responses to vegetation architecture. *Southwest. Nat.* **34**, 319–29.

Perry D. A. (1995) Self-organizing systems across scales. *Trends Ecol. Evol.* **10**, 241–4.

Pimentel D., Stachow U., Takacs D. A. *et al.* (1992) Conserving biological diversity in agricultural/forest systems. *Bioscience* **42**, 354–62.

Ponder W. & Lunney D. (1999) *The Other 99%. The Conservation and Biodiversity of Invertebrates*. Surrey Beattie & Sons, Sydney.

Rivers-Moore N. A. & Samways M. J. (1996) Game and cattle trampling, and the impacts of human dwellings on arthropods at a game park boundary. *Biodivers. Conserv.* **5**, 1545–56.

Shattuck S. O. (1999) *Australian Ants: Their Biology and Identification*. CSIRO Publishing, Melbourne.

Shipley B. & Keddy P. A. (1987) The individualistic and community-unit concepts as falsifiable hypotheses. *Vegetatio* **69**, 47–55.

Steinberger Y., Aldon E. F. & Whitford W.G. (1991) Ground-dwelling arthropods of the Rio Puerco Watershed, New Mexico. *Arid Soil Res Rehab* **5**, 147–53.

Taylor R. W. (1983) Descriptive taxonomy: past, present and future. In: *Australian Systematic Entomology: A Bicentenary Perspective* (eds E. Highley & R. W. Taylor) pp. 54–68. CSIRO, Melbourne.

Turton S. M. & Sexton G. J. (1996) Environmental gradients across four rainforest-open forest boundaries in northeastern Queensland. *Aust. J. Ecol.* **21**, 245–54.

van der Maarel E. (1990) Ecotones and ecoclines are different. *J. Veg. Sci.* **1**, 135–8.

Wiens J. A. (1992) Ecological flows across landscape boundaries: A conceptual view. In: *Landscape Boundaries* (eds A. Hansen & F. di Castri) pp. 217–35. Springer, New York.

Wiens J. A., Schooley R. L. & Weeks R. D. (1997) Patchy landscapes and animal movements: Do beetles percolate? *Oikos* **78**, 257–64.

Wiens J. A., Stenseth N. C., Van Horne B. & Ims R. A. (1993) Ecological mechanisms and landscape ecology. *Oikos* **66**, 369–80.

Williams-Linera G. (1990) Vegetation structure and environment of forest edges in Panama. *J. Ecol.* **78**, 356–73.

Wilson M. V. & Mohler C. L. (1983) Measuring compositional change along gradients. *Vegetatio* **54**, 129–41.

With K. A. (1994) Ontogenetic shifts in how grasshoppers interact with landscape structure: An analysis of movement patterns. *Funct. Ecol.* **8**, 477–85.

With K. A. & Cirst T. O. (1995) Critical thresholds in species' responses to landscape structure. *Ecology* **76**, 2446–59.

Young I., Blanchart E., Chenu C. *et al.* (1998) The interaction of soil biota and soil structure under global change. *Glob. Chan. Biol.* **4**, 703–12.