Bias in the effect of habitat structure on pitfall traps: An experimental evaluation

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Abstract   Habitat structure has been implicated as a source of bias for pitfall-trap data but most evidence is observational or anecdotal. This study used an experimental approach to quantify biases due to habitat structure. In a randomized block design, I manipulated native grassland to create three types of habitat structure and measured pitfall-trap catches of grassland ants. Small patches of modified habitat were surrounded by otherwise unmodified grassland with the assumption that population density remained unaffected by the modification and that the effects observed were due to changes in trappability. I assessed magnitude, direction, predictability, and consistency of bias for the following types of data: population abundance for single species, relative abundance among species, species composition of assemblages, and species richness. The magnitude of the bias in population abundance was large for most species. However, since the direction of the bias varied predictably with habitat structure, pitfall-trap data can be used to judge differences in population abundance in some situations. The magnitude of the bias in relative abundance was less than for abundance. However, there was inconsistency in the direction and magnitude of bias among species. Thus, interpretation of relative abundance data in pitfall-trap studies may be compromised. Species richness and species composition were biased by habitat structure but were affected significantly only when the groundcover was very dense, suggesting a threshold effect of habitat structure. To help to interpret survey data, pitfall-trap studies should routinely measure attributes of habitat structure and incorporate an experimental component to characterize the bias.

Key words: biodiversity assessment, field experiment, Formicidae, population assessment, survey methods.

INTRODUCTION

Pitfall traps are commonly used to address a question of difference in population size or community structure in time or space. However, an effect of habitat structure on trappability could result in biased data for studies that compare locations with different habitat structure, or when habitat structure changes in time. Despite widespread recognition of this and other potential sources of bias (reviews by Luff 1975; Thomas & Sleeper 1977; Southwood 1978; Adis 1979; Halsall & Wratten 1988; Topping & Sunderland 1992; Spence & Niemelä 1994), pitfall traps continue to be used frequently in many areas of ecological research, for both vertebrates and invertebrates. This is perhaps because methods other than pitfall trapping are more difficult and expensive to implement, particularly for surface-active invertebrates. Sometimes pitfall trapping may be the only feasible method, such as when population densities are low or when minimal impact methods are required for sensitive sites. Because of the advantages of pitfall trapping, approaches need to be

developed to factor out bias or to aid interpretation of biased data (Niemelä *et al.* 1990; Spence & Niemelä 1994; Digweed *et al.* 1995; Melbourne *et al.* 1997). In this paper, I consider the biases that emerge when locations with different habitat structure are compared, determine the extent to which different types of data are affected by bias and consider approaches to aid interpretation of biased data.

The capture rate of a pitfall trap is a function of population density and trappability. Trappability is here defined as the probability of capture of an individual in the population. Differences in trappability in time or space may lead to biased estimates for population-level data. One well-recognized influence on trappability is the activity level of individuals in a population (Mitchell 1963). Indeed, pitfall-trap data are often said to represent the 'activity density' of a population (Thiele 1977). Activity levels can be affected, independently of population density, by a variety of factors (Southwood 1978), particularly those that directly affect the physiological state or behaviour of the animal, such as weather (Whicker & Tracy 1987; Honék 1988; Niemelä *et al.* 1989), leading to biased estimates of population density. Community-level data share the same problems as population-level data but in addition are affected by differences in trappability

among species, which can arise either from differences in activity levels (Honék 1988), or through trap avoidance or escape behaviour (Luff 1975; Halsall & Wratten 1988; Topping 1993). Differences in the direction and magnitude of biases among species may cause community-level data to vary in time or space, independently of real changes in community structure.

The limitations just described are not critical when the question of interest is a relative difference in population density or community structure in time or space. Then, it is not necessary to know the absolute density or structure; biased data (e.g. the activity density of the 'pitfall-sampled' community) are sufficient to address the question of 'differences'. However, it must be assumed that biases are the same between the times or locations that are being compared. For comparisons in time, such as between seasons, this assumption is probably unreasonable at least because of changing weather conditions and animal behaviour. For comparisons in space, this assumption is often reasonable provided that weather conditions are not different between locations or can be averaged out over time (Baars 1979).

For studies that compare locations with different habitat structure, the assumption that biases are the same between the locations that are being compared is critical. Trappability must not change with habitat structure. Here, habitat structure is defined as the spatial configuration of the animal's environment, particularly the environment immediately surrounding the trap. Examples of elements of habitat structure include the density of vegetation, the roughness of the soil surface, or the spatial arrangement of microlandscape features. Habitat structure could affect trappability by affecting the movement behaviour of animals, either through microclimatic effects or by a more direct response of individuals to the physical features of the habitat. Studies that compare locations with different habitat structure are perhaps the most common. Some examples from the recent literature include forest fragments versus the surrounding landscape (Punttila *et al.* 1994), grazed versus ungrazed plots (Dennis *et al.* 1997), burnt versus unburnt sites (Greenberg *et al.* 1994; Cole *et al.* 1997), comparisons among agroecosystems (Cárcamo *et al.* 1995; Perfecto & Snelling 1995), or biodiversity studies that compare different habitat types (Abensperg-Traun *et al.* 1996; Gomez & Anthony 1996; Hadden & Westbrooke 1996; Samways *et al.* 1996). Sometimes comparisons made in time are coincidentally also comparisons between different habitat structures, because habitat structure may change over time. The effect of habitat structure on trappability, independent of its effect on population size or community structure, could present a serious problem when interpreting the results from these types of studies.

The effect of habitat structure on trappability was first experimentally examined by Greenslade (1964).

In his main experiment, he clipped away a 30 cm radius area of grass from around three pitfall traps and compared this to three traps in intact grass. He found that catches of some carabid beetles were higher in the traps that had grass clipped from around them. The result was attributed to the lower impedance of the habitat surrounding cleared traps. Although there is anecdotal evidence consistent with Greenslade's experimental findings (e.g. Wallin 1985; Honék 1988) his study is apparently the only published experimental investigation into the effect of habitat structure on trappability. Since studies that compare locations with different habitat structure are common, more research is needed to identify limitations to the use of pitfall traps and to develop approaches to aid interpretation of biased data. I conducted a field experiment to determine the effect of habitat structure on trappability of grassland ants for the following types of data: population abundance for single species, relative abundance among species, species composition of assemblages, and species richness.

METHODS

Study site and manipulations

The study site was located within a 20 hectare area of *Themeda triandra* dominated grassland (35°12′40′′E, 149°06′50′′S), in the Australian Capital Territory (ACT), Australia. This grassland consisted of dense *T. triandra* with a thick litter layer of dead and senescent plant material to a height of about 20 cm. The study site was a uniform area, 60×50 m, divided into 30 10×10 m plots (Fig. 1). Two pitfall traps were installed 2.5 m apart at the centre of each plot. Pitfall traps were similar to the design used by Margules (1993). Each trap consisted of a plastic cup, 9 cm in diameter, inserted into a polyvinyl chloride sleeve, sunk flush with ground level. A 60 cm long, 5 cm high, galvanized iron drift fence was positioned across the centre line of the cup and a galvanized iron roof was positioned over the cup, flush with the drift fence. A preservative fluid, consisting of 50% ethylene glycol with water, was used. Further details of the study site and pitfall traps are given in Melbourne *et al.* (1997).

The experimental design included three levels of habitat structure, which were created by modifying (or not modifying) the structure of the habitat within an 80 cm radius of each pitfall trap. This radius was chosen to be somewhat larger than the drift fence. The three levels of habitat structure encompassed a range of vegetation densities and were designed to match the structure of different native grassland communities found in the ACT. For the most dense level ('unmodified') no modification was made to the structure of the surrounding habitat. For the least dense level ('cleared')

all above-ground vegetation and litter was removed from within an 80 cm radius of each pitfall trap. To create a level of density intermediate between 'unmodified' and 'cleared', only litter and senescent plant material was removed from within an 80 cm radius of each pitfall trap, such that inter-tussock spaces were created ('litter removed'). All debris was removed from 'cleared' and 'litter removed' plots using a vacuum device. A randomized block design was used with 10 blocks and 10 replicates for each level of habitat structure (Fig. 1). Habitat structure treatments were randomly assigned to plots within blocks. In all analyses, data from the two pitfall traps in each plot were summed and made up one replicate. Traps were installed before experimental manipulations were per-
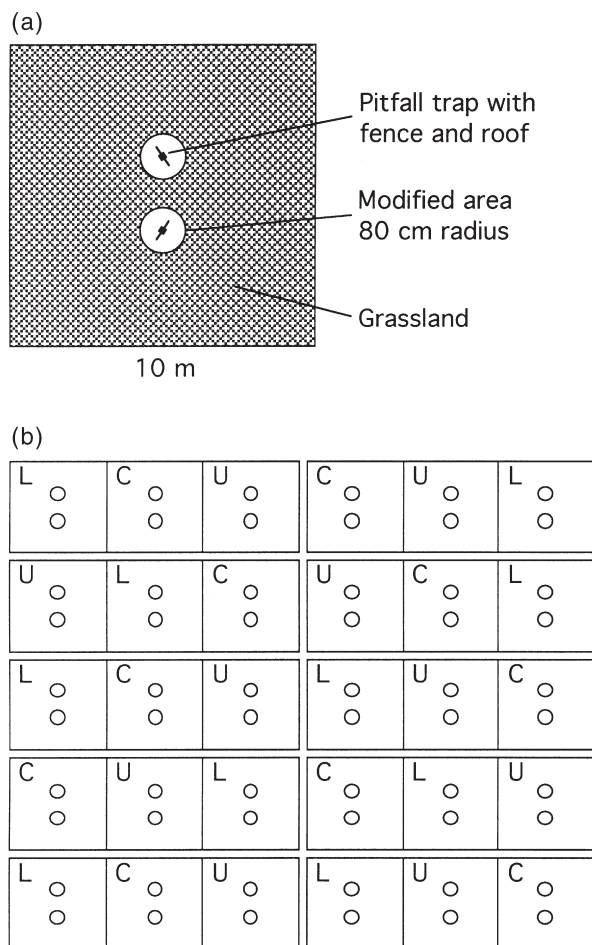

(a)

Pitfall trap with fence and roof

Modified area 80 cm radius

Grassland

10 m

(b)

Fig. 1. Schematic representation of (a) experimental plots and (b) the experimental area. (a) Each plot consisted of a 10×10 m area with two pitfall traps positioned 2.5 m apart. Habitat structure was modified (or not modified) in a circular area of radius 80 cm surrounding each trap. (b) Plots were arranged in a randomized block design, with three plots to a block and treatments randomly assigned to plots within blocks. Treatments were: U, unmodified; L, litter removed; C, cleared.

formed but remained closed for 10 days after the manipulations were completed to allow disturbance effects to dissipate. Traps were then opened for two weeks in autumn (5–20 April 1993).

All ants caught were sorted to morphospecies as described in Andersen & Reichel (1994). Representative samples of morphospecies were identified by S. O. Shattuck (pers. comm. 1996). Many species could not be identified to named species with confidence. These species were identified to species groups where possible. In this paper, species groups are indicated by the use of parentheses (International Commission of Zoological Nomenclature 1985). Voucher specimens of each morphospecies have been deposited in the Australian National Insect Collection, CSIRO Entomology, Canberra.

Experimental assumptions

Two assumptions were made in the experiment. First, that the modifications to habitat structure made in the area immediately surrounding the pitfall traps did not affect the size of ant populations. Thus, any effects observed would be due to a change in trappability rather than to a change in the population size of a given species. This assumption is based on the scale of the manipulations. The size of each manipulation (the sum of the two modified circular areas in each plot) was $4 m^2$, or 4% of a 10×10 m plot (Fig. 1a). This small area was not expected to alter substantially the population size of any species, in the time frame of the experiment. In other words, the true population size at the scale of 10×10 m plots was assumed to be the same, on average, among the different habitat structure manipulations. A second assumption was that any observed effects were due to differences in the structure of the habitat rather than to other effects associated with the manipulations, such as physical disturbance of the habitat. Possible effects due to disturbance include disruption of ant nests and attraction of animals to the disturbed area because of an increase in food items. However, such initial disturbance effects associated with installation of pitfall traps probably last for less than one week for ants (Greenslade 1973), less than two weeks for carabid beetles (Digweed *et al.* 1995) and a few days for Collembola (Joose & Kapteijn 1968) and some other invertebrate groups (Greenslade 1973). I left a 10-day period, during which traps were closed, between the habitat manipulations and the commencement of trapping. This period was a trade off between allowing initial disturbance effects to dissipate and to minimize delayed effects, such as regrowth of vegetation or population response to the new habitat.

Statistical analyses

Mixed model analyses of variance (ANOVA) were used to model the effect of habitat structure on: (i) the abun-

dance of the five most abundant ant species considered separately, and (ii) the number of species caught. Block was included in the ANOVA model as a random effect. The abundance data for all species required log transformation, which successfully stabilized the variance. *P*-values were calculated from *F*-ratios to test the null hypothesis that there was no effect of habitat structure on pitfall-trap catches. There were no *a priori* hypotheses requiring comparisons between particular means and thus a multiple comparison procedure was used. A protected LSD (least significant difference) was calculated from: $t \times \text{SED}$, where t = critical value of student's *t*-distribution with appropriate degrees of freedom at $\alpha = 0.05$ and SED = standard error of the difference between means (Fisher 1935).

Logistic regression (McCullagh & Nelder 1989) was used to model the effect of habitat structure on the relative abundance of the five most abundant species. Logistic regression was used because 'relative abundance' has an approximately binomial form, that is, the abundance of a given species is a proportion of the abundance of all species combined. To estimate the change in deviance associated with habitat structure, block was first added to the model followed by habitat structure. Block was included in the model whether it was significant or not because it describes the (random) variation associated with experimental blocks. Deviance ratios and standard errors were calculated using the dispersion parameter set to the residual mean deviance. *P*-values were calculated from deviance ratios to test the null hypothesis that there was no effect of habitat structure on pitfall-trap catches. A common approach to analyzing relative-abundance data is ANOVA of untransformed or arcsine-transformed percentages. This approach gave similar means, identified the same outliers and gave higher levels of statistical significance. However, the ANOVA assumption of constant variance was violated and attempts to stabilize the variance with various data transformations were not as successful as the use of logistic regression, which is more appropriate for the distributional properties of relative-abundance data. Logistic regressions and ANOVAs were performed using the statistical package GENSTAT 5, release 3.1 (Numerical Algorithms Group, Oxford).

The effect of habitat structure on species composition was investigated using multivariate techniques as follows. First, the species composition of each plot was compared with all other plots using the Czekanowski-Sorensen measure of dissimilarity, which is one of a class of measures that provide a robust estimate of ecological distance (Faith *et al.* 1987). Second, to detect outliers, a cluster analysis was performed on the association values using the UPGMA (unweighted pair group arithmetic averaging) method (Sneath & Sokal 1973) with slight dilation (beta = − 0.1; Belbin 1994). Outliers were then excluded from all other analyses. Third, hybrid multidimensional scaling (HMDS) was used to ordinate the sites based on the association values (Faith *et al.* 1987; Belbin 1991, 1994). A cut-value of 0.63 was used for HMDS based on inspection of a histogram of the association values (Belbin 1994). The number of dimensions required to describe the data adequately was determined using the guidelines given in Clarke (1993) after inspecting the stress values from solutions in two to five dimensions obtained from the best of 10 random starts. The final solution for the chosen number of dimensions was obtained from 100 random starts using a stopping rule of a maximum of 50 iterations or a minimum stress difference of 0.005. Solutions from non-metric and metric MDS also were inspected. Fourth, a permutation test (ANOSIM; Clarke 1993) was used to determine whether there was a significant effect of habitat structure on species composition. The ANOSIM test described by Clarke (1993) is based on rank similarities (non-metric ANOSIM) but the association values themselves also can be used (metric ANOSIM; Belbin 1994). The latter approach possibly has more statistical power. Both approaches were used here. Following the test for an overall effect, the test was repeated for pairs of the treatment level. All multivariate analyses were performed using PATN 3.3 (Belbin 1994).

RESULTS

Experimental manipulation of habitat structure in *Themeda triandra* grassland affected all types of data (abundance, relative abundance, species richness, species composition). In general, trappability increased as the structure of the habitat became more open. For convenience of presentation, pitfall-trap catches are here referred to using the same terminology as the quantities they would normally be used to estimate. Thus, for example, 'abundance' here implicitly means 'the number of animals caught in pitfall traps' since it was only the number of animals caught in pitfall traps that could be affected by the manipulations of habitat structure. The true population abundance at the scale of 10×10 m plots was assumed to be the same, on average, among the different habitat structure classes. In other words, the data were assumed to be affected (biased) not the ecological quantity itself. Note also that the bias referred to here is in addition to other sources of bias. It is assumed that the baseline data are inherently biased by the factors discussed in the Introduction. The issue addressed here is whether additional bias is introduced, or the inherent bias changes, with habitat structure.

Population abundance

Abundance data were biased by habitat structure for four of the five most abundant ant species (Fig. 2). For

all species for which there was a significant effect of habitat structure, trappability increased as the habitat became more open. However, comparisons of means indicated that there was variation among species in their responses to particular levels of habitat structure. The abundance of *Iridomyrmex (rufoniger)* sp. A increased with each decrease in vegetation density, the abundance of *Rhytidoponera (metallica)* sp. increased significantly only in the 'cleared' pitfall traps, and the abundance of *Pheidole* sp. A and *Paratrechina* sp. increased to a similar extent in both the 'litter removed' and 'cleared' pitfall traps.

Relative abundance among species

Relative-abundance data were biased by habitat structure for three of the five most abundant species (Fig. 3). Indeed, the results for each species were idiosyncratic; that is, for most species there was not a monotonically ordered pattern with vegetation density and there was considerable variation among species. It appears also that the rank relative abundance and rank abundance of species was affected (Table 1). For example, the relative abundance of *I. (rufoniger)* sp. A (about 17%) in the 'litter removed' pitfall traps was lower than the relative abundance of *Paratrechina* sp.
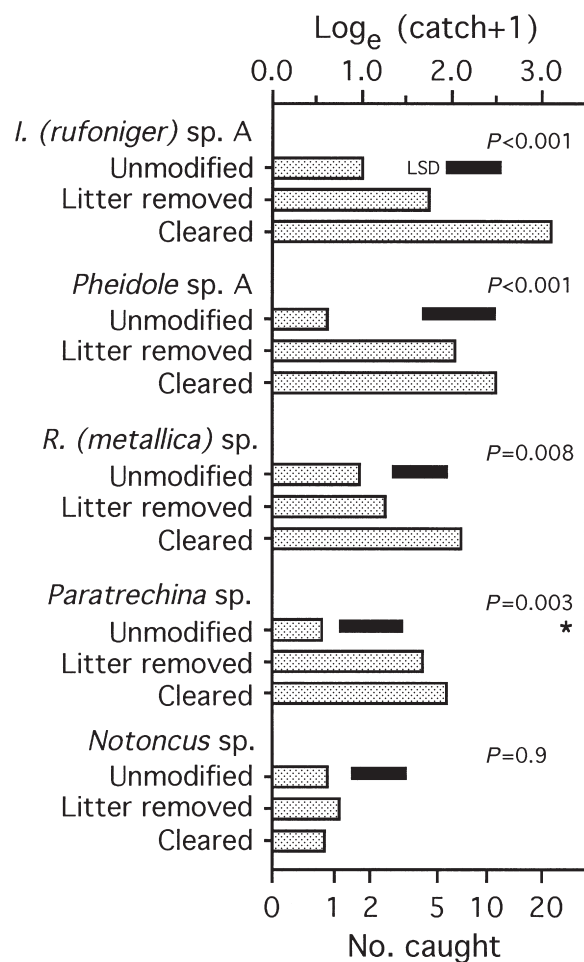

Fig. 2. The abundance in pitfall traps of five ant species in response to experimental manipulation of habitat structure surrounding the trap. Results show mean abundance estimated using ANOVA for each species separately. *P*-values indicate the level of significance for habitat structure. Black bars indicate the least significant difference for each species (LSD), which is equal to approximately two times the standard error of the difference between means. Comparison of means using the LSD indicates the significance of the difference between two means, within species, at $\alpha = 0.05$. ⋆ = outlier, excluded from model ($P = 0.2$ with outlier included).
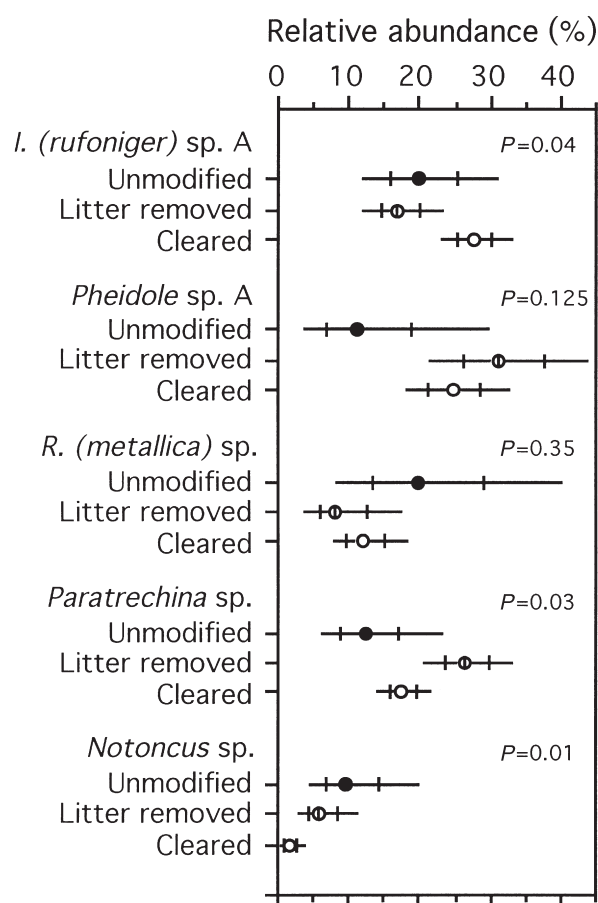

Fig. 3. The relative abundance in pitfall traps of five ant species in response to experimental manipulation of habitat structure surrounding the trap. Results show mean relative abundance estimated using logistic regression for each species separately. *P*-values indicate the level of significance for habitat structure. Two-tiered error bars indicate the standard error (inner tier) and 95% confidence interval (outer tier) for the mean. One outlier was excluded from the model for *Iridomyrmex (rufoniger)* sp. A (relative abundance = 85% in a 'cleared' plot) and also for *Paratrechina* sp. (relative abundance = 83% in an 'unmodified' plot). With outliers included in the model, $P = 0.009$ and $P = 0.3$, respectively.

(about 26%) but this pattern was reversed in the 'cleared' pitfall traps (Fig. 3, Table 1). Also of note was the pattern of the variance for relative abundance, from large variance in the 'unmodified' pitfall traps to small variance in the 'cleared' pitfall traps (Fig. 3).

Frequency of occurrence

The frequency of occurrence for almost all of the 19 species caught in the study increased as the habitat structure became more open (Table 2). The main effect was for the most dense habitat ('unmodified'), in which frequency of occurrence was very low for many species. Species that were represented in the experiment by less than 10 individuals were caught only in the 'litter removed' and 'cleared' treatments in all but two cases (Table 2). For most of the abundant species, the frequency of occurrence was higher in the modified plots than the 'unmodified' plots and was either equal between

Table 1. The rank order of five ant species, from highest to lowest, for mean abundance and mean relative abundance of the pitfall-trap catch in response to experimental manipulation of habitat structure

Species	Abundance			Relative abundance		
	U	L	C	U	L	C
Iridomyrmex (rufoniger) sp. A	1	2	1	1	3	1
Pheidole sp. A	3	1	2	3	1	2
Rhytidoponera. (metallica) sp.	1	4	3	1	4	4
Paratrechina sp.	5	2	4	3	2	3
Notoncus (ectatommoides) sp.	3	5	5	5	5	5

Ranks were calculated from the means given in Fig. 2 and 3. Means were considered different when the larger mean was 1.10 times larger than the smaller mean, otherwise ranks were considered to be tied.

U, unmodified, L, litter removed, C, cleared.

Table 2. The 19 ant species caught in the experiment and the frequency of occurrence for each species in pitfall traps with different surrounding habitat structure

Species	Code	Frequency of occurrence			Total caught
		Unmodified	Litter removed	Cleared	
Ponerinae					
Heteroponera imbellis (Emery)	GR03	0.1	0.7	0.3	20
Hypoponera sp. A	GR04	0	0.5	0.6	35
Hypoponera sp. E	GR06	0.1	0	0.5	8
Hypoponera sp. F	GR07	0	0.1	0.1	2
Rhytidoponera. (metallica) sp.	GR09	0.8	1.0	1.0	147
Myrmicinae					
Meranoplus sp.	GR11	0.1	0.3	0	8
Monomorium sp. C	GR14	0	0.1	0	1
Pheidole sp. A	GR18	0.4	0.9	1.0	313
Dolichoderinae					
Iridomyrmex (rufoniger) sp. A	GR29	0.8	1.0	1.0	361
Iridomyrmex (rufoniger) sp. B	GR30	0	0.1	0	2
Iridomyrmex (bicknelli) sp.	GR32	0	0.1	0	1
Iridomyrmex sp. A	GR28	0	0	0.3	8
Iridomyrmex sp. C	GR31	0	0.1	0.1	2
Ochetellus glaber (Mayr)	GR26	0	0	0.1	1
Formicinae					
Camponotus sp.	GR36	0	0	0.1	1
Melophorus sp. A	GR37	0	0.1	0.2	3
Melophorus sp. B	GR38	0	0.1	0	1
Notoncus (ectatommoides) sp.	GR40	0.4	0.5	0.6	48
Paratrechina sp.	GR42	0.7	0.8	0.8	264

Frequency of occurrence was calculated from the number of plots in which the species was caught, divided by the total number of plots (10) for each habitat structure class. The total number of individuals caught for each species also is given. Species have been grouped by subfamily. Also shown are voucher codes that correspond to specimens submitted to the Australian National Insect Collection, CSIRO Entomology, Canberra.
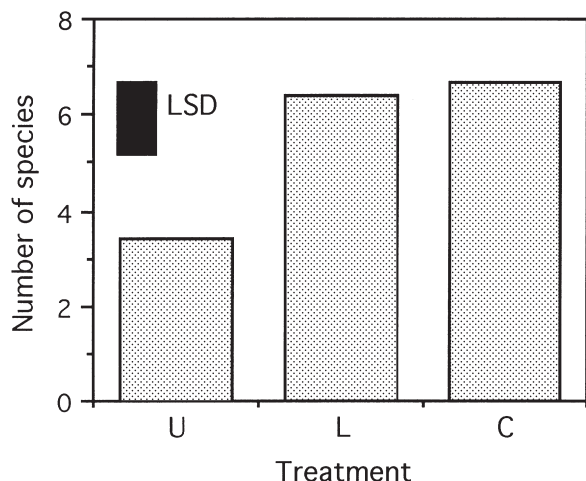
Fig. 4. The number of species caught in pitfall traps in response to experimental manipulation of habitat structure surrounding the trap. Results show mean number of species caught estimated using ANOVA. There was a significant effect of habitat structure ($P < 0.001$). LSD stands for least significant difference, which is equal to approximately two times the standard error of the difference between means. Comparison of means using the LSD indicates the significance of the difference between two means at $\alpha = 0.05$. U, unmodified; L, litter removed; C, cleared.
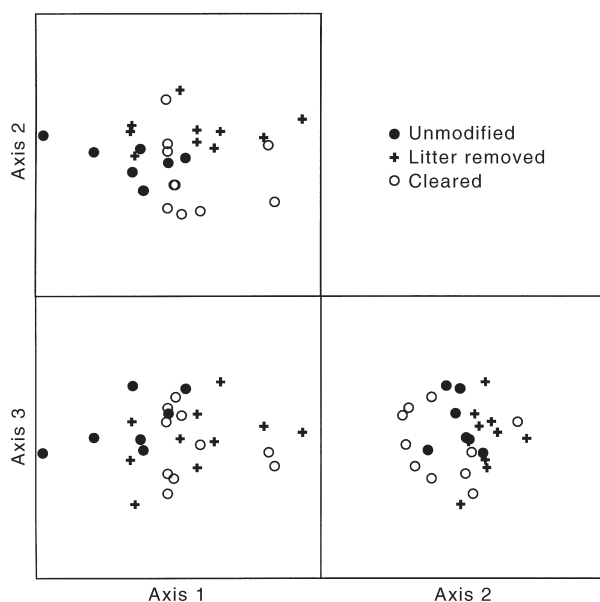

Fig. 5. Scatterplot matrix of the 3-dimensional solution from HMDS. The ordination represents the composition (presence/absence) of ant species caught in pitfall traps in response to experimental manipulation of the habitat structure surrounding the trap. Each point represents one experimental plot (i.e. one pair of pitfall traps). Axes are scaled equally. The ordination illustrates the significant effect of habitat structure on species-composition data (non-metric ANOSIM, $P = 0.01$) and demonstrates that the 'litter removed' and 'cleared' pitfall traps are more similar to each other than to the 'unmodified' traps (Table 3).

the 'litter removed' and 'cleared' plots or slightly higher in the 'cleared' plots.

Species richness and composition

There was a significant effect of habitat structure on species-richness data ($P < 0.001$, Fig. 4). Species richness in the 'litter removed' and 'cleared' pitfall traps was almost twice as high as in the 'unmodified' pitfall traps.

There was a significant effect of habitat structure on species-composition data (non-metric ANOSIM, $P = 0.01$; metric ANOSIM, $P = 0.004$), which is reflected in the separation of habitat-structure types in ordination space (Fig. 5). Pairwise comparisons indicate that the difference in species composition was most significant for 'unmodified' compared to 'cleared' and 'unmodified' compared to 'litter removed' pitfall traps (Table 3). However, only the 'unmodified' versus 'cleared' contrast using the metric test was significant after Bonferonni correction (for an overall type I error rate of $\alpha = 0.05$, $\alpha' = 0.017$). There did not appear to be a significant difference between 'litter removed' and 'cleared' pitfall traps (Table 3), however, these two habitat-structure types were essentially separated in ordination space (Fig. 5) suggesting some degree of difference in species composition. Three dimensions were required for HMDS to represent adequately (stress $= 0.12$) the composition of species after three outlying plots (Fig. 6), all from the 'unmodified' class, were removed. Non-metric and metric MDS gave similar ordination solutions to HMDS. The presence of the outliers indicates that, as well as being more different to the other modified classes, there also was greater variation in species composition within the 'unmodified' class. With outliers included, the effect of habitat structure on species composition data also was significant (non-metric ANOSIM, $P < 0.001$; metric ANOSIM, $P < 0.001$).

Table 3. Pairwise comparisons of species composition between the different habitat structure classes

Comparison	*P* value	
	Non-metric	Metric
U *vs* L	0.041	0.026
U *vs* C	0.029	0.003
L *vs* C	0.117	0.115

P values were calculated using analysis of similarity (ANOSIM). Non-metric *P* values were calculated using the ranks of the association values whereas metric *P* values were calculated using the association. The values Czekanowski association measure was used.

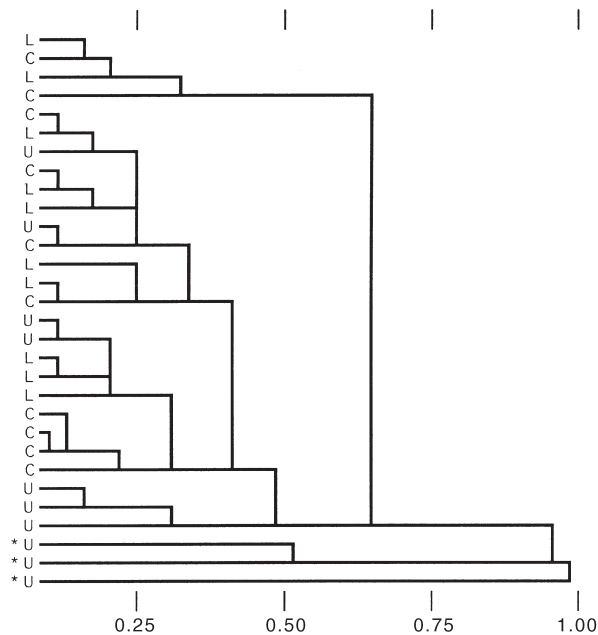U, unmodified; L, litter removed; C, cleared.

Fig. 6. Cluster analysis of plots using UPGMA. The dendrogram represents the composition (presence/absence) of ant species caught in pitfall traps in response to experimental manipulation of the habitat structure surrounding the trap. Three outliers (*) were identified. Scale indicates dissimilarity.

DISCUSSION

Bias and recommendations for assessment procedures

How seriously the interpretation of pitfall-trap data is compromised by bias depends on four characteristics of the bias: (i) magnitude, (ii) direction, (iii) predictability, and (iv) for multispecies data, consistency of magnitude and direction among species. Here, I emphasize studies where the question of interest is a difference in population size or community structure between different habitat types, rather than studies attempting to obtain absolute estimates. I consider assessment procedures for four data types: population abundance for single species, relative abundance among species, species composition of assemblages, and species richness.

For grassland ants, population-abundance data were biased by habitat structure for most species and the magnitude of the bias was large, up to 10 times difference in abundance between structural classes (Fig. 2). Therefore, any attempt to compare population abundance between different habitats would need to correct for this bias. Correction would be difficult to achieve when the magnitude of the bias is different among species, as it was for grassland ants. For this situation, the magnitude of the bias would not be predictable without experimental testing for the species of interest.

One possibility is that some easily measured trait (e.g. body size) is related to the magnitude of the bias. For the ants considered here, there is a pattern of increasing bias with decreasing body size but there are too few species to test this conjecture.

In the absence of a means to predict the magnitude of the bias, pitfall-trap data could be used to judge differences in population abundance when the direction of the bias is known, albeit in a limited number of situations (Fig. 7). For grassland ants, there was a monotonic increase in the bias as the habitat structure became more open (Fig. 2). Thus, in a population assessment study for grassland ants, it would be possible to determine whether population abundance was lower in open compared to dense habitats but not vice versa (Fig. 7) but it would not be possible to determine accurately the magnitude of the difference. For the grassland ants in this study, the direction of the bias was the same for nearly all species (Fig. 2, Table 2), which is a useful generalization. Melbourne *et al.* (1997) used the guidelines given in Fig. 7 to interpret the results from a pitfall-trap survey of five different types of grassland for slugs and crickets. The response of slugs and crickets to habitat structure was first determined experimentally. Since habitat structure did not bias abundance data for slugs, the survey results were considered robust. In contrast, for crickets, bias in the abundance (higher trappability in open grasslands) meant that only the direction of the difference in abundance between habitats could be determined; crickets were more abundant in one of the densest grasslands. Carabid beetles may not have the same consistency in the direction of bias as ants. Greenslade (1964) observed a variety of responses to habitat structure for carabid beetles, including higher trappability of predatory carabids in open plots, no bias for larger phytophagous species and lower trappability in open plots for smaller phytophagous species. This suggests that the results obtained for grassland ants cannot be generalized to other species. It will be necessary to determine the bias experimentally for different organisms in different habitats before survey results can be interpreted.

The magnitude of the bias in relative abundance (Fig. 3) was generally less than that for abundance but inconsistency in the direction and magnitude of bias among species (Fig. 3, Table 1), along with greater variance, means that the interpretation of multispecies relative-abundance data is more seriously compromised. To correct the bias for each species would rarely be logistically feasible for large multispecies assemblages. Consequently, commonly used multispecies measures of community structure or diversity that include a relative abundance component will be difficult to interpret when pitfall traps are used to compare locations with different habitat structure. These include the family of measures that reduce the species richness

and relative abundance information into a single index, such as the Shannon–Weiner index and Pielou's J′ (reviewed by Magurran 1988) as well as species abundance models such as the log normal distribution and the logarithmic series (May 1975; Pielou 1975; Magurran 1988). Multivariate techniques such as ordination and clustering that include this relative abundance component also will be difficult to interpret, as will the 'functional group' approach to community assessment (Greenslade & Halliday 1983; Andersen 1995). I did not directly test the measures and indices mentioned here because it makes no sense to do so. For most measures, species identity is not important so that an increase in the relative abundance of one species may be offset by a decrease in another, leading to no change in the index despite real changes in relative abundance.

Directly evaluating the bias in the relative-abundance data, as done here, provides a more powerful test of the reliability of these measures.

Species-richness and species-composition data were biased by habitat structure but were seriously affected only by the most dense habitat structure class (Figs 4,5,6). This effect appears to be due to the effect of habitat structure on capture probabilities. Assuming that the frequency of occurrence data reflect the probability of capturing a species when it is actually present, there was a tendency for capture probabilities to increase as the habitat became more open but the main effect of habitat structure on capture probabilities involved the most dense habitat, in which frequency of occurrence was very low for many species (Table 2). This resulted in species compositions for the dense 'unmodified' plots that were essentially a small and random sample of the more common species present at the experimental site. Thus, species richness estimates were lower and species composition estimates were different for the dense plots compared to the more
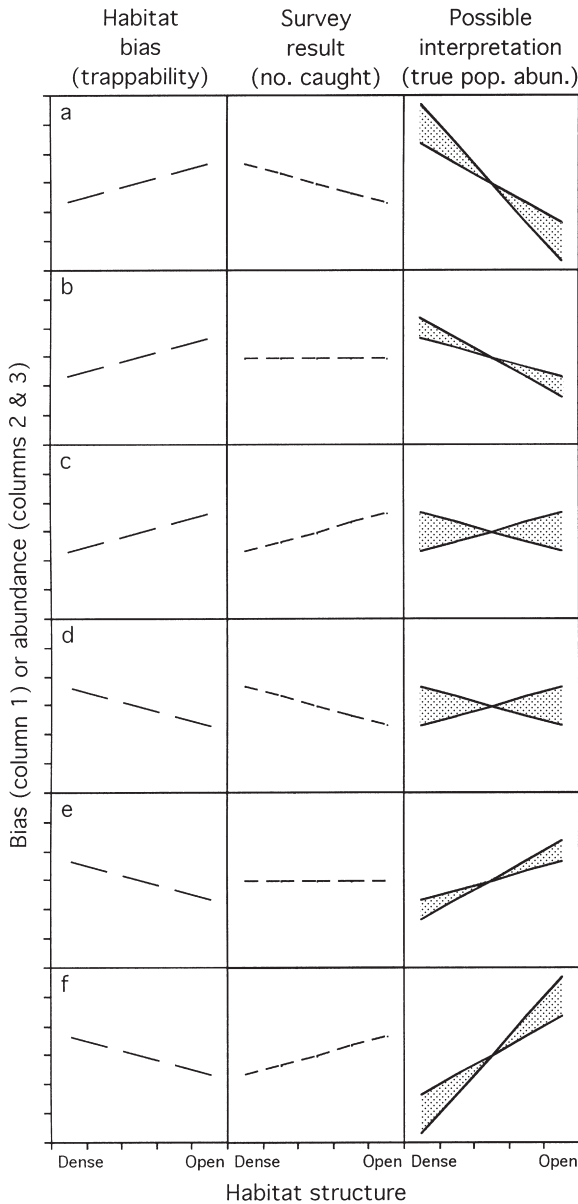

Fig. 7. Possible interpretations of abundance data in pitfall-trap surveys for different patterns of bias caused by habitat structure. The first column shows the pattern of bias (or trappability) in relation to habitat structure. This might, for example, be determined experimentally. For simplicity, the relationship between the bias (log measured abundance minus log real abundance) and habitat structure is shown as a linear function. The second column shows the number of animals caught in a hypothetical field survey of sites with different habitat structure. The third column shows the possible interpretation of field-survey data (i.e. the true population abundance) given the bias but assuming that only the direction of the bias (the sign of the slope in column one) is known. Shading indicates that the slope of the line may vary. It is only possible to determine the difference in the true abundance between survey sites with different habitat structure (column three) when the survey results (column two) have a different pattern to the bias (a, b, e, f). Further, in these cases it is only possible to determine the direction of the difference in the true abundance, not the magnitude of the difference (i.e. in the third column, the sign of the slope may be determined but not the gradient). When the survey results have the same pattern as the bias, any interpretation is possible (i.e. in the third column, neither the sign nor the gradient of the slope may be determined; c, d), in which case no confident conclusions can be drawn. Note also that, when bias is present, 'no difference between survey sites' is a possible interpretation only when the survey result has the same pattern as the bias (i.e. in the third column, the slope can only equal zero in c and d). It follows that, since no confident conclusions can be drawn for (c) and (d), one can never be confident of a 'no difference' conclusion when bias due to habitat structure is present. When there is no bias (not shown here) it is possible to determine both the direction and the magnitude of the difference in abundance. The habitat structure axis is arbitrary but could, for example, represent a gradient from dense to open habitats.

open plots (Figs 4,5,6). There was less difference in frequency of occurrence between the more open habitat classes ('litter removed' and 'cleared'; Table 2), which was reflected by the greater similarity in species composition and species richness estimates (Figs 4,5). This pattern, along with the sharp transitions observed for abundance data (three species out of five, Fig. 2) suggests that there is a threshold effect of vegetation density on trappability. It would be useful to conduct further studies where habitat structure is manipulated across a greater range of densities to elucidate better the functional relationship between vegetation density and trappability. In conclusion, pitfall traps can be used to assess differences in species richness, species composition, and frequency of occurrence provided that differences in habitat structure do not span such thresholds.

Modifications and additions to the pitfall trapping method would help to interpret survey data. First, field surveys could incorporate an experimental component to characterize the bias. For example, trapping could use both cleared and uncleared traps at the same location. By plotting the ratio of cleared to unmodified traps against habitat structure, the direction of the bias and shape of the bias function (i.e. Fig. 7 column 1) could be determined, including the detection of thresholds. However, consideration needs to be given to the size of manipulated areas and the length of time required for disturbances associated with manipulations to dissipate, both of which need to be determined experimentally for different taxa and different habitats. Another consideration is that inherent biases due to trap design (e.g. trap size, drift-fence length, type of preservative) have the potential to interact with habitat structure. Thus, it might be useful to vary both trap design and habitat structure. Second, attributes of habitat structure should be measured at each location. Standard suites of measurements need to be determined for different taxa but could include, for example, vegetation density, vegetation height, microtopography (surface roughness), and temperature near the ground. It is unlikely that any one method (e.g. clearing alone) would provide a standard protocol but experimental manipulations, further discussed below, in conjunction with measurement of habitat structure, could provide enough information to determine important properties of the bias.

Mechanisms and future experiments

It will be necessary to consider mechanisms so that better generalisations can be made about how trappability will be affected by habitat structure for which taxa and in what way. The trappability of animals changes with habitat structure, either because of a dilution effect or because of effects on the movement behaviour of animals. The dilution hypothesis stems from the fact that habitats with a more complex structure have more surface area available for animals to move around on, hence, the number of pitfall traps per unit area is effectively reduced. For example, in dense vegetation, animals may move around not only on the ground but also above the ground. Thus, while population or community measurements are traditionally calculated as if the surface of the ground was two dimensional, animals perceive the surface area of the habitat in three dimensions. The importance of this effect will be related to the scale at which the organism perceives its environment so that, for example, grass will add significant surface area for a small invertebrate like an ant but little surface area for a reptile or small mammal.

Two hypotheses have been suggested to explain why changes in movement behaviour occur: (i) because of changes in microclimate (Honék 1988) and (ii) because of the response of the species to the physical layout of the habitat (Greenslade 1964; Crist et al. 1992). In the first hypothesis, several effects of habitat structure on the microclimate near the ground are expected, including changes to solar radiation, humidity and temperature (Geiger 1965). The potential effect of increasing temperature is usually regarded as resulting from faster movement or more movement activity overall (Honék 1988). While temperature clearly plays a part in pitfall-trap catches at the larger scale in relation to weather (Honék 1988; Niemelä et al. 1989), few studies have considered the effect of temperature in relation to the microclimate resulting from habitat structure. Honék (1988) and Wallin (1985) considered higher catches of some species on bare ground exposed to the sun to be due to the thermophilic nature of the species but their evidence is anecdotal. In any case, the effect of habitat structure on temperatures near the ground will be complex and will depend on the time of day and the season (Geiger 1965). For example, at night, temperatures on bare ground could be lower than a habitat with dense ground cover because of greater convective and radiative losses. Thus, effects of habitat structure due to temperature and other microclimatic factors will depend on the diurnal and seasonal timing of activity for a given species.

The second hypothesis is that changes in movement behaviour will result because of the response of species to the physical layout of the habitat. This includes effects on the shape of movement pathways, including effects on tortuosity and net displacement, which will affect the susceptibility of the animal to capture (Crist & Wiens 1995) and will be dependent on the spatial scale at which the animal perceives habitat structure (Crist et al. 1992; Wiens et al. 1995). Speed of movement also may be affected due to the impedance of the habitat (Greenslade 1964). Morrill et al. (1990) found that speed of movement was an important determinant of pitfall-trap efficiency for some carabids and tene-

brionids, and Andersen (1983) and Greenslade (1973) have observed that ants that move fast are especially prone to capture in pitfall traps. However, the effect of speed of movement appears to be variable among species since Halsall & Wratten (1988) could find no effect of speed of movement on pitfall-trap catches of carabids.

In summary, the effect of habitat structure on trappability could involve effects of dilution, microclimate and response of the species to the physical layout of the habitat, acting independently or in concert. Well-designed experiments will be needed to determine the most important mechanisms for different taxa. Examples include simultaneous manipulation of habitat structure and microclimate, simultaneous manipulation of surface area and other attributes of habitat structure (to distinguish between the dilution hypothesis and other mechanisms), and variation in the size and shape of cleared areas (to determine the role of diffusion processes). Such experiments may allow better generalisations to be made about the effect of habitat structure on trappability for different taxa and could point to modifications that would improve the pitfall trapping method.

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REFERENCES

Abensperg-Traun M., Smith G. T., Arnold G. W. & Steven D. E. (1996) The effects of habitat fragmentation and livestock-grazing on animal communities in remnants of gimlet *Eucalyptus salubris* woodland in the Western Australian wheatbelt. 1. Arthropods. *J. Appl. Ecol.* **33**, 1281–301.

Adis J. (1979) Problems of interpreting arthropod sampling with pitfall traps. *Zool. Anz.* **202**, 177–84.

Andersen A. N. (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. (1995) A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. *J. Biogeogr.* **22**, 15–29.

Andersen A. N. & Reichel H. (1994) The ant (Hymenoptera, Formicidae) fauna of Holmes Jungle, a rainforest patch in the seasonal tropics of Australia's Northern Territory. *J. Aust. Entomol. Soc.* **33**, 153–8.

Baars M. A. (1979) Catches in pitfall traps in relation to mean densities of carabid beetles. *Oecologia* **41**, 25–46.

Belbin L. (1991) Semi-strong hybrid scaling, a new ordination algorithm. *J. Veg. Sci.* **2**, 491–6.

Belbin L. (1994) *PATN, Pattern Analysis Package: Technical Reference*. CSIRO Division of Wildlife & Ecology, Canberra.

Cárcamo H. A., Niemelä 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. (1993) Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* **18**, 117–43.

Cole E. C., McComb W. C., Newton M., Chambers C. L. & Leeming J. P. (1997) Response of amphibians to clearcutting, burning, and glyphosate application in the Oregon coast range. *J. Wildl. Manag.* **61**, 656–64.

Crist T. O., Guertin D. S., Wiens J. A. & Milne B. T. (1992) Animal movement in heterogeneous landscapes: an experiment with *Eleodes* beetles in shortgrass prairie. *Funct. Ecol.* **6**, 536–44.

Crist T. O. & Wiens J. A. (1995) Individual movements and estimation of population size in darkling beetles (Coleoptera: Tenebrionidae). *J. Anim. Ecol.* **64**, 733–46.

Dennis P., Young M. R., Howard C. L. & Gordon I. J. (1997) The response of epigeal beetles (Col.: Carabidae, Staphylinidae) to varied grazing regimes on upland *Nardus stricta* grasslands. *J. Appl. Ecol.* **34**, 433–43.

Digweed S. C., Currie C. R., Cárcamo H. A. & Spence J. R. (1995) Digging out the 'digging-in effect' of pitfall traps: Influences of depletion and disturbance on catches of ground beetles (Coleoptera: Carabidae). *Pedobiologia* **39**, 561–76.

Faith D. P., Minchin P. R. & Belbin L. (1987) Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* **69**, 57–68.

Fisher R. A. (1935) *The Design of Experiments*, 1st edn. Oliver and Boyd, Edinburgh.

Geiger R. (1965) *The Climate near the Ground*, 4th edn. Harvard University Press, Cambridge, Massachusetts.

Gomez D. M. & Anthony R. G. (1996) Amphibian and reptile abundance in riparian and upslope areas of five forest types in western Oregon. *Northwest Sci.* **70**, 109–19.

Greenberg C. H., Neary D. G. & Harris L. D. (1994) Effect of high-intensity wildfire and silvicultural treatments on reptile communities in sand-pine scrub. *Conserv. Biol.* **8**, 1047–57.

Greenslade P. J. M. (1964) Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *J. Anim. Ecol.* **33**, 301–10.

Greenslade P. J. M. (1973) Sampling ants with pitfall traps: digging-in effects. *Insectes Soc.* **20**, 343–53.

Greenslade P. J. M. & Halliday R. B. (1983) Colony dispersion and relationships of meat ants *Iridomyrmex purpureus* and allies in an arid locality in South Australia. *Insectes Soc.* **30**, 82–99.

Hadden S. A. & Westbrooke M. E. (1996) Habitat relationships of the herpetofauna of remnant buloke woodlands of the Wimmera plains, Victoria. *Wildl. Res.* **23**, 363–72.

Halsall N. B. & Wratten S. D. (1988) The efficiency of pitfall trapping for polyphagous predatory Carabidae. *Ecol. Entomol.* **13**, 293–9.

Honék A. (1988) The effect of crop density and microclimate on pitfall trap catches of Carabidae, Staphylinidae (Coleoptera),

and Lycosidae (Araneae) in cereal fields. *Pedobiologia* **32,** 233–42.

International Commission of Zoological Nomenclature (1985) *International Code of Zoological Nomenclature*, 3rd edn. International Trust for Zoological Nomenclature in association with British Museum (Natural History), London.

Joose E. N. G. & Kapteijn J. M. (1968) Activity-stimulating phenomena caused by field-disturbance in the use of pitfall traps. *Oecologia* **1,** 385–92.

Luff M. L. (1975) Some features influencing the efficiency of pitfall traps. *Oecologia* **19,** 345–57.

Magurran A. E. (1988) *Ecological Diversity and its Measurement*. Croom Helm, London.

Margules C. R. (1993) The Wog Wog habitat fragmentation experiment. *Environ. Conserv.* **19,** 316–25.

May R. M. (1975) Patterns of species abundance and diversity. In: *Ecology and Evolution of Communities* (eds M. L. Cody & J. M. Diamond), pp. 81–120. Harvard University Press, Cambridge.

McCullagh P. & Nelder J. A. (1989) *Generalised Linear Models*, 2nd edn. Chapman and Hall, London.

Melbourne B. A., Gullan P. J. & Su Y. N. (1997) Interpreting data from pitfall-trap surveys: crickets and slugs in exotic and native grasslands of the Australian Capital Territory. *Mem. Mus. Vict.* **56,** 361–7.

Mitchell B. (1963) Ecology of two carabid beetles, *Bembidium lampros* (Herbst) and *Trechus quadristriatus* (Schrank). II. Studies on populations of adults in the field, with special reference to the technique of pitfall trapping. *J. Anim. Ecol.* **32,** 377–92.

Morrill W. L., Lester D. G. & Wrona A. E. (1990) Factors affecting the efficiency of pitfall traps for beetles (Coleoptera: Carabidae and Tenebrionidae). *J. Entomol. Sci.* **25,** 284–93.

Niemelä J., Haila Y., Halma E., Pajunen T. & Punttila P. (1989) The annual activity cycle of carabid beetles in the southern Finnish taiga. *Ann. Zool. Fenn.* **26,** 35–41.

Niemelä J., Halme E. & Haila Y. (1990) Balancing sampling effort in pitfall trapping of carabid beetles. *Entomol. Fenn.* **1,** 233–8.

Perfecto I. & Snelling R. (1995) Biodiversity and the transformation of a tropical agroecosystem: ants in coffee plantations. *Ecol. Applic.* **5,** 1084–97.

Pielou E. C. (1975) *Ecological Diversity*. Wiley, New York.

Punttila P., Haila Y., Niemelä J. & Pajunen T. (1994) Ant communities in fragments of old-growth taiga and managed surroundings. *Ann. Zool. Fenn.* **31,** 131–44.

Samways M. J., Caldwell P. M. & Osborn R. (1996) Ground-living invertebrate assemblages in native, planted and invasive vegetation in South Africa. *Agric. Ecosyst. Environ.* **59,** 19–32.

Sneath P. H. A. & Sokal R. R. (1973) *Numerical Taxonomy*. W. H. Freeman and Company, San Francisco.

Southwood T. R. E. (1978) *Ecological Methods*, 2nd edn. Chapman and Hall, London.

Spence J. R. & Niemelä J. K. (1994) Sampling carabid assemblages with pitfall traps: the madness and the method. *Can. Entomol.* **126,** 881–94.

Thiele H. U. (1977) *Carabid Beetles in their Environments*. Springer Verlag, Berlin.

Thomas D. B. & Sleeper E. L. (1977) The use of pitfall traps for estimating the abundance of arthropods, with special reference to the Tenebrionidae (Coleoptera). *Ann. Entomol. Soc. Am.* **70,** 242–8.

Topping C. J. (1993) Behavioural responses of three linyphiid spiders to pitfall traps. *Entomol. Exp. Appl.* **68,** 287–93.

Topping C. J. & Sunderland K. D. (1992) Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. *J. Appl. Ecol.* **29,** 485–91.

Wallin H. (1985) Spatial and temporal distribution of some abundant carabid beetles (Coleoptera: Carabidae) in cereal fields and adjacent habitats. *Pedobiologia* **28,** 19–34.

Whicker A. D. & Tracy C. R. (1987) Tenebrionid beetles in the shortgrass prairie: daily and seasonal patterns of activity and temperature. *Ecol. Entomol.* **12,** 97–108.

Wiens J. A., Crist T. O., With K. A. & Milne B. T. (1995) Fractal patterns of insect movement in microlandscape mosaics. *Ecology* **76,** 663–6.