



Spatial variability in species composition in birds and insects

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If spatial patterns of change within a habitat were similar for both vertebrates and insects, then vertebrates would provide useful surrogates for designing reserves for the conservation of invertebrates. Data from two eucalypt habitats were analysed to determine levels of habitat richness, site richness and species turnover in birds and insects. For birds the relatively low species richness and turnover indicated that sites within the habitat were similar in composition. In wet eucalypt forests Diptera were very speciose with over 1,000 morphospecies sorted. Species turnover was slightly higher than for birds, indicating a large number of species change from site to site. In dry eucalypt woodland, insects trapped through the winter months were not speciose but turnover between sites was very large. This suggests reserves designed to conserve insects may need to be larger than for birds in order to include the high site variability and richness of insect communities.

Spatial patterns of birds and insects were investigated further, to determine if sites that were closer together were more similar for both birds and insects. No patterns were found for birds in either habitat suggesting birds are not responding to changes in the environment at this scale. Diptera in wet eucalypt forest showed higher similarity between close sites than distant sites, while for winter insects in dry eucalypt woodland the relationship was significant when two outlier points were removed. Overall, birds are not good surrogates for insects in either habitat as no relationship between birds and insects in site-to-site similarity was found.

Keywords: turnover, species richness, spatial variability, birds, Diptera

Introduction

Species composition within a habitat is expected to change through time and space (MacArthur, 1965; Cornell, 1985; many examples summarized in Begon *et al.*, 1996). Local processes (e.g., predation, stochastic events and immigration) and the natural variability in environmental parameters over relatively small spatial scales (i.e., habitat heterogeneity), influence spatial and temporal patterns of change (e.g., Clark and Clark, 1984; Weiher and Boylen, 1994; Kaspari, 1996; Partel *et al.*, 1996). An understanding of the spatial and temporal variability within a habitat should, therefore, be an integral part of the planning of reserves to conserve the biological diversity of a habitat.

Conserving biodiversity is usually envisaged to be accomplished when part of the habitat is placed in a reserve. I use the term 'habitat' as a synonym for vegetation community as vegetation communities are typically adopted by land managers as a mechanism for partitioning a landscape into manageable units. It is assumed that species will use the whole distribution of a vegetation community as a habitat and that habitats are homogeneous with respect to species composition.

Therefore, a reserve that encompasses part of a habitat will conserve all species occupying that habitat. However, if species composition varies over greater spatial scales than that part of the habitat within a reserve, then the reserve will fail to adequately preserve the biological diversity within that habitat. As such, managers need to understand the rate of change of species composition from site to site and with a site through time.

For a particular habitat there will be a species list which encompasses all species found at all sites within that habitat, often termed habitat diversity or species richness. There is confusion in the literature regarding the use of the term 'diversity', which is used as a weighted index of richness (incorporating abundance), and as a measure of species richness without correcting for abundance. To avoid this confusion, I will use richness as a measure of the number of species in a defined area. The relationship between regional (or habitat) richness and the richness found at a particular site is quantifiable (Whittaker, 1972; Wilson and Shmida, 1984; Harrison *et al.*, 1992). Some taxa may have a high site richness relative to habitat richness resulting in species composition changing little from site to site.

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There is high overlap and therefore low turnover from site to site. At the other extreme some taxa may have low site richness relative to the habitat richness, resulting in species composition changing dramatically from one site to the next. There is low overlap and therefore a high turnover of species composition from site to site within a habitat. These taxa pose a difficulty for managers to conserve, as many sites are needed for the protection of all species in a habitat.

Furthermore, if local processes are important in determining the composition of species at a site, then sites that are closer are expected to be more similar. As one moves through a habitat there should be a change of species composition from the beginning to the end with the two most distant sites being least similar. If this is true, this provides a mechanism to design reserves incorporating spatial variability. In this particular case, spatial variability is predictable over geographic distance.

For any particular taxon, it would be useful to know the richness in a habitat, the level of turnover from site to site and whether turnover is predictable with geographic distance within a habitat. This will clearly aid in reserve design. It would also be valuable to be able to generalize to other similar habitats. So the question arises, 'Is the turnover rate from site to site consistent for a particular taxon when you move to another similar habitat?' This paper compares the rates of turnover and similarity between sites for two taxa surveyed in two similar habitats in southeastern Australia. Birds and insects were used for this comparison as insects are rarely utilized in reserve design and are either ignored, or assumed to vary in the same way as vertebrate groups, such as birds.

Methods

Surveys of insects and birds were undertaken in two habitats at sites that spanned distances of 60–150 kilometres. Wet eucalypt forest, dominated by *Eucalyptus pilularis*, blackbutt, occur on coastal slopes from Bundaberg in Queensland to Bega in southern NSW, a latitudinal distance of over 1000 km (Chippendale, 1988). The forests are important for timber production and range from drier forests with a sclerophyllous understorey to wetter forests on higher slopes and richer soils. Wetter forests have a mesic understorey with rainforest species common. Eight sites in the wet eucalypt forest were sampled over a two-year period (July 1995–March 1997) every four months (six sampling periods). At each site, Diptera were sampled using three modified flight intercept traps set out for one

week. Insects were caught using a black net, 1 m², stretched between poles with a trough below to catch animals that fell from the netting. At the top, a funnel, leading to a collecting jar, caught those species that attempted to fly over the netting. Samples were sorted to morphospecies. Birds were also censused at each site along a 600 × 50 m transect (3 ha). An observer walked through the centre of this transect for two hours recording all species seen and heard within the transect. Data are pooled over all time periods for this analysis. The eight sites were within 60 kilometres of each other and were situated in the Taree/Wauchope district (32° 40'S, 152° 45'E) which is near the centre of the distribution of blackbutt communities.

Dry eucalypt woodland was sampled in 1995 in the Sydney district (34° 00'S, 151° 00'E). Ten sites on ridge tops or upper slopes were sampled. The sites were dominated by a variable combination of *Eucalyptus sieberi* (silvertop ash), *E. haemastoma/racemosa* (scribbly gum) and *E. gummifera* (bloodwood). These woodlands occur on poor sandy soils and have a sclerophyllous dense understorey. Sites were sampled every month for five months from May to September. Birds were surveyed at each site for two hours using eight spot counts, each of radius 30 m (total of 2.26 ha), that were placed consecutively along a 480 m transect. Spot counts were pooled for each transect. Flying insects were sampled using two flight intercept traps placed out for one week. All insects were sorted to morphospecies and months were pooled for each site.

Some differences in methodology between the two habitats exist. The dry sclerophyll woodland was sampled intensively during the cooler months of one year. The dry sclerophyll woodland estimates, therefore, represent only winter species of invertebrates and birds in that community. Birds are unlikely to vary widely as only a small proportion of the bird community are summer migrants and winter samples are therefore likely to record most species. However, insect composition is likely to be very different between seasons and the interpretation is restricted to understanding spatial patterns of winter insects. The sampling regime in wet sclerophyll forest has been shown to sample the majority of Diptera in the sampling area and therefore provides a good estimate of overall richness (French, unpublished). The difference in methodology of sampling birds for these two studies is not believed to influence the results. Investigation of the species accumulation curves revealed that both techniques sampled the bird communities well and therefore provide good estimates of richness in these habitats. The increased area sampled per unit time in



wet sclerophyll forests is related to a more experienced team of observers during this study.

Beta diversity (Whittaker, 1972) was calculated for each taxon in each habitat. There are a range of measures of species turnover which have been evaluated in the literature (Whittaker, 1972; Wilson and Shmida, 1984; Harrison *et al.*, 1992). However, the original measure of turnover (Whittaker, 1972) has been found to be most useful and robust (Wilson and Shmida, 1984). Beta diversity is calculated: $\beta = s/\alpha - 1$, where s = the total number of species in the study area, and α = the average number of species found within the sites.

Association matrices using the Bray Curtis similarity measure were initially calculated for each dataset and sites were ordinated using non-metric multi-dimensional scaling (Carr, 1996). The Bray Curtis measure of similarity for each pair of sites was then regressed with distance between these sites. Anosim analysis was used to determine if differences occurred between northern, central and southern sites within each habitat. To determine the ability of birds to predict insect patterns, the similarity matrices were correlated using 'Relate' in the Primer package.

Results

Habitat diversity and turnover

For birds, the two habitats were consistent in species richness and turnover (Table 1). Relative to insects, birds had very low richness with a maximum of 73 species being recorded in wet eucalypt forests overall. Richness at the regional level was only twice that of site richness in both habitats, resulting in the two lowest measures of turnover in this study.

Sampling in wet eucalypt forests revealed large numbers of species of flies, despite the fact that Chironomids were not sorted due to difficulties in separating adults into morphospecies. On average, sites yielded 480 species of Diptera from over one thousand species found

Table 1. Richness and Whittaker's measure of turnover for birds and insects in two eucalypt habitats. Richness is the number of species recorded.

	Wet eucalypt forest		Dry eucalypt woodland	
	Birds	Diptera	Birds	Insects
Regional richness	73.0	1065.0	54.0	311.0
Average site richness	26.9	480.1	36.2	73.5
Species turnover	1.02	1.21	1.08	3.23

throughout the sampling area. Turnover therefore was only marginally higher than that for birds although a large number of species changed from site to site because of the high species richness of the habitat.

Samples of insects in dry sclerophyll woodland in winter revealed only a few species. During this time period sites were very different to each other. Regional richness was four times higher than average site richness resulting in a very high turnover. The samples of insects from the two habitats showed little consistency in either habitat diversity or turnover.

Spatial patterns of variability

For birds, ordination analysis revealed few predictable patterns in either habitat (Fig. 1a and c). Sites were spread randomly and no grouping occurred in relation to geographic distance (Wet euc. forest: Global R = 0.175, $p = 0.24$; dry euc. woodland: Global R = 0.120, $p = 0.21$). Sites that were closer together were not more similar than those further apart (Wet euc. forest: $r^2 = 0.02$, $p = 0.52$; dry euc. woodland: $r^2 = 0.01$, $p = 0.43$; Fig. 2a and c).

In contrast, insect turnover was more predictable in space. Ordination analysis revealed good separation geographically, particularly for Diptera in wet eucalypt forest. (Fig. 1b and d). The more northern sites were not significantly different to the southern sites, but both were more different from the central sites (Global R = 0.800, $p = 0.005$). Regression analysis revealed a strong significant relationship ($r^2 = 0.57$, $p = 0.00$; Fig. 2b). The pattern in dry eucalypt woodland was not so clear (Fig. 2d). Northern sites were significantly different to southern sites with the central sites not differing from either. The regression analysis was not significant ($r^2 = 0.003$, $p = 0.29$), however, when the two outlier points were excluded from the analysis, the relationship between distance and similarity was significant ($r^2 = 0.08$, $p = 0.03$).

Patterns of similarity between sites for birds cannot be used to predict the similarity for insects in either habitat. No correlation between the two data sets was found (wet eucalypt forest: Global RHO = 0.025, $p = 0.45$; dry eucalypt woodland: Global RHO = 0.12, $p = 0.21$).

Discussion

For birds, species turnover was consistent between habitats. The low to moderate turnover and richness of birds indicates that a few sites can encompass the full suite of species found in the habitat. Designing reserves, using only this criteria, would result in

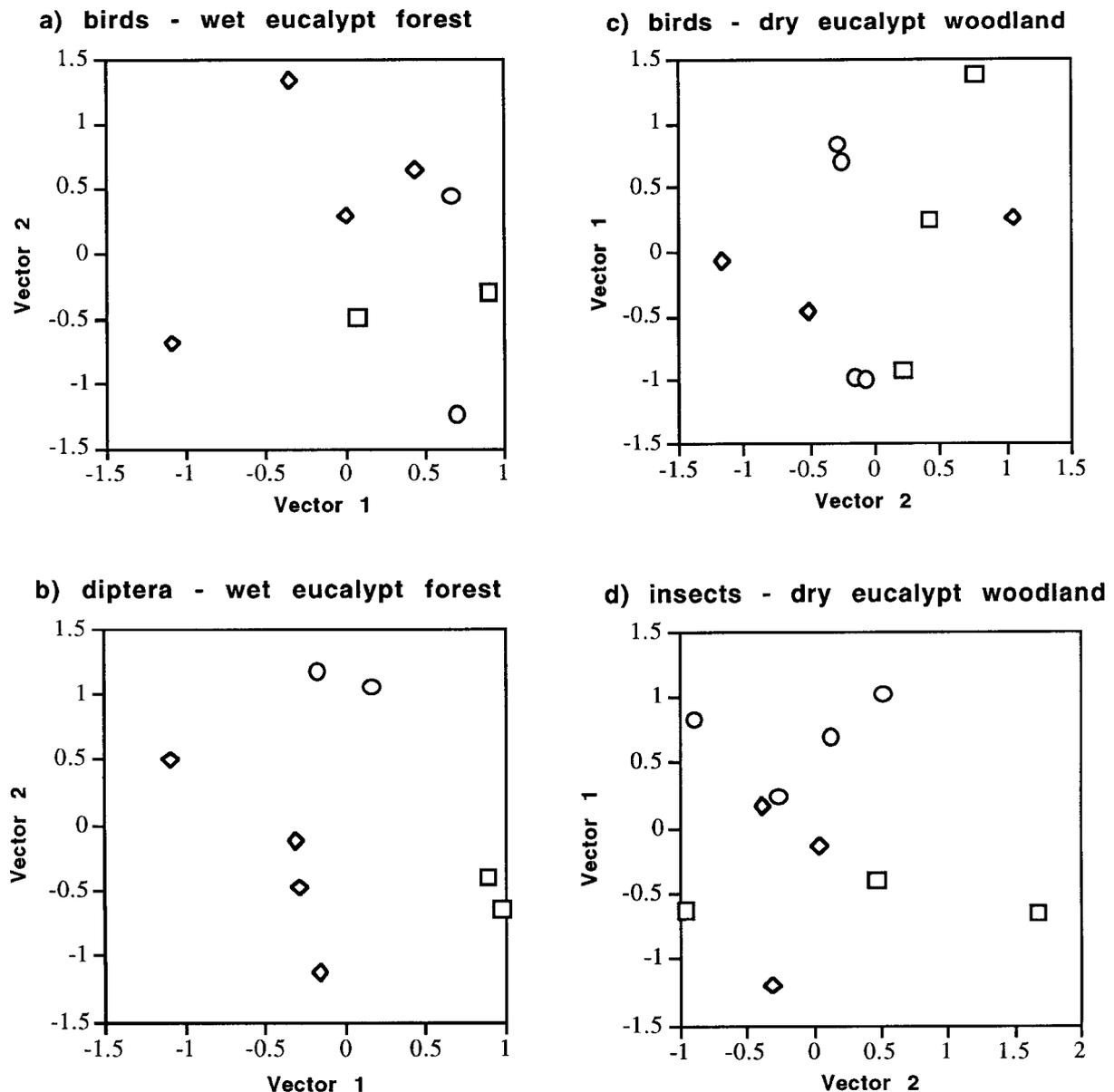


Figure 1. Ordination analysis of birds and insects in wet eucalypt forest and dry eucalypt woodland. Squares represent the northern sites within the habitat, triangles represent the central sites and circles represent the southern sites.

relatively small reserves for birds, relative to insects. However, using only species richness to determine reserve design ignores processes important to the viability of species (e.g. minimum population sizes, home range size, probability of extinction, seasonal uses of habitats) which must be incorporated for sensible management.

Furthermore, for birds, there was little evidence that any changes in species composition were related to a linear change in the landscape within the two habitats studied. At this scale of study, birds do not respond to

geographic factors that change through the landscape. There appears more predictability with larger spatial scales. At a scale of hundreds of kilometres, Cody (1993) found that turnover in bird composition increased with increasing distance between sites in rainforest communities and in semi-arid communities. This indicates that larger spatial scales are likely to be important in designing reserves to conserve the diversity of birds.

In contrast, for invertebrates, species turnover and similarity between sites suggest that smaller spatial scales might be important. On the north coast, species

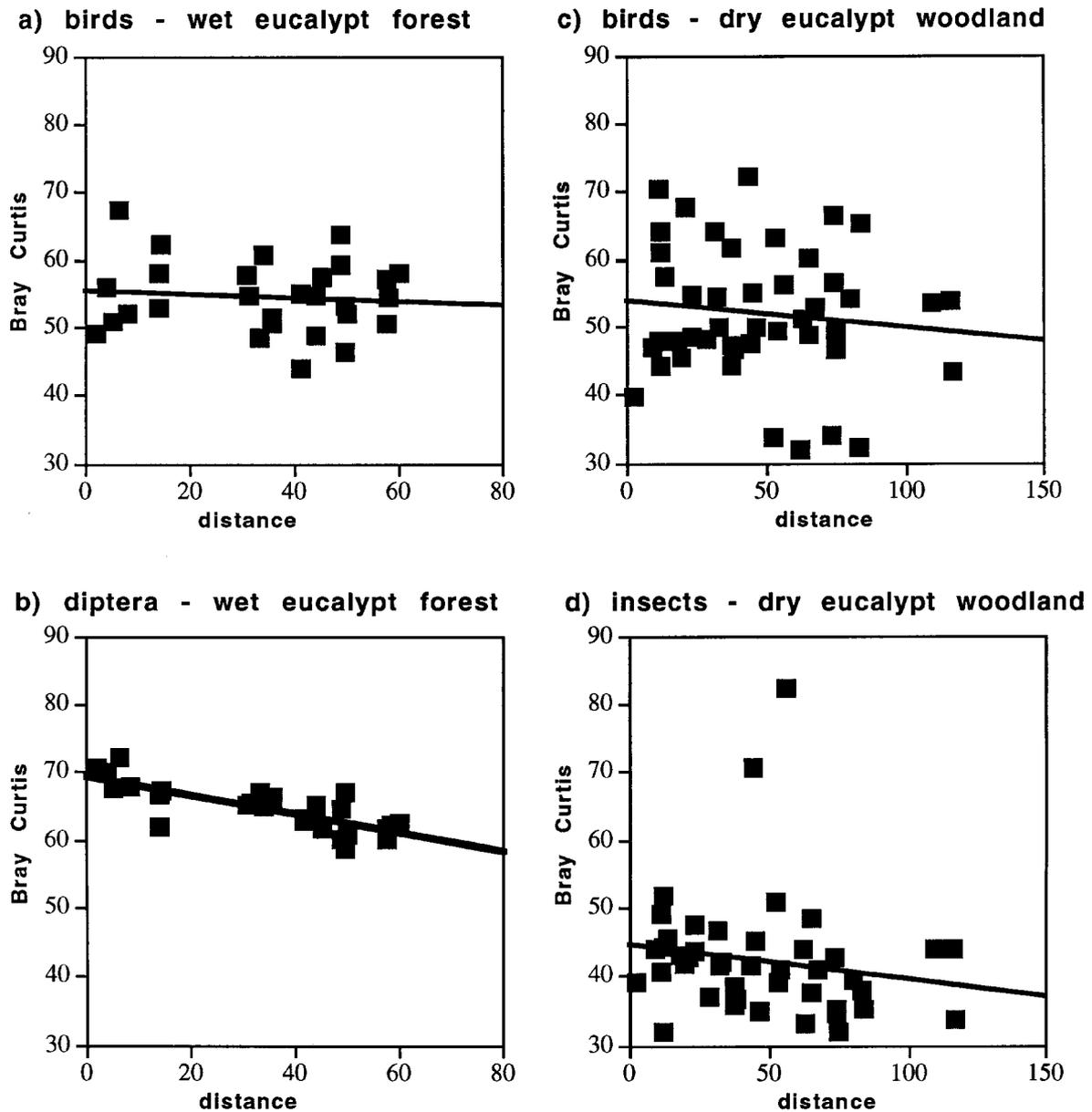


Figure 2. Regression analysis of similarity between sites with distance for birds and insects in wet eucalypt forest and dry eucalypt woodland. Similarity is measured using Bray Curtis indices of similarity. For birds, the regression was not significant for either habitat (Wet euc. forest: $r^2 = 0.02$, $p = 0.52$; dry euc. woodland: $r^2 = 0.01$, $p = 0.43$). For insects the regression was significant ($r^2 = 0.57$, $p = 0.00$) in wet eucalypt forest and in dry eucalypt woodland when the two outlier points were removed from the analysis ($r^2 = 0.08$, $p = 0.03$).

richness of flies was high in wet eucalypt forests. Even accompanied with a moderate rate of turnover, this result suggests that in order to include all species in a reserve, the number of reserves or the size of reserves will have to be greater than that for birds. Turnover was predictable across the landscape with closer sites showing greater similarity than more distant sites. This implies that reserves for flies in wet sclerophyll forest

must be situated throughout the habitat and further work may allow an understanding of the frequency of the reserves across the habitat. For the dry eucalypt woodland, data so far suggest that there is lower diversity of insect species in winter months. However, the very high turnover from site to site means more or larger reserves are needed to ensure conservation of these species.



Species richness at a site gives no information on the size of habitat necessary for an individual. Nor does it provide information on whether other habitats are necessary. As with birds, a knowledge of ecological processes needs to be included in reserve design to ensure that population sizes, essential habitats and evolutionary potential are conserved: factors likely to increase the amount of habitat needed in reserves rather than decrease it. Because of this lack of knowledge, using the presence of a species at a site in order to design reserves is fraught with difficulties as the assumption is that conserving the site will conserve those species currently present in it. While we know a great deal about the size of home ranges of birds, our understanding for each insect species is virtually non-existent.

The interaction between spatial and temporal patterns needs to be investigated further (Lowman, 1982). This is suggested by the data from dry eucalypt woodland which represent a set of regular monthly samples pooled for the purposes of this study. The low diversity but high turnover in these winter invertebrates would be masked in an analysis collected over the whole year and then pooled. In this situation, summer invertebrates are likely to dominate the sample and determine the results. Management decisions based on such analyses may affect the conservation of these winter species with significant impacts on the community through loss of insects at a crucial time.

Surrogacy is a highly sought-after methodology by land managers (Margules and Stein, 1989; Ryti, 1992; Oliver *et al.*, 1998). The idea of only managing for one or a few easily measured taxa, knowing that this taxa reflects the responses of other taxa, is an economically palatable concept, although the scientific proof behind the idea is scant. However, if the similarity between close sites is greater than between further sites for a range of taxa, then one taxa can be used as a surrogate for another taxa in determining the frequency of reserve placement in the landscape. In terms of management it would be economically useful to use vertebrates as surrogates for invertebrates. Our study showed that birds are not good surrogates for invertebrates and that within a habitat, these taxa do not follow the same spatial patterns of diversity. This complements other studies which have shown similar results when surrogacy has been looked at between habitats and regions (e.g., Wilcox *et al.*, 1986; Kremen, 1992; Prendergast *et al.*, 1993; Oliver *et al.*, 1998). A reserve system designed for bird conservation is unlikely to conserve invertebrate diversity.

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