



Equal diversity in disparate species assemblages: a comparison of native and exotic woodlands in California

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ABSTRACT

The species richness of ecosystems can remain stable over time, despite changes in species composition and changes in the dominant plant species. While this pattern of stability is known to occur temporally, it has been examined poorly in a spatial context. To examine this spatially, the species richness, diversity and composition of native woodlands (of oak and bay trees) and exotic woodlands (of eucalypt trees) were compared in California. Species richness was nearly identical for understorey plants, leaf-litter invertebrates, amphibians and birds; only rodents had significantly fewer species in eucalypt sites. Species diversity patterns (using the Shannon–Wiener Index) were qualitatively identical to those for species richness, except for leaf-litter invertebrates, which were

significantly more diverse in eucalypt sites during the spring. Species composition was different between sites, as evidenced by a principal components analysis, coefficients of similarity, and the relatively few species shared between native and eucalypt sites. Thus, the consistency in richness and diversity observed for most groups, in most seasons, occurred despite significant differences in species composition. These results are consistent with previous demonstrations of temporal stability, suggesting that species richness may often be stable, both temporally and spatially, despite changes in composition and regardless of the dominant vegetation.

Key words Amphibians, birds, California, *Eucalyptus globulus*, invertebrates, mammals, plants, *Quercus agrifolia*, species richness, stability.

INTRODUCTION

The processes that determine the richness, i.e. numbers, of species for any given location have been the focus of much research in ecology and biogeography (e.g. Ricklefs & Schluter, 1993; Brown & Lomolino, 1998). Brown *et al.* (2001) have suggested that species richness, an emergent property of ecosystems, may often be relatively stable over time. They show that richness of species has remained relatively constant despite large changes in species composition, in three different systems: a rodent assemblage in Arizona, USA that shifted from a desert grassland to a desert shrubland (over 22 years), a bird assemblage in Michigan, USA that shifted from a post-logging shrubland to a closed-canopy forest (over 50 years) and, using pollen records, two plant assemblages in Europe that had various shifts in composition (over c. 10 000 years). They suggest that this pattern of stability can occur whenever the factors determining productivity, i.e. the availability of energy or other limiting resources, are

relatively constant and when the regional pool of species is sufficiently large to create an opportunity for compensatory colonizations and extinctions (see Brown *et al.*, 2001 for other potentially important conditions). They speculate further that these conditions should be met most strongly, not on islands or island-like habitats, but instead in non-isolated ecosystems where rates of immigration from the regional pool of species are highest. If this is correct, the richness of ecosystems should commonly be relatively fixed, even in the face of large changes in the dominant vegetation and regardless of changes in species composition. If this pattern can be shown to be robust, then the characterization of species richness will have progressed significantly.

In support of the pattern, an initial survey of the literature by Brown *et al.* (2001) lists 20 studies whose data show relatively fixed richness values, despite changes in species composition. Ideally, numerous additional studies with data that are relevant to this pattern would be examined in a variety of ecologically diverse settings. Unfortunately, however, there are probably only a limited number of such studies, since long-term records of both species numbers and composition in relatively non-isolated systems are uncommon. Therefore, it may be profitable to examine alternative forms of evidence.

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One possibility is to consider whether this temporal pattern, i.e. stable richness through time, has a spatial analogue, i.e. stable richness between sites. This would involve comparing sites that are adjacent or nearby, but which differ in their dominant vegetation type. If these sites have similar levels of productivity and access to the same pool of colonizing species then they should provide a spatial analogue to the temporal comparisons made by Brown *et al.* (2001). In a spatial context, however, many sites will not meet these requirements since differences in dominant vegetation types are often due to differences in the factors determining productivity, as well as to differences in disturbance, a factor that can strongly affect species richness (e.g. Sousa, 1979). Here a comparison is made between communities where these requirements can be met: woodland habitats that are dominated by native vs. exotic trees.

Exotics are species that have been introduced by humans, or have been able to expand their range because of anthropogenic disturbances, into regions where they were not historically present. Of those species that have been introduced, only a subset establishes self-sustaining populations in the absence of human assistance, i.e. become naturalized (Sax & Brown, 2000). Their numbers, however, are still large. For example, in California alone, over 1000 species of vascular plants have become naturalized (Randall *et al.*, 1998). The effects of naturalized species are often strong and have been known to cause changes at the community, ecosystem, and landscape levels (e.g. Elton, 1958; Carlton, 1979; Mack, 1981; Case & Bolger, 1991; D'Antonio & Vitousek, 1992; Simberloff & Stiling, 1996). Indeed, exotic species pose a serious threat to biodiversity on a global scale (Crawley, 1997). Despite this threat, however, exotic species may nevertheless prove useful in understanding the underlying mechanism of many ecological processes (Sax, 2001). In particular, they can provide the context for comparisons of species richness between different vegetation types.

Species richness is expected to decline in ecosystems when exotic plants are able to exclude most or all other plant species, e.g. *Mesembryanthemum crystallinum* L. in coastal grasslands of California (Vivrette & Muller, 1977). Similarly, species richness may also be expected to change when an exotic plant has altered the disturbance regime of an ecosystem, e.g. by increasing the frequency of fire, as in *Bromus tectorum* L. in grasslands of the western United States (D'Antonio & Vitousek, 1992). Less clear, however, is whether species richness of an ecosystem will change when the dominant trees of a native forest or woodland are replaced by exotic ones, a situation in which levels of productivity and disturbance can remain relatively unaltered. Ecosystems dominated by exotic trees are often expected to have or attract a diverse set of species, as evidenced by research that examines the utility of using exotic trees as a catalyst for regenerating native vegetation (e.g. Geldenhuys, 1997; Lugo,

1997; Parrotta *et al.*, 1997). Indeed, many comparisons of species richness have previously been made in exotic and native woodlands.

In north-western Spain, where *Eucalyptus globulus* Labill. (the blue gum eucalypt) and *Pinus pinaster* Aiton have been planted, Bara Temes *et al.* (1985) found that composition and density (species richness was not reported) of leaf-litter invertebrates (surveyed with 0.063 m² core samples, collected once in each of four seasons) were similar in native forests (eight sites), eucalypt plantations (eight sites) and pine plantations (eight sites), but that the species richness of understorey plants (sampled within 1600 m² plots) was greater in native forests. In the highlands of Ethiopia, Michelsen *et al.* (1996) found that richness of understorey plants (sampled within 100 m² plots in plantations and 400 m² plots in native forests) was as high in plantations of *E. globulus* (nine sites), *E. grandis* W. Hill (four sites), *E. saligna* Sm. (six sites) and *Pinus patula* Schiede ex Schltdl & Cham. (four sites) as in native forests (four sites). In the central Mexican state of Michoacán, Garcia *et al.* (1998) found that species richness and abundance of birds (sampled with five 10-min-long point counts per site) was as high in stands of *E. camaldulensis* Dehnh. (six sites) as in native forests (79 sites). In Sabah, north-east Borneo, Chey *et al.* (1998) found that species richness of canopy arthropods (sampled with mist-blown insecticide beneath three trees per site on each of four occasions over the period of a year) was lower in plantations of *E. deglupta* Blume (five sites) than in the native forest (one site), but that these differences were considerably reduced if arthropods from the understorey vegetation of the eucalypt stands were included. Also in Sabah, Mitra & Sheldon (1993) found that species diversity of birds (using the Shannon–Wiener Index, with data sampled with replicated 3-h surveys of 9-ha sites) was as high in 7-year-old plantations of *Albizia falcataria* (L.) Fosberg (three sites) as in native forests (two sites), but was greatly reduced in younger plantations (eight sites). In Australia, Friend (1982) found that species richness of mammals (sampled with a total of 9783 trap nights, 200 h of spotlight surveys and the analysis of 663 scats) was as high in older plantations of *Pinus radiata* D. Don plantations (four sites) as in native forests (four sites), but was reduced in younger plantations (three sites), i.e. those less than five years of age. Also in Australia, Springett (1976) found that densities of soil microarthropods (surveyed with 10 core samples of 0.01 m² per site, taken once per month over the period of a year) were as high in exotic plantations of *P. pinaster* Ait. (three sites) as in a native woodland (one site), but that richness was reduced in the plantations.

Together, these studies indicate that consistency in richness occurs commonly, but not universally, and that there can be substantial variation in the response of different taxonomic components of an ecosystem, e.g. of arthropods and mammals. This suggests that comparisons will be most valuable when they investigate multiple taxonomic components of

Table 1 Site characteristics: the mean elevation, mean slope, mean slope orientation and habitat boundaries of each site

Site	Elevation	Slope	Orientation	Site boundaries
Native ₁	201 m	14.7°	NW	Native forest, riparian vegetation and grassland
Native ₂	214 m	13.5°	W	Native forest, riparian vegetation and grassland
Native ₃	427 m	14.0°	W-NW	Native forest, riparian vegetation and grassland
Eucalypt ₁	159 m	13.3°	SW	Native forest, riparian vegetation and grassland
Eucalypt ₂	201 m	12.5°	SW	Eucalypt forest and grassland
Eucalypt ₃	183 m	11.0°	W	Eucalypt forest and grassland

these systems. It also raises the issue of whether individual taxonomic components or the entire species assemblage of an ecosystem represent the best metric for these comparisons. Further, some of the above studies indicate a significant effect of plantation age upon levels of species richness, with older ones having more species, and being closer in richness to native forests than younger ones. This is probably due to successional processes and the variation in the time necessary for different species to colonize newly available habitats, indicating that comparative studies should consider differences in stand age.

Plantations of *E. globulus* in California, which were planted extensively at the beginning of the twentieth century, provide a useful comparative system. These trees, which are native to south-eastern Australia and Tasmania, are the most commonly planted eucalypt trees in the world (Jacobs, 1979). In California many *E. globulus* woodlands grow in close proximity to native woodlands. Here, these woodlands were used to compare species richness, diversity (i.e. the Shannon–Wiener Index) and composition of five taxonomic groups: vascular plants of the understorey, leaf-litter invertebrates, amphibians, rodents and birds. These comparisons test the hypothesis that species richness and diversity can remain stable spatially across ecosystems, despite differences in the dominant vegetation type, and regardless of differences in species composition.

METHODS

Study area

This study was performed in the Berkeley Hills, a coastal mountain range, east of the San Francisco Bay in central California. These mountains have loam soils and experience a mediterranean climate, with precipitation in the winter and drought throughout the remainder of the year (McBride, 1974; Welch, 1977). Common plant communities, including the percentage of area covered are as follows: grasslands 43%, native woodlands/forest 27%, shrublands 21% and introduced *E. globulus* plantations 7% (McBride, 1974). The *E. globulus* plantations were planted between 1910 and 1913 and have not been cut or burned since that time. Six study

sites were selected, three in *E. globulus* plantations and three in native forests dominated by *Quercus agrifolia* Nee (coast live oak) and *Umbellularia californica* (Hook. & Arn.) Nutt. (California bay tree). Each site was approximately 1 ha in size. Sites were not distributed contiguously, but instead spread out across the landscape (the closest two sites were approximately 0.75 km apart, while the furthest two were approximately 11 km apart). These sites were chosen to minimize physical differences in site elevation, slope and slope orientation (Table 1). Native forest sites were bordered at lower elevations by riparian vegetation, at upper elevations by grassland and at similar elevations, along either side of the site, by delineated borders with contiguous native forest (Table 1). The first eucalypt site was also bordered by riparian vegetation, grasslands and native forest, while the remaining two eucalypt sites were bordered by grassland and delineated borders with contiguous eucalypt plantations (Table 1). All sites had a well-developed understorey of plants and a substantial layer of leaf-litter.

Sampling procedures

Understorey plants

Each study site was sampled in both autumn, September–November 1991 and spring, February–April 1992. Note that these two seasons were chosen in order to contrast the wettest and driest times of the year, when presumably the largest seasonal differences in species richness and composition would be detectable. Understorey plants were sampled using 0.25 m² quadrats, in which the presence or absence of plant species were recorded. Quadrats were sampled in a stratified manner at 10-m intervals along 40-m long transects. At least five transects, placed in a parallel series at 15-m intervals, were sampled in each site. Additional transects were added if the sampling curve of cumulative number of species censused vs. number of samples taken had not plateaued (Southwood, 1978). Species present along any of the transects, but not present within the quadrats, were also recorded. Finally, species observed incidentally, but not sampled using the above procedures, were recorded as well (during approximately 23 h at each site).

Leaf-litter invertebrates

Twelve leaf-litter core samples, 155 mm in diameter, were collected at each site in late October 1991 and mid-February 1992. Core samples were collected in a stratified manner similar to that described above. After collection, samples were immediately transported to a laboratory, processed in berlese funnels (which took several days) and preserved in ethanol. All processed invertebrates were counted and identified immediately or given a unique code and identified later by a taxonomist (many were not identified to the species level and were recorded as morphological species). The invertebrates consisted primarily of arthropods: arachnids (e.g. spiders and mites) and insects (e.g. Coleoptera and Collembola), but in addition to arthropods also included an annelid, nematode and mollusc species. The number of samples processed per site and season was limited to that needed to attain a plateau in the sampling curve (Southwood, 1978). A plateau for invertebrates was defined as occurring when no more than two new species were identified in two consecutive samples. This resulted in processing a total of 123 species and 16 791 individuals.

Amphibians

Naturally occurring ground cover items, such as logs and small boulders, were turned over and examined during 30-min searches at each site. The area under each item was examined for 30 s if nothing was found or if amphibians were found, for 30 s following the last observation. Each site was censused using this procedure once in the autumn, October or November 1991, and twice in the spring, February and March 1992. Additionally, 20 artificial cover items (40 × 40-cm plywood boards) were placed in each study site in December at 20-m intervals along four 80-m transects placed in a parallel series at 15-m intervals. The area under each artificial cover item was examined in February and March 1992. Amphibians were also recorded if observed opportunistically during the course of other fieldwork (approximately 23 h per site).

Rodents

Rodent populations were sampled in March of 1992. At each study site, 50 traps were set along five 40-m transects. Two live traps, a Sherman and a Longworth, were set at 10-m intervals along each transect. Three parallel transects were placed at 15-m intervals in the most central portion of each site and two transects were established along the site edges. The traps were baited with rolled oats and peanut butter, set in the afternoon and checked on each of two successive mornings. Animals captured were identified, weighed and sexed. Those captured on the first morning were marked with phosphorescent powder to aid in their identification if recaptured. All stands were sampled within a 10-day period to minimize

the effects of climatic differences, moon phases and other temporal variations on capture rates (Stickel, 1968).

Birds

Birds were censused at each study site during 30-min counts, initiated 30 min after sunrise and 30 min before sunset in both the autumn, October or November 1991, and the spring, March 1992. In addition, birds were counted for a 1-h period at each site, beginning 3 h after sunrise, in April 1992. Birds were also recorded if observed opportunistically during the course of other field work (approximately 23 h per site).

Data analysis

All analyses were based upon both survey and opportunistically observed data, except for leaf-litter invertebrates and rodents for which no opportunistic data were collected. The principal measure of diversity used in this study was species richness, which is a count of the number of species present. Richness provides a robust and accurate measure of species diversity as long as sampling methods are standardized, as they were in this study. A second measure of diversity, the Shannon–Wiener Index of diversity, which incorporates both richness and evenness of distribution, was also used (Krebs, 1989). Only species richness was calculated for bird populations, since individuals were not distinguished. All comparisons of mean values of taxonomic groups between site types were restricted to intra-season comparisons. For example, the mean richness of plants in eucalypt sites in the spring was compared with the mean richness of plants in native sites in the spring. These comparisons were made with two-tailed *t*-tests. This use of multiple *t*-tests, without a Bonferroni correction, is a conservative test of the hypothesis since they increase the likelihood of finding significant differences between sites. In addition to tests of individual taxonomic components, it can be valuable to consider comparisons of richness across all taxa, since changes in a single taxonomic component could be compensated for by another. Therefore, the means of the total richness of both woodland types were compared with a two-tailed *t*-test. Total richness of each site was calculated by summing all species censused there, i.e. summing plants, invertebrates, amphibians, rodents and birds; this was performed for species censused in the spring, when the greatest numbers of taxonomic components were examined.

Differences in species composition between sites were examined with a principal components analysis (PCA). They were also examined with the coefficient of Jaccard and the coefficient of Sorensen (Krebs, 1989). Finally, I examined the number of species shared between all of the different possible combinations of the six sites, when split into two groups of three sites each; this produces 10 combinations of comparisons: first, eucalypt₁, eucalypt₂, and eucalypt₃ vs. native₁, native₂,

and native₃, second, eucalypt₁, eucalypt₂, and native₁ vs. eucalypt₃, native₂, and native₃, and so on through the other eight combinations. All of these compositional analyses were based upon the presence or absence of plants and invertebrates (the two most speciose groups). The mean abundance of individual species of invertebrates and plants were also calculated. This was done for each species by summing its abundance scores and dividing by the number of sites where it was present. For invertebrates, the log of mean abundance was used to normalize their values. For plants, frequency, the ratio of presence to absence across quadrats, was used as a proxy for abundance, since the number of individuals per quadrat could not readily be determined for species with a clonal growth form. Note that plants observed at a site, but not within a quadrat were assigned a frequency of zero to denote their presence and low abundance within that site.

RESULTS

In the spring, the mean species richness values of native and eucalypt sites were nearly identical for understorey plants, leaf-litter invertebrates, amphibians and birds, with only rodents yielding a significant difference (Fig. 1a). These taxon-specific richness values are highly correlated between native and exotic sites, $r = 0.99$, and the slope of the relationship, 0.95, is extremely close to the null hypothesis of no difference between sites (Fig. 1b). In the autumn, no significant differences in species richness were observed between site types (rodents were not sampled). The comparisons of mean species diversities (calculated with the Shannon–Wiener Index) were qualitatively identical to those for species richness, with one exception; eucalypt stands had a significantly higher diversity of leaf-litter invertebrates in the spring (t -value = 3.75, d.f. = 4, $P < 0.02$). Measures of total species richness (the sum of all taxonomic components censused in the spring) had mean values that were not significantly different between woodland types ($\bar{x}_{\text{eucalypt}} = 74.7$, $\bar{x}_{\text{native}} = 79.0$, t -value = 0.41, d.f. = 4, $P > 0.71$).

In contrast to richness and diversity, species composition varied greatly between native and eucalypt woodlands. The majority of species sampled did not occur in both woodland types, the values for those that did occur in both being: plants 39%, invertebrates 49%, amphibians 40%, rodents 50% and birds 42%. The first axis of a PCA, which represented a weighted average of the presence or absence of plant and invertebrate species, differentiated between sites by woodland type, with significantly different means in native and eucalypt woodlands (t -value = 8.69, d.f. = 4, $P < 0.001$). Pairwise site comparisons of similarity, using the coefficients of Jaccard and Sorensen, indicated that all within site type comparisons were more similar than all across site-type comparisons (Table 1). Of the 10 ways to divide six sites into two groups of three sites each, the groups composed exclusively of native sites and exclusively of exotic sites had the least number of

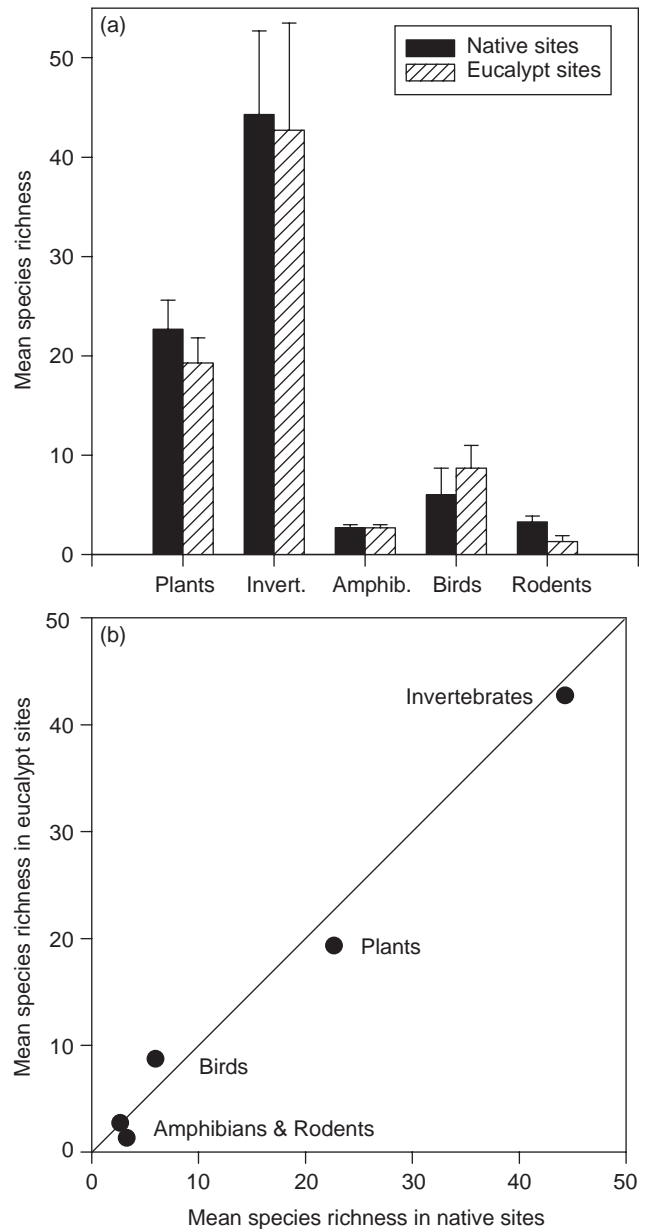


Fig. 1 (a) Mean species richness (in the spring) of understorey plants, leaf litter invertebrates, amphibians, birds and rodents in native and eucalypt sites. Error bars represent one standard deviation from the mean. No values were significantly different between site types, except for rodents (t -value = 4.24, d.f. = 4, $P < 0.02$). (b) The preceding data plotted against a line of equality (slope of one), which represents a null model of no difference between site types. Note the close proximity of mean values to the line of equality and that a correlation between mean values is highly significant with a slope close to 1 ($P < 0.001$, $r = 0.99$, slope = 0.95).

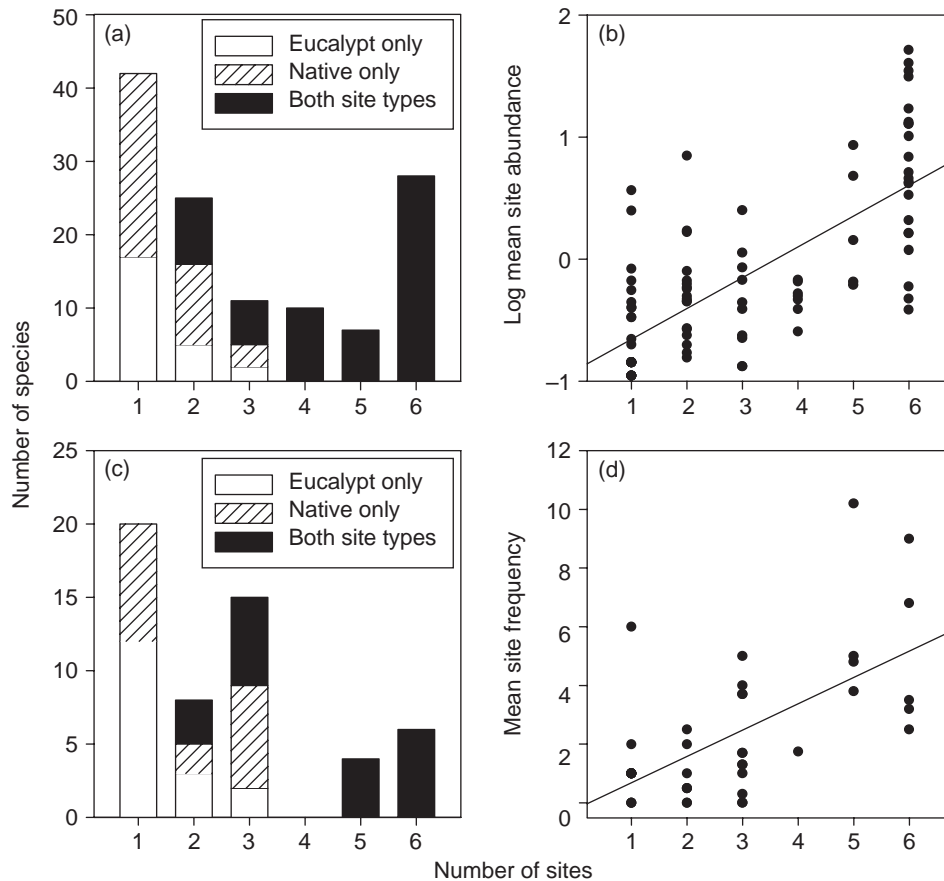


Fig. 2 (a) Number of species of leaf-litter invertebrates (in both autumn and spring) that occurred in different numbers of sites, further divided by their presence in different site types: only eucalypt, only native, or both. (b) Number of sites (in the spring) that species of invertebrates were present in, plotted against the log of their mean site abundances ($n = 92$, $P < 0.001$, $R^2 = 0.53$). (c) Number of species of understorey plants (in both autumn and spring) that occurred in different numbers of sites, further divided by their presence in different site types: only eucalypt, only native, or both. (d) Number of sites (in the spring) that species of plants were present in, plotted against their mean site frequency ($n = 44$, $P < 0.001$, $R^2 = 0.40$). Note that mean site frequency is a proxy for mean site abundance (see methods for details).

species in common, i.e. the least number of shared species. Also, many species present in only one woodland type (native or eucalypt) were also only present at one site, as illustrated by the invertebrates and plants (Fig. 2a,c). Only rarely, in 8% of the species, were species present in only one woodland type, and found in all three of those sites. In contrast, most species present in both woodland types were found in all or most sites (Fig. 2a,c). Finally, the number of sites where a species was recorded was positively correlated with its mean site abundance, measured as the log of mean site abundance for invertebrates and with the roughly equivalent, mean site frequency, for plants (Fig. 2b,d).

DISCUSSION

In this study, the mean numbers of species in native and eucalypt woodlands were nearly identical for most taxonomic

components of these systems: understorey plants, leaf-litter invertebrates, amphibians and birds (Fig. 1). The only significant difference was shown by rodents, which were the most species poor group surveyed, representing less than two percent of the total number of species. Diversity values were qualitatively similar to richness values, with one exception, a greater diversity of leaf-litter invertebrates occurred in eucalypt woodlands in the spring. Therefore, it can be stated broadly that for most groups, and in most seasons, richness and diversity values were nearly equivalent in native and exotic woodlands. Additionally, the mean values of total species richness (the sum of all taxonomic components) within these woodlands were also nearly identical. In contrast, species composition was substantially different between site types, as evidenced by the PCA, the similarity coefficients (Table 2) and the relatively low number of species shared by eucalypt and native sites. Together, these results show that the

Table 2 Similarity coefficients of pair wise site comparisons — Site comparisons are ranked from most to least similar by the similarity coefficients of both Jaccard and Sorensen (based on the presence and absence of leaf-litter invertebrate and understorey plant species). Note that all within site type comparisons were more similar than all across site type comparisons, e.g. any eucalypt site is more similar to any other eucalypt site, than it is to any native site. Further, the mean coefficients of within site type comparisons were significantly higher than the mean coefficients of across site type comparisons (Jaccard t -value = 6.68, d.f. = 13, $P < 0.001$; Sorensen t -value = 6.55, d.f. = 13, $P < 0.001$)

Paired site comparisons	Coefficient of Jaccard	Coefficient of Sorensen
Eucalypt ₁ × Eucalypt ₃	0.570	0.726
Native ₁ × Native ₃	0.558	0.716
Native ₂ × Native ₃	0.544	0.705
Eucalypt ₂ × Eucalypt ₃	0.537	0.699
Eucalypt ₁ × Eucalypt ₂	0.515	0.679
Native ₁ × Native ₂	0.500	0.667
Eucalypt ₂ × Native ₃	0.479	0.647
Eucalypt ₂ × Native ₁	0.472	0.642
Eucalypt ₁ × Native ₂	0.445	0.616
Eucalypt ₃ × Native ₂	0.433	0.604
Eucalypt ₁ × Native ₃	0.430	0.601
Eucalypt ₁ × Native ₁	0.395	0.566
Eucalypt ₂ × Native ₂	0.395	0.566
Eucalypt ₃ × Native ₃	0.370	0.540
Eucalypt ₃ × Native ₁	0.367	0.537

substitution of exotic woodlands for native ones has led to species assemblages with nearly equal diversities but different compositions.

These results may not at first seem to be intuitively reasonable. The negative impacts of exotic species on many native systems have been catastrophic, e.g. the effects of the brown tree snake in Guam (Fritts & Rodda, 1998). However, in this study, the substitution of eucalypt trees for native ones has not had catastrophic effects on species diversity. The reasons for this are most likely complex, but the most important aspect of the explanation seems to be the existence of a well-established understorey of plants. In native eucalypt woodlands of Australia, the presence of understorey plants has a strong effect on both the number and composition of animal species present (e.g. Fox & McKay, 1981). Therefore, it seems reasonable that understorey plants in eucalypt woodlands of California would also be important in determining diversity and composition of other organisms. This is because understorey plants appear to be the foundational element of the species assemblage in these woodlands. They provide large quantities of leaf-litter that is critical for the leaf-litter invertebrates (Wallwork, 1976). The leaf-litter invertebrates in turn support the amphibians, whose diets are composed primarily of leaf-litter arthropods (Zweifel, 1949; Stebbins, 1954). The

rodents are dependent on both the understorey plants and the leaf-litter fauna, as their diets consist of seeds, fruits, arthropods, leaves and fungi (Jameson, 1952), while the birds acquire resources from the plants, invertebrates, and vertebrates.

Even though the understorey plants, and secondarily the leaf-litter invertebrates, may provide a similar resource base in both woodland types, their differences in species composition might still be expected to affect the diversity of dependent groups, namely amphibians, mammals and birds, as well as the leaf-litter fauna itself with respect to the understorey plants. These differences, however, may be mitigated by two factors. First, those species that are shared between site types tend to be relatively abundant; secondly, those species that are present only within one site type or at one site tend to be relatively rare (Fig. 2). This means that most of the understorey plants and leaf-litter invertebrates that are abundant in native woodlands are also abundant in eucalypt woodlands, while most rare species that are only found in one woodland type are not abundant there. This may tend to homogenize the understoreys, and leaf-litter faunas, of both woodland types and reduce the relative importance of their compositional differences upon dependent groups.

Nevertheless, important differences in composition do exist, as indicated by several lines of evidence, including those few species that were consistently present in one site type, but consistently absent from the other. This pattern suggests that environmental differences that are important to these species occur between woodland types. These environmental differences may be due to the presence of secondary compounds present in the leaf-litter of eucalypt or native forests, to the more open nature of eucalypt canopies, to other physical differences between sites, or to the absence of other key species (del Moral & Muller, 1969; Poore & Fries, 1987).

One strong point of this investigation is the multiple taxonomic components that were compared, allowing more robust conclusions to be reached than would otherwise be possible. Unfortunately, the examination of multiple groups necessitated a reduction in the effort spent surveying any one of them. This trade-off should not present a problem as long as: (1), a roughly equal quantity of effort was spent surveying groups in both woodland types and (2), the majority of species present at each site were surveyed (which can be determined with cumulative sampling effort plots — Southwood, 1978). These requirements were met for plants, leaf-litter invertebrates, amphibians and rodents. For birds, however, while all abundant species were probably identified, it is likely that some rare species were missed, as suggested by the number of species observed opportunistically. Therefore, patterns of bird richness should be interpreted with some caution, even though they are largely consistent with the other groups surveyed.

In summary, the results of this study are consistent with the work of Brown *et al.* (2001), who suggest that species richness will often remain relatively stable despite changes in the

dominant vegetation type, and despite changes in species composition. Further, this study expands their concept by showing that species richness can be relatively stable not only in a temporal context but also in a spatial one. Thus, species richness may often be largely invariant to changes in species composition, and may instead be a deterministic consequence of local environmental factors and the regional pool of species. Finally, this study shows that the dominance of an ecosystem by an exotic plant species, and in particular *E. globulus*, will not necessarily result in a reduction of species diversity.

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