

The effects of large-scale fragmentation on bryophytes in temperate forests

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Summary

1. Bryophyte response to landscape fragmentation has not been investigated in replicated studies in temperate forests. Many bryophytes disperse widely but have narrow habitat requirements, suggesting that their responses to fragmentation may differ from other taxa.

2. We studied 16 sites in native eucalypt remnants located within an intensively managed plantation of exotic *Pinus radiata*. Eight further sites were dominated by exotic pines, and eight more were in large, continuous areas of native eucalypt forest located at the plantation boundary. We investigated how landscape context, remnant size and time since remnant isolation influence the bryophyte assemblage. Rocks, logs, soil, upturned trees and standing dead and live trees were sampled at each site.

3. Eucalypt remnants supported all but six of a total of 58 bryophyte taxa. Radiata pine sites were missing 40% of the species found in native forest, and pine was the only landscape context class not to have unique species. There was little difference in the richness or assemblage composition between the remnants and the unfragmented eucalypt forest.

4. Bryophyte assemblages differed between substrates but were similar across the same substrates even in different landscape context classes (except for rocks). Strip-shaped remnants had more bryophytes in common with continuous forest than patch-shaped remnants, while moss richness increased with remnant size.

5. *Synthesis and applications.* Native eucalypt remnants surrounded by intensively managed radiata pine plantation appeared to have retained, or regained, much of their bryoflora. Pine plantations were relatively depauperate, although burned eucalypt logs that remained after clearing native forest provided key substrates for many species and were crucial for maintaining bryophyte diversity. Forest managers aiming to retain bryophyte diversity should conserve native remnants of all sizes and retain suitable structural attributes, such as large decayed logs. Our findings support the hypothesis that many bryophytes have the mobility to overcome dispersal problems posed by fragmented landscapes if appropriate habitat or substrate is available.

Key-words: Australia, eucalypt forest, exotic pine, liverwort, matrix, moss, remnant

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Introduction

There is an ongoing need to understand species response to fragmentation because landscape fragmentation continues apace world-wide and because the impacts of

landscape fragmentation can vary markedly between and within taxonomic groups (Debinski & Holt 2000). Bryophytes are an ideal plant group for evaluating habitat fragmentation effects because of their high diversity among the world's forest types, foreshortened generation times, and their presence in even extreme habitats (Smith 1982; Pritchard & Bradt 1984; Jarman & Kantvilas 1995; Pharo & Blanks 2000; Cook *et al.* 2002; Jules & Shahani 2003). Although bryophyte response to disturbances such as fire is well known

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(Duncan & Dalton 1982; Pharo & Beattie 1997), we know of only one study on the effects of habitat fragmentation. Tropical epiphyllous (leaf-inhabiting) bryophytes had lower richness, abundance and among-site compositional variation in small (1 and 10 ha) remnants in a matrix of secondary forest and agricultural land compared with both larger (100 ha) remnants and continuous forest (Zartman 2003). There are a few studies that have examined naturally isolated 'islands', for example a rainforest fragment in drier forests (Kantvilas & Jarman 1993), islands in a lake (Tangney, Wilson & Mark 1990) and forest fragments in sphagnum bog (Berglund & Jonsson 2001; Moen & Jonsson 2003), where the surrounding is more akin to the 'sea' of classical island biogeography theory than a disturbed habitat where the matrix would have once been inhabited by the target taxa.

There is good evidence, however, that the landscape can provide important habitat for many species (Debinski & Holt 2000; Norton, Hannon & Schmiegelow 2000; Cook *et al.* 2002; Jules & Shahani 2003; Lindenmayer, McIntyre & Fischer 2003). Existing studies suggest that an exotic pine matrix may not be an 'inhospitable sea' for some plants, despite clear negative effects of the plantation on both plant and animal diversity (Armstrong *et al.* 1996; Lindenmayer *et al.* 1999; Lindenmayer, Cunningham & Pope 1999; Hansson 2000). The remnant areas of this study were surrounded by exotic pine forest, and the appraisal of these exotic plantations, long regarded as inhospitable habitat for bryophytes, is important. The plantation estate in Australia is relatively large (Wood *et al.* 2001) and expanding rapidly in many parts as a result of Australia's recent Regional Forest Agreements and socio-economic changes in rural land-use patterns (Burns, Walker & Hansard 1999; Lindenmayer & Hobbs 2004).

The two main subgroups of bryophytes, liverworts and mosses, might respond differently to fragmentation, with liverworts favouring more sheltered, moist conditions (Barkman 1958; Gradstein, Van Reenen & Griffin 1989; Kantvilas & Jarman 1993). Most of the species in a recent study in the Amazon by Zartman (2003) were liverworts, which may have been one of the reasons why there was a clear response to fragmentation.

Bryophyte presence is likely to depend on substrate availability and quality (van Zanten & Pocs 1981; Marino 1988; Söderström 1989; Iwatsuki 1990; Miles & Longton 1992; Cleavitt 2001; Pharo & Beattie 2002). Bryophytes may be able to reach and establish on suitable substrate within a largely unfavourable environment. This study investigated relationships between bryophyte diversity and substrate, landscape context, interactions between substrate and landscape context, and remnant variation (shape, age, size). The main aims were to compare bryophyte diversity in (i) remnants of native vegetation surrounded by pine plantations, (ii) sites in large areas of continuous native vegetation and (iii) sites dominated by radiata pine *Pinus radiata*. Due to problems of low power when

analysing individual species, we focused on species richness and species composition to determine how this group of spore-dispersed plants responded to the independent variables.

Materials and methods

THE STUDY SITES

The study took place within the Buccleuch and Bondo State Forests near Tumut, southern New South Wales, Australia (Fig. 1), over an area of approximately 15 × 20 km (Lindenmayer *et al.* 1999). The study comprised 32 sites, of which 16 were in eucalypt remnants surrounded by an extensive radiata pine plantation, eight were dominated by radiata pine trees and managed intensively as a plantation, and eight were located within large continuous areas of native eucalypt forest adjacent to the plantation. All sites were matched for climate and geology. Isolation times ranged from 15 to 60 years, which is important given that a major review of fragmentation studies found that strong patterns might be missed in the short term (< 14 years) (Debinski & Holt 2000). Eucalypt remnants were selected to ensure that a variety of sizes, shapes, forest types and ages of surrounding plantation were represented (Table 1). Remnants were divided into four size classes (less than 3 ha, 3–10 ha, 11–20 ha, more than 20 ha) and were either patch shaped (elliptical or round) or strip shaped (long and narrow). The vegetation surrounding the remnants was classified as heterogeneous if there was marked variation (> 20 years) in the ages of the adjacent radiata pine plantations (such as clearfell on one edge of the remnant and a mature plantation on the other). Only three sites were heterogeneous (Table 1) and the effect of this heterogeneity was not analysed statistically. Three native forest types were examined in the study and were named for their dominant tree species: swamp gum *Eucalyptus camphora* R.T. Baker, narrow-leaved peppermint *Eucalyptus radiata* DC. ssp. *radiata* and ribbon gum *Eucalyptus viminalis* Hook.

DEPENDENT VARIABLES

At each of the 32 sites, a 10 × 10-m plot was thoroughly searched for bryophytes. Data on plants from each of the substrates were kept separately: rock, log, soil, upturned tree/log, stump/dead tree and live trees (*Acacia dealbata*, *Acacia melanoxylon*, *Acacia siculiformis*, *Baeckea virgata*, *Cassinia aculeata*, *Eucalyptus camphora*, *Eucalyptus pauciflora*, *Eucalyptus radiata*, *Eucalyptus viminalis*, *Exocarpos cupressiformis*, and *Pinus radiata*). Trees were sampled to approximately 2 m height about the ground. Further searches targeting additional substrates not found within the 10 × 10-m plot were conducted in an area of 100 × 50 m at each site. These additional samples were needed to ensure that as much of the diversity on a site was sampled as possible.

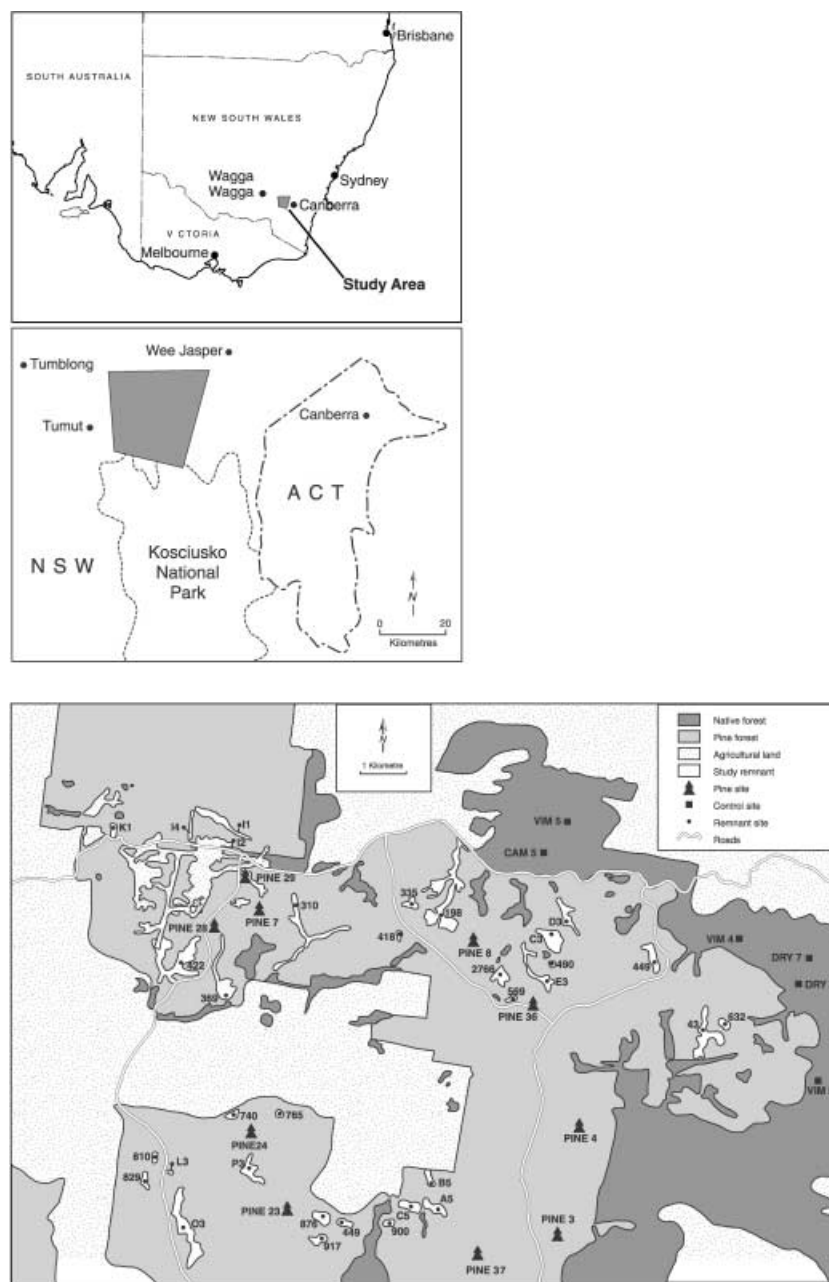


Fig. 1. The location of the main study area at Tumut, Australia, demonstrating that there is no overt spatial correlation between the three main site types: remnants, *Pinus radiata* sites and sites in large areas of native *Eucalyptus* forest. The sites shown are a sample of those surveyed for vertebrates, and only a few of these were included in the bryophyte survey, but they are representative of our sampling. Sites in large areas of native forest are coded for their forest type (e.g. Cam, Rad, Vim), and pine sites are denoted Pine9, Pine10, etc. The remnants are coded with a single letter and/or number.

ANALYSES

Analysis of variance was used to compare the species richness of the three major site types or landscape context classes (namely eucalypt remnants, large areas of native vegetation, pine). Normality was investigated using the Anderson–Darling test and variance equality was checked with Bartlett’s test (Minitab 2000). All Durbin–Watson statistics were close to 2, indicating that there was no bias relating to the order in which sites were sampled. We found no spatial correlation between sites, with the species matrix and the matrix of distances

between sites having little in common ($Rho = -0.027$, $P = 0.649$, using Spearman rank correlation and 999 permutations, with the Relate function in PRIMER; Clarke & Gorley 2001).

Differences in species composition between landscape context classes were investigated using analysis of similarities (ANOSIM), which is analogous to analysis of variance (Clarke 1993). ANOSIM uses a non-parametric permutation procedure (in this case 999 permutations) applied to the rank Bray–Curtis similarity matrix. To display the multivariate species data, clustering was performed using unweighted pair group metric averaging

Table 1. Details of the 16 remnants at Tumut in south-eastern Australia. An additional eight sites in large, continuous areas of *Eucalyptus* forest and eight sites in the radiata pine sites were included in this study. Forest types are named for the dominant tree species: Cm, swamp gum *Eucalyptus camphora*; Ra, ribbon gum *Eucalyptus radiata*; Vi, narrow-leaved peppermint *Eucalyptus viminalis*. Surrounding forest age is young if 25 or fewer years. Pine forest age was heterogeneous if > 20 years differences in ages of the pine plantations adjacent to remnant

Site name	Size class (ha)	Shape	Surrounding forest age	Uniform or heterogeneous in pine forest age	Forest type
335 (patch 1)	1–3	Patch	Old	Heterogeneous	Ra
418 (patch 2)	1–3	Patch	Old	Uniform	Cm
740 (patch 3)	3–10	Patch	Young	Heterogeneous	Ra
906 (strip 1)	11–20	Strip	Old	Uniform	Cm
1401 (strip 2)	> 20	Strip	Old	Uniform	Vi
1537 (patch 4)	11–20	Patch	Old	Uniform	Ra
1863 (strip 3)	11–20	Strip	Old	Uniform	Ra
C (strip 4)	> 20	Strip	Old	Uniform	Ra
C3 (patch 5)	11–20	Patch	Young	Uniform	Ra
D1 (strip 5)	1–3	Strip	Old	Uniform	Cm
E1 (patch 6)	3–10	Patch	Young	Uniform	Cm
E3 (strip 6)	11–20	Strip	Young	Uniform	Vi
F1 (patch 7)	> 20	Patch	Young	Uniform	Vi
J3 (strip 7)	> 20	Strip	Old	Uniform	Vi
K3 (strip 8)	> 20	Strip	Old	Uniform	Cm
L3 (patch 8)	1–3	Patch	Young	Heterogeneous	Ra

Table 2. Bryophyte data by site type. Number of substrate level samples taken from each of the five main substrate types is indicated in parentheses

Landscape context class	Pine	Patch remnants	Strip remnants	Continuous forest	Total
Number of sites	8	8	8	8	32
Total number of species	26	40	40	35	58
Restricted to site type	0	8	5	7	20
Species recorded only once	0	6	4	7	17
Maximum species per site	15	19	21	19	N/A
Minimum species per site	6	13	11	9	N/A
Mean species per site	9.8	15.6	15.5	14.5	13.8
Standard deviation per site	2.6	2.0	4.1	3.7	3.9
Species on rocks ($n = 23$)	8	15	18	10	23
Species on logs ($n = 31$)	17	10	10	13	21
Species on soil ($n = 29$)	13	18	25	18	37
Species on uprooted trees ($n = 19$)	9	18	12	8	24
Species on tree trunks ($n = 53$)	9	15	14	19	26

and Bray–Curtis similarity in PC-ORD (McCune & Mefford 1999).

Results

We found 58 bryophytes in our study: 45 mosses and 13 liverworts. Three species accounted for most of the liverwort records. Of a total of 145 occurrences of liverworts (vs. 411 for mosses), 61 of those were *Chiloscyphus semiteres*, 29 were *Frullania probosciphora* and 28 were *Cephalozia exiliflora*. The remaining 10 species of liverwort were recorded three or fewer times.

CONTEXT EFFECTS: SPECIES RICHNESS AND ABUNDANCE

Of the 58 bryophyte taxa found in the region, 26 species (40%) occurred in the eight sites within radiata pine-dominated plantations. There were 35 species in the eight sites of continuous native forest, 40 species in the

eight patch-shaped remnants, and 40 species in the strip-shaped remnants (Table 2). When the remnants were combined, we found a total of 51 species.

No bryophyte taxa were confined to the radiata pine sites. Eight were confined to the patches, five to the strips and seven to the continuous forest (Table 2). When patch- and strip-shaped remnants were combined, we found 17 species unique to these sites.

The average richness of the radiata pine sites was significantly lower than the remnants and continuous eucalypt sites ($P < 0.001$; Table 3). The result was weaker when the eucalypt remnants were divided into patch- and strip-shaped remnants, but the overall effects were still strong and highly significant ($P = 0.003$; Table 3 and Fig. 2). Species richness was similar for the three native vegetation landscape context classes (i.e. continuous forest, patch- and strip-shaped remnants; Fig. 2). When the native vegetation sites were assigned to forest types, rather than divided on a landscape-context basis (e.g. remnant/non-remnant), the results were the same

Table 3. Analysis of variance results for bryophyte richness and key variables

Variable	<i>n</i>	d.f.	All bryophytes		Mosses		Liverworts	
			<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Landscape context class								
Remnant, pine, continuous forest	32	2	9.26	< 0.001***	8.51	< 0.001***	4.88	0.015*
Patches, strips, pine, continuous forest	32	3	5.96	0.003**	5.49	0.004**	3.16	0.040*
Remnant, continuous forest (no pine)	24	1	0.55	0.467	1.18	0.288	6.04	0.022*
Patches, continuous forest	16	1	0.58	0.458	1.27	0.278	3.87	0.069
Strips, continuous forest	16	1	0.26	0.617	0.57	0.463	5.65	0.032*
Patches, strips	16	1	0.01	0.940	0.03	0.868	0.04	0.851
Forest type	32	3	5.74	0.003**	5.20	0.006**	1.27	0.305
Forest type without pines	24	2	0.08	0.922	0.32	0.731	0.68	0.519
Substrate variables								
Substrate type (rocks, logs, soil, upturned tree bases, tree trunks)	152	4	4.46	0.002**	8.13	< 0.001***	5.54	< 0.001***
Number of substrates per site (< 5, 5–6, 7–9)	32	2	6.64	0.004**	6.47	0.005**	2.51	0.099
Remnant variables								
Remnant age (< 25 years, > 25 years)	16	1	1.20	0.291	0.90	0.359	0.30	0.592
Younger remnants (<i>n</i> = 6), continuous forest	14	1	0.05	0.822	0.33	0.571	8.49	0.010**
Older remnants (<i>n</i> = 10), continuous forest	18	1	1.80	0.205	2.28	0.157	1.94	0.188
Size (1–3 ha, 3–10 ha, 11–20 ha, 20+ ha)	16	3	2.77	0.087	4.28	0.029*	0.59	0.632

P* < 0.05, *P* < 0.01, ****P* < 0.001.

as those described above. That is, there was a highly significant forest type effect when radiata pine sites were included (*P* = 0.003) but no significant differences when pines were excluded and the three native forest types tested (*P* = 0.92; Table 3).

Mosses and liverworts responded differently to landscape context. Radiata pine sites were the least moss species-rich, continuous forest of intermediate richness, and the remnants the most species-rich (*P* = 0.004; Fig. 2). There was limited variation in liverwort richness between the four landscape context classes, although the difference was statistically significant. Liverworts

were most species-rich in the continuous forest, followed closely by the pine sites. The patch remnants and strip remnants were of similar species richness (Fig. 2). The results for both mosses and liverworts were stronger when the remnants were pooled, rather than being separated into patch- and strip-shaped remnants (Table 3).

When we examined differences in moss and liverwort species richness between the native vegetation classes (i.e. radiata pine sites were excluded), the liverworts were significantly less species rich in the remnants (mean 4.44 species) compared with the continuous forest (mean 5.75 species; *P* = 0.022; Table 3). The results for mosses echoed bryophytes as a group, with no significant differences between the remnants and the continuous eucalypt sites (Table 3).

CONTEXT EFFECTS: SPECIES COMPOSITION

There appeared to be a continuum of change in bryophyte species composition from eucalypt remnant sites, through continuous forest to pine sites. Most of the pine sites separated out in a dendrogram, although two of the pine sites clearly grouped with the native vegetation sites (Fig. 3). One of the patch-shaped remnants (site 740) supported a composition of species that was different to the rest of the sites (Fig. 3). The next group to separate in the clustering included six of the eight radiata pine sites, three continuous forest sites and one strip-shaped remnant (site C), indicating that these sites were different in composition to the other sites (Fig. 3). The remaining 21 sites showed some grouping of the continuous forest sites (Cam1, Cam4, Rad9, Vim5) but there was substantial intermixing of patch-shaped remnants, strip-shaped remnants and continuous eucalypt forest (Fig. 3).

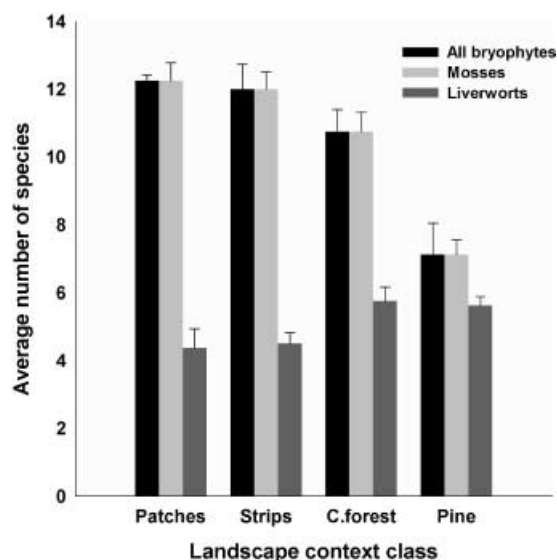


Fig. 2. Species richness of bryophytes as a group, mosses only and liverworts only in different site types. Standard errors shown. Patches, patch-shaped remnants; Strips, strip-shaped remnants; C. forest, continuous forest.

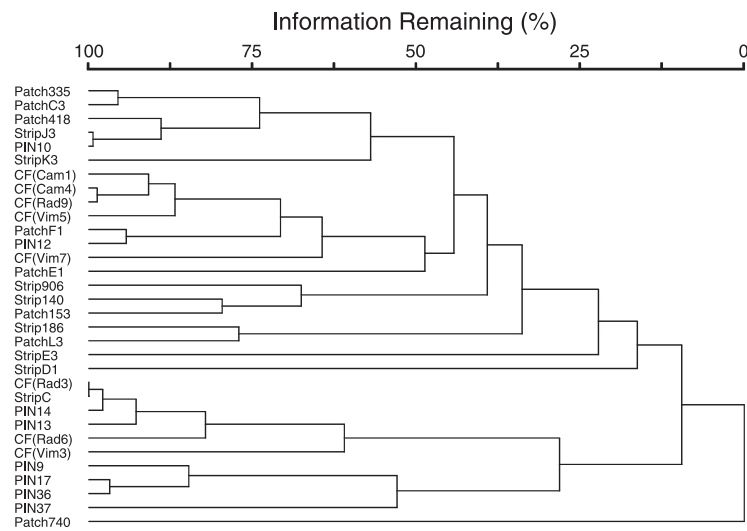


Fig. 3. Dendrogram resulting from clustering using Bray–Curtis and unweighted pair group averaging. CF, continuous forest; Strip, strip-shaped remnant; Patch, patch-shaped remnants; PIN, *Pinus radiata* plantation. Continuous forest sites were named for their forest type (Cam, *Eucalyptus camphora*; Rad, *Eucalyptus radiata*; Vim, *Eucalyptus viminalis*).

Species composition differed significantly between the remnants, continuous forest and radiata pine sites ($P = 0.026$; Table 4). When remnants were separated into patches and strips, differences were greater between the four landscape context classes (patch- and strip-shaped remnants, continuous forest and radiata pine; $P = 0.002$). When radiata pine sites were removed from the analyses, there was no difference between the remnants and the continuous eucalypt forest ($R = 0.01$, $P = 0.457$). This outcome was not surprising in light of the clustering results, which showed some grouping of the radiata pine sites but an intermixing of the continuous forest and eucalypt remnants (Fig. 3).

Despite the mixing on the dendrogram, ANOSIM revealed a significant difference between the patch-shaped remnants and continuous forest ($R = 0.30$, $P < 0.001$). There was no difference between the strip-shaped remnants and continuous forest ($R = 0.02$, $P = 0.342$) or patch- and strip-shaped remnants ($R = 0.05$, $P = 0.237$).

Liverworts did not differ between remnant, continuous forest and radiata pine sites ($P = 0.219$; Table 4). Pairwise comparisons showed that for mosses on the native vegetation sites, the largest differences were for patch-shaped remnants and continuous forest ($P < 0.001$; Table 4). In contrast, there was no significant difference

Table 4. Analysis of similarity results for bryophyte species composition and key variables

Variable	No. sites/ samples	All bryophytes (<i>n</i> = 152)		Mosses (<i>n</i> = 142)		Liverworts (<i>n</i> = 91)	
		<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>
Landscape context class							
Remnant, pine, continuous forest	32	0.15	0.026*	0.145	0.029*	0.057	0.219
Patches, strips, pine, continuous forest	32	0.20	0.002**	0.169	< 0.001***	0.123	0.004**
Remnants, continuous forest	24	0.008	0.428	0.041	0.291	−0.068	0.713
Patches, continuous forest	16	0.281	< 0.001***	0.282	< 0.001***	0.059	0.092
Strips, continuous forest	16	0.021	0.348	−0.035	0.657	0.105	0.054
Patches, strips	16	0.053	0.242	0.061	0.218	0.003	0.406
Forest type	32	0.19	< 0.001***	0.173	0.003**	0.173	0.002**
Forest type without pines	24	0.126	0.031*	0.12	0.047*	0.131	0.029*
Forest type in continuous forest only	8†	0.095	0.296	0.129	0.243	−0.007	0.571
Substrate variables							
Substrate type (rocks, logs, soil, upturned tree bases, tree trunks)	152*	0.30	< 0.001***	0.274	< 0.001***	0.284	< 0.001***
Tree species (<i>n</i> = 12 including a category for dead standing trees)	53	0.23	< 0.001***	0.194	0.005**	0.101	0.103
Remnant variables							
Remnant age (< 25 years, > 25 years)	16	0.164	0.084	0.199	0.040*	−0.047	0.638
Younger remnants (<i>n</i> = 6), continuous forest	14	0.353	< 0.001***	0.304	0.007**	0.165	0.053
Surrounding pines uniform or heterogeneous age	16	0.018	0.459	0.044	0.413	−0.084	0.639
Size (1–3 ha, 3–10 ha, 11–20 ha, 20+ ha)	16	0.061	0.274	0.072	0.276	−0.036	0.613

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

†Only 280 permutations possible (therefore if one permutation is greater than the observed, P -value is 0.004).

between these two groups for liverworts ($P = 0.092$; Table 4).

SUBSTRATE EFFECTS: SPECIES RICHNESS

We examined an average of 4.8 substrates per site in each of the 32 sites, yielding a total sample of 152 substrates. The range of substrates at each site varied from only two (logs and the ground) in one of the pine sites, to nine in one of the continuous forest sites (logs, ground, rocks, upturned tree base, and five different species of trees). This translated into higher bryophyte richness where there were more substrates ($P = 0.004$; Table 3). The result was very similar for mosses ($P = 0.005$) but weaker for liverworts ($P = 0.099$). Radiata pine sites appeared to provide a poorer range of substrates (mean 3.5) compared with the native vegetation (mean 5.0 for patch-shaped remnants, 5.4 for strip-shaped remnants and 5.1 for continuous forest). However, there was considerable variability within sites and no statistical difference between the means (d.f. = 3, $F = 2.49$, $P = 0.081$).

When the total number of species found on each substrate was compared across the landscape context classes, there were more species on logs in pines than on logs in either continuous forest or the remnants (Table 2). Seventeen of the 26 species recorded in radiata pine-dominated sites were on logs. Five of these species were not found on other substrates in the pine, and of these one (*Orthodontium lineare*, known to prefer charred logs; Scott & Stone 1976) was restricted to woody substrates. Of the total of 40 samples on logs in pine sites, 37 were on burned eucalypt logs and only three on pine logs. Soil was also an important substrate (Table 2), with half the 26 species found in the radiata pines living on the ground.

Two-way analysis of variance showed that substrate was more important than landscape context class in explaining bryophyte diversity (patch–strip–continuous forest–pine: $n = 152$, d.f. = 3, $F = 0.39$, $P = 0.688$; rock–log–soil–upturned tree–live tree: $n = 152$, d.f. = 4, $F = 4.46$, $P = 0.002$). When patch- and strip-shaped remnants were combined, the result changed little (landscape context class: d.f. = 2, $F = 0.54$, $P = 0.584$). Some of the most species-rich substrates (eucalypt logs) were found in the least species-rich landscape context class (radiata pine sites). The results were stronger for both mosses and liverworts separately (Table 3 and Fig. 4).

Radiata pine sites were particularly poor as habitat for epiphytic bryophytes. Despite searching a 100×50 -m area at each site, only four of the eight pine sites had epiphytes, whereas all native forest sites had epiphytes. At three of these sites, bryophytes were growing either at the base or roots of radiata pine trees, a habitat that had often accumulated some soil and therefore ameliorated conditions. At the fourth site, a native tree species *Acacia melanoxylon* had established in the plantation and supported bryophytes.

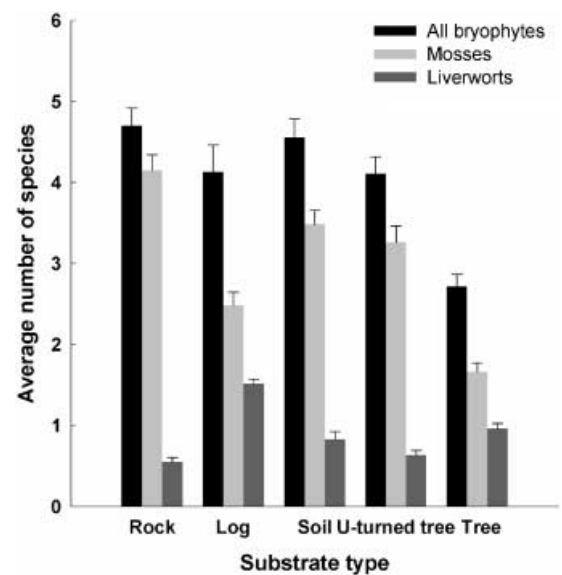


Fig. 4. Species richness of bryophytes, mosses and liverworts on different substrates. Standard errors shown. U-turned tree, upturned tree base.

SUBSTRATE EFFECTS: SPECIES COMPOSITION

Bryophyte species composition was responsive to substrate type ($P < 0.001$). Pairwise comparisons between each of these substrates were all highly significant, except for soil and upturned trees ($R = 0.06$, $P = 0.081$). Field observations showed that upturned trees provided sheltered microsites on both soil and roots, and it was the soil still adhering to the roots that normally supported bryophytes, hence the similar species composition to the samples taken from bare ground. The largest differences in species composition were between rocks and logs ($R = 0.68$, $P < 0.001$) and rocks and upturned tree bases ($R = 0.50$, $P < 0.001$). Mosses and liverworts showed similar results both overall (Table 4) and at the pairwise level. The strongest contrasts were between substrates offering quite different conditions for bryophytes.

The category of 'tree trunks' was examined separately by looking at individual tree species. There were 11 different vascular plant species and a 12th category for dead trees/stumps. There were highly significant differences in species composition between these 12 categories overall ($R = 0.23$, $P < 0.001$). Pairwise comparison of species compositions on different tree species was problematic because only two of the 11 tree species supported bryophytes on more than five occasions: *Eucalyptus radiata* (12 samples) and *Acacia melanoxylon* (eight samples). Moss composition was significantly different on different tree species ($R = 0.005$), but not liverwort composition ($R = 0.103$). Of the 46 occurrences of liverworts on trees, 36 of them were two species (17 occurrences of *Chiloscyphus semiteres*, 19 of *Frullania probosciphora*). The remaining six liverworts found on trees were present three or fewer times.

Table 5. Analysis of similarity results for the interaction between landscape context class and substrate. Separate data sets were established for each landscape context class and tested to determine whether there was an effect of substrate. n = number of samples/substrates

	n	Remnants		Patches		Strips		Continuous forest		Radiata pine	
		R	P	R	P	R	P	R	P	R	P
Global test		0.279	< 0.001***	0.288	< 0.001***	0.281	< 0.001***	0.296	< 0.001***	0.325	< 0.001***
Pairwise comparisons											
Rock–log	51	0.774	< 0.001***	0.674	< 0.001***	0.742	< 0.001***	0.673	< 0.001***	0.649	< 0.001***
Rock–soil	49	0.149	0.054	0.252	< 0.001***	0.256	< 0.001***	0.367	< 0.001***	0.321	< 0.001***
Rock–upturned tree base	39	0.333	< 0.001***	0.414	< 0.001***	0.487	< 0.001***	0.503	< 0.001***	0.579	< 0.001***
Rock–standing tree	73	0.075	0.174	0.170	0.002**	0.188	< 0.001***	0.259	< 0.001***	0.273	< 0.001***
Log–soil	60	0.489	< 0.001***	0.463	< 0.001***	0.385	< 0.001***	0.402	< 0.001***	0.385	< 0.001***
Log–upturned tree base	50	0.513	< 0.001***	0.447	< 0.001***	0.312	< 0.001***	0.246	< 0.001***	0.281	< 0.001***
Log–standing tree	84	0.315	< 0.001***	0.290	< 0.001***	0.274	< 0.001***	0.231	< 0.001***	0.315	< 0.001***
Soil–upturned tree base	48	0.046	0.242	0.013	0.383	0.076	0.600	0.045	0.126	0.104	0.036*
Soil–standing tree	82	0.160	0.002**	0.259	< 0.001***	0.224	< 0.001***	0.288	< 0.001***	0.329	< 0.001***
Upturned tree base–standing tree	72	0.219	0.002**	0.266	< 0.001***	0.279	< 0.001***	0.275	< 0.001***	0.367	< 0.001***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

The interaction between substrate and landscape context class was tested indirectly by one-way ANOSIM of substrate for each of the different landscape context classes separately and then each of the substrates separately (Clarke 1993). The results were unambiguous, with strong substrate effects (Table 5) but negligible effects of landscape context class (Table 6). For the comparisons within each landscape context class, the only substrates that were consistently similar in species composition were two where bryophytes were anchored in soil ('soil' and 'upturned tree bases').

Bryophyte species composition did not differ between sites with different numbers of substrates ($P = 0.114$; Table 4). To reduce the chance that this result was affected by the large number of groups and the groups that only had one member (only one site had eight substrates and only one had nine substrates), sites were grouped into those with four or less substrates, five or six substrates and seven to nine substrates. This produced an even weaker result ($R = 0.08$, $P = 0.135$).

REMNANT VARIABLES

Moss diversity differed significantly between remnants of different sizes ($P = 0.029$). However, the relationship

was not simple, with lower numbers in both the smallest (< 3 ha) and largest (> 20 ha) remnants compared with the two intermediate sizes (3–10 ha, 11–20 ha). We could find no reason for this outcome, because remnant size was not correlated with other variables, such as number of substrates or forest type. There was no difference for liverworts alone ($P = 0.632$), which led to a non-significant result for bryophytes as a group ($P = 0.087$; Table 3). There were no differences in species composition between the different sizes ($P = 0.274$; Table 4).

There was no significant difference in bryophyte species richness between young (25 or fewer years old) and old (more than 25 years) remnants ($P = 0.291$; Table 3). By comparing relatively recently isolated remnants and older ones separately with native continuous forest, we found more liverworts in the continuous forest (mean 5.8, SD 1.2) compared with the younger remnants (mean 4.3, SD 0.9; Table 3).

For bryophytes as a group, species composition differed between relatively recently isolated remnants and continuous forest ($P < 0.001$; Table 4) but not older remnants and continuous forest ($P = 0.180$). There was also a difference in moss species composition between relatively recently isolated and older remnants ($P =$

Table 6. Analysis of similarity results for the interaction between landscape context class and substrate. Separate data sets were established for each substrate and tested to determine whether there was an effect of landscape context class. n = number of sites

	n	Rock		Log		Soil		Upturned tree base		Standing tree	
		R	P	R	P	R	P	R	P	R	P
Global test	32	0.24	0.045*	–0.003	0.492	0.113	0.065	0.086	0.206	0.043	0.167
Pairwise comparisons											
Remnants–continuous forest	24	0.221	0.115	0.04	0.316	0.176	0.024*	–0.091	0.717	0.001	0.441
Remnants–radiata pine	24	0.313	0.061	–0.045	0.699	0.034	0.341	0.220	0.061	0.160	0.091
Continuous forest–radiata pine	16	–0.222	0.886	0.023	0.340	0.094	0.160	–0.154	0.732	0.100	0.180

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

0.040), but no difference for liverworts ($P = 0.638$), which explains the weaker result for bryophytes as a group (Table 4).

Discussion

RESPONSE TO LANDSCAPE CONTEXT

Pine sites were not bryophyte 'deserts'. However, they lacked 40% of the total number of species found in the native vegetation, lacked unique species, and had a depressed average richness compared with native vegetation. In contrast, eucalypt remnants were valuable habitat for bryophytes, being species-rich and with little difference in composition to the large areas of continuous forest. All but six of the 58 species found in this study were present in the remnants and 17 were only found in the remnants. Both strip- and patch-shaped remnants had a higher total number of species than the continuous eucalypt forest, although mean numbers of species were not significantly different. Analyses of both landscape context and forest type showed that the main contrast was between native eucalypt forest and the exotic radiata pine plantation.

There are no comparable studies of bryophyte response to landscape context and few studies have examined vascular plant response to landscape context. A study of eucalypt-dominated remnants in the dry forests of Tasmania showed that landscape context was important for vascular plants (Gilfedder & Kirkpatrick 1998). Remnants in an urban matrix had higher vascular plant richness compared with remnants in an agricultural matrix. North American studies of vascular plant communities have also found that the landscape matrix can provide important habitat for many species (Jules *et al.* 1999; Cook *et al.* 2002).

IMPORTANCE OF SUBSTRATE

This study showed substrate type to be a better predictor of species richness than landscape context. In other words, in terms of both species richness and composition at the substrate level, it mattered more what substrate was sampled than which landscape context class it was sampled from. Ojala, Monkkonen & Inkeroinen (2000) also concluded that epiphytic bryophyte species richness on *Populus tremula* trees was independent of landscape structure across heavily fragmented Norwegian forests and more continuous Russian forests, but positively related to *Populus tremula* abundance and the size of the trunk. Others have argued that microhabitat availability might be a crucial factor in determining bryophyte presence (Herben, Rydin & Söderström 1991; Humphrey *et al.* 2002).

We found that sites with greater numbers of substrates supported more bryophytes; a result that is well documented in a variety of habitat types (Lee & La Roi 1979; Palmer 1986; Vitt, Li & Belland 1995; Pharo & Blanks 2000). Work on small mammals and inverte-

brates has also concluded that conditions within remnants, rather than remnant size and isolation *per se*, can be critical for the occurrence of species (Margules 1996; Knight & Fox 2000). Our results highlight the complex implications of habitat fragmentation when the surrounding matrix is not entirely uninhabitable. The landscape appears to be more of a continuum of habitats, depending on the habitat requirements and biology of the particular species and groups of species in question (Knight & Morris 1996; Knight & Fox 2000; Hobbs & Yates 2003; Lindenmayer, McIntyre & Fischer 2003).

Radiata pine sites often failed to provide a full suite of substrate types for epiphytic bryoflora, with four of the eight pine sites supporting no epiphytes while all native vegetation sites had epiphytes. At the other four sites, bryophytes were found on pine tree roots, at the base of pine trees, or on native tree species established within the otherwise pine-dominated sites. Even in areas where pines are native, bryophytes can be restricted to the stable areas at the base of *Pinus* spp. (Palmer 1986).

Windrows of burned eucalypt logs left from clearing the original native forest to establish the pine plantation at Tumut were important substrates for bryophytes. Windrows are piles of woody debris bulldozed into long, parallel rows that clear the area for replanting. Approximately 90% of bryophyte samples collected in the radiata pine sites were from these remnant eucalypt logs. This suggests that, when the eucalypt logs have broken down completely, some of these pine-invading bryophyte species will disappear. Logs are particularly important habitat in forests where there is a dense layer of litter and the dominant trees are poor hosts (Jarman & Kantvilas 1994). Both the dry sclerophyll forests and pine plantations of this study fall into that category.

Deadwood is known to be a key habitat for bryophytes in temperate and boreal forests (Söderström 1993; Crites & Dale 1998; Humphrey *et al.* 2002; Zechmeister *et al.* 2003) and windrows of eucalypt logs can be valuable for other taxa in plantations, such as mammals and birds (Friend 1982; Curry 1991). Silvicultural practices that result in reduced substrate diversity, such as removing windrows to control pest herbivores (le March 2000), will almost certainly result in a depauperate bryoflora in these same environments.

RESPONSE TO REMNANT VARIABLES

Remnant responses were complex and may be a function of within-group life-history differences. Significant relationships were identified between the attributes of eucalypt remnants and both overall bryophyte richness and species composition. Strip-shaped remnants supported a bryoflora more similar to the continuous eucalypt forest than did the patch-shaped remnants. Substrate differences did not explain this pattern, with only rocks showing a significant difference when each substrate was analysed separately for the effect of landscape context class. Sites were chosen so that there was

a variety of forest types, ages and sizes for both patch- and strip-shaped remnants. The main difference between patch- and strip-shaped remnants was that all three remnants surrounded by pine plantation of heterogeneous age (more than 20 years) were patch-shaped. A larger number of species on uprooted trees was found in patch-shaped remnants, so there may also be an effect of ongoing disturbance in some of the patches, either directly through changes in microclimate or indirectly through changes in habitat provision.

Mosses were most species rich in the intermediate size remnants in this investigation. In contrast, there was a clear response to remnant size in a study of tropical leaf-inhabiting bryophytes in central Amazonia, with smaller remnants being less species-rich (Zartman 2003). In both Zartman's (2003) study and this one, the fragments have been isolated for at least 15 years, which should be long enough for the bryoflora to have adjusted to new conditions. In our study there may be more complex spatial effects influencing numbers of moss species in remnants, such as the distance to other areas of native vegetation. Alternatively, remnant disturbance history may influence moss richness.

Bryophyte response to remnant age was less complex than the results for remnant size. Liverworts were species poor in the relatively recently isolated remnants compared with the continuous forest. Overall species composition of bryophytes was different. Some bryophytes, and liverworts in particular, may be slow to become established in new habitats. The only liverwort studied for spore production, *Ptilidium pulcherrimum*, has a considerably lower output of spores than mosses (Söderström & Herben 1997). However, most of the mosses studied were 'weedy' species and perhaps not representative (Söderström & Herben 1997). The other variable implicated in long distance dispersal is wind (Muñoz *et al.* 2004). Spores launched from a long seta and in open fields, rather than forests, appear to have the best chance of being carried long distances by winds (Söderström & Herben 1997). Seta length and other variables that may be related to dispersal distance, such as spore size, asexual propagule size and spore longevity, all vary greatly between species of both liverworts and mosses. Therefore, bryophyte response to fragmentation in the more open habitat of agricultural landscapes may differ from the patterns in this study.

Eucalypt remnants had lower mean liverwort richness than both continuous forest and pines. Liverworts also showed no significant difference in species composition between remnants, continuous forest and pines, which appears largely to be because of the similar composition of the patches and continuous forest. Liverwort richness was low across all sites, which was not surprising given that these are relatively dry forests and liverworts are most species rich in moist areas (Gradstein, Van Reenen & Griffin 1989; Kantvilas & Jarman 1993). The results for liverworts largely reflect the substrate preferences of three common species and the location of the 10 uncommon species. *Cephaloziella exiliflora*

prefers burned logs and both *Frullania probosciphora* and *Chiloscyphus semiteres* tolerate dry conditions and are flexible in their substrate requirements (Scott 1985). All three are widely distributed (Scott 1985), therefore it is not surprising that landscape context class effects were less pronounced for liverworts than for mosses.

Our study sites had been examined previously for the response of mammals and birds to landscape context (Lindenmayer *et al.* 1999; Lindenmayer, Cunningham & Pope 1999; Lindenmayer *et al.* 2000; Lindenmayer, Cunningham & Donnelly 2002). Four main points emerge from comparing responses of both the taxa from the same study sites at Tumut and results of other studies. First, exotic pine plantations suppressed richness compared with native forest. Secondly, the main contrast was between the pine plantations and the native eucalypt forest, with remnants providing valuable habitat, often regardless of size. Thirdly, responses of individual species were variable. Although we did not examine the response of individual taxa in this study, the variability of responses within taxa such as mammals and birds, invertebrates (Margules 1996) and liverworts and lichens (Moen & Jonsson 2003) is a common theme in fragmentation studies (Debinski & Holt 2000). Finally, an understanding of the biology of the taxa in question is vital in predicting the response to fragmentation. In the case of bryophytes, it appears that mobility and small size resulted in a stronger response to substrate than forest type, although the two are not independent. Substrate effects were critical in understanding patterns, with soil and burned eucalypt logs supporting much of the diversity in radiata pine sites. Plantations that maintain remnant vegetation and maintain key substrates such as decayed eucalypt logs will be vital for regional bryophyte diversity.

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