

# Structure of biological soil crust communities in *Callitris glaucophylla* woodlands of New South Wales, Australia

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## Abstract

**Question:** What is the nature of the relationships between cover, diversity and abundance of biological soil crusts, cover and diversity of vascular plants, and annual rainfall, soil texture and forestry practices in *Callitris glaucophylla* woodlands?

**Location:** Arid and semi-arid *Callitris glaucophylla*-dominated woodlands of eastern Australia.

**Methods:** We documented soil crust-forming mosses, lichens and liverworts at 83 woodland sites along a gradient of declining rainfall. Linear and non-linear regression were used to examine relationships between soil crust species and attributes of vascular plant communities, and a similarity matrix (species abundance × sites) was subjected to Non-metric Multi-Dimensional Scaling (MDS), and Analysis of Similarities (ANOSIM) to show the degree of association between groups of taxa, and soil texture, rainfall classes and forestry practices.

**Results:** We collected 86 taxa. Mosses were dominated by the family *Pottiaceae*, and lichens were dominated by squamulose forms. Average annual rainfall was highly correlated with soil crust community composition, and loamy soils supported a greater cover and diversity of taxa compared with sandy soils. Increases in tree cover were associated with significant, though weak, increases in abundance, but not diversity, of crusts. Crusts tended to be more diverse in areas that (1) had a sparse cover of ground-storey plants; (2) were relatively stable – as indicated by the proportion of perennial and/or native plants; (3) had more stable soil surfaces; and (4) were unlogged. Litter cover, overstorey thinning, and livestock grazing had no appreciable effect on crust diversity or cover.

**Conclusions:** *Callitris glaucophylla* woodlands provide substantial habitat for soil crust organisms, and the dense tree cover and closed canopies of *Callitris* do not appear to have a major influence on the structure of biological crust communities. Unlike other woodland systems, relatively few patches would be required to reserve a high diversity of crust species.

**Keywords:** *Callitris glaucophylla*; Cryptogam; Diversity; Non-vascular plant; Semi-arid woodland; Soil lichen.

**Nomenclature:** McCarthy (1991) for lichens; Streimann & Klazenga (2002) for mosses; Scott (1985) for liverworts.

## Introduction

Studies of the impacts of changes in ecosystem structure and function on woodland biota have tended to focus on the more visible components of the ecosystem such as mammals, birds, reptiles and vascular plants (e.g. Lindenmayer et al. 1999; Fischer & Lindenmayer 2002; Wethered & Lawes 2003). An often overlooked, but functionally important taxonomic group of organisms is the non-vascular plant group (see Pharo & Beattie 2001). Soil inhabiting (terricolous), non-vascular organisms are an important component of forest and woodland ecosystems. They are complex assemblages of mosses, liverworts and lichens that form a biological crust on the soil surface giving the surface soil environment a degree of structural and functional stability (West 1990). Biological soil crusts are widespread throughout the arid and semi-arid regions of the world including savanna woodlands and open forests (West 1990; Eldridge 2001).

The composition of soil crust communities is strongly influenced by soil surface biogeochemistry (e.g. surface texture, pH, plant cover, mineral content), land use (e.g. forestry, farming), and available light and moisture (West 1990; Metting 1991; Sveinbjörnsson & Oechel 1992; Ponzetti & McCune 2001). Changes in edaphic conditions can influence species diversity and composition (Metting 1991; Qian et al. 1999). For example, higher species diversity has been recorded on fine-textured compared with coarse-textured soils (Anderson et al. 1982). Species assemblages are also sensitive to habitat disturbances such as trampling (Hodgins & Rogers 1997), stump removal (Andersson & Hytteborn 1991), and logging (Newmaster & Bell 2002). Given adequate conditions, however, biological soil crust organisms have the ability to recover from disturbances (Newmaster & Bell 2002; Pharo et al. 2004), though recovery rates are typically slow.

In the Southern Hemisphere, much is known about

the structure and function of biological soil crust communities in arid and semi-arid landscapes (see Eldridge 2001 and references therein). In eastern Australia, the soil surface under *Callitris glaucophylla* (white cypress pine) is known to support a floristically diverse community of biological soil crust organisms, but the vascular plant community is generally sparse (Thompson & Eldridge 2005). *Callitris glaucophylla* (Cupressaceae) occurs over large areas of continental Australia on a range of soil types. It does not self-thin (Lacey 1972), and tends therefore to form mono-specific stands that suppress the cover of vascular plants, reputedly leading to an increased risk of water erosion (Thompson & Eldridge 2005). Anecdotal evidence suggests, however, that reductions in vascular plant cover may be compensated by increases in other forms of ground cover, particularly biological soil crusts and litter from the trees. The result is that biological soil crusts may be playing a substantial role in the functioning of *C. glaucophylla* woodlands where tree densities are sufficient to suppress the cover of vascular plants. Despite their putative importance in *C. glaucophylla* communities, the distribution and abundance of crusts and their constituent species has not been rigorously assessed.

We report here on a study of the diversity and cover of biological soil crusts at 83 sites in the *Callitris glaucophylla*-dominant woodlands in eastern Australia. We had four predictions about the structure of the soil crust community within *C. glaucophylla*-dominant woodlands. Firstly, given the strong links between soil texture (clay content), soil stability, and the distribution of soil crust taxa worldwide (e.g. Anderson et al. 1982), we anticipated that fine-textured soils would support a greater diversity and cover of crust species compared with sandy surfaces. Secondly, we predicted that reduced rainfall from relatively wet eastern woodlands to relatively dry western woodlands would be associated with increases in biological crust cover, diversity and abundance corresponding to declines in cover of vascular plant cover. Thirdly, notwithstanding any changes due to rainfall, we expected that increases in tree, ground-storey and litter cover would be accompanied by declines in diversity and abundance of crust species. Finally, given that biological soil crusts are useful indicators of landscape health (in the sense that vital ecosystem processes are fully functional) and stability (Eldridge & Koen 1998), we anticipated strong correlations between the cover and composition of biological soil crusts and the proportions of both perennial and native ground-storey plants at a site, which we regard as measures of landscape health. We tested these predictions by examining the cover and floristics of soil crust communities on fine- and coarse-textured soils at *C. glaucophylla* woodland sites along a rainfall gradient.

## Methods

### Study area

*Callitris glaucophylla* woodlands occur primarily over large areas of eastern Australia primarily in New South Wales (NSW) and Queensland (QLD). *C. glaucophylla* is a small to medium, single trunk evergreen tree, occasionally reaching heights up to 30 m (Boland et al. 1984). The pre-European community structure is thought to have comprised a mosaic of *Eucalyptus* spp., *Allocasuarina leuhmannii*, *Acacia aneura*, *Casuarina* spp. and *Geijera parviflora* trees (Lacey 1972). However, forestry operations and clearing for agriculture have substantially altered *C. glaucophylla* community structure so that most woodlands are now essentially mono-specific. *C. glaucophylla* is managed for forestry and is an important commercial timber species because of its natural resistance to termites. In addition to forestry, many *C. glaucophylla* woodlands are leased for grazing on both leasehold or freehold land, or on land managed by State Forests of NSW which permit controlled stock grazing. Despite their importance for timber production, there is a growing recognition of their significance as habitat for plants and animals.

Climate across the study area is characteristically Mediterranean, with warm to hot summers and mild winters. Ca. 20% more rain falls in the six cooler months (March - August) compared with six warmer months. *C. glaucophylla* occurs on a variety of land forms ranging from sloping ridges in the eastern part of the study area to level plains in the western part of the State. The soils were generally well-drained Kandosols and some Chromosols (Isbell 1996) with surface textures ranging from sands to clay loams. The soils are neutral to slightly acidic pH (ca. 5-7) at the surface, have generally low nutrient levels and often a high erosion potential. Soils are generally very deep, with exposure of bedrock only at the margins of hill slopes and ranges. At the time of the study the area was experiencing severe drought conditions.

### Site selection

A review of the geographic distribution of *Callitris glaucophylla* provided a basis for selection of field sites. In NSW, *C. glaucophylla* occurs primarily within State Forests, National Parks and along roadside corridors, but smaller areas occur on private property in the Central Division and within leasehold land in the Western Division. Sites were selected opportunistically along an east-west transect from Eugowra (33°24' S, 148°22' E) in the east to Pooncarie (33°22' S, 142°34' E) in the west

and sampled sites as far north as Cobar (31°30' S, 145°50' E) and south to the Victorian border (35°49' S, 146°14' E). Sampling encompassed a large distributional range of *C. glaucophylla* within NSW (Lacey 1972) including significant regions of *C. glaucophylla* woodland in the Riverina (southern NSW) and the Cobar Pedepain. The survey also encompassed a range of land tenures (e.g. forestry, roadside corridors and leasehold or freehold property). All field sites were dominated by *C. glaucophylla*, with only an occasional *Eucalyptus* or *Allocasuarina luehmannii* sharing any canopy space.

### Field sampling

Field sampling took place over a six week period in late 2001 and early 2002. Each of the 83 sites consisted of a 0.1 ha (20 m × 50 m) plot. This plot layout formed the basis for other studies not reported here. For the current study, all measurements were made from within a 20 m × 20 m plot located in the centre of the 0.1 ha plot. We measured the cover of ground-storey vascular and non-vascular plants, and collected small quantities of soil crust samples for detailed laboratory identification. A soil sample from the top 5 cm was taken from each corner of the plot and bulked for laboratory particle size analysis. Soil surface condition was assessed within five 0.5-m<sup>2</sup> quadrats spaced every 4 m along a 20 m transect running through the centre of the plot.

Field sites were categorized as State Forest, roadside corridor (including travelling stock reserve), or private property. The extent of grazing could not be quantified apart from noting that sites were either grazed or ungrazed at the time of field survey. Evidence of grazing included the presence of cattle or sheep, dung, or watering troughs. Evidence of forestry activities i.e. degree of thinning and/or logging was recorded and confirmed using records from State Forests NSW.

### Soil surface condition

The morphology of the soil surface was assessed in each quadrat according to the methods of Tongway (1995) and Tongway & Hindley (2004) using a total of 12 surface features (Table 1). Surface roughness is defined as the vertical distance between the lowest and highest points in the quadrat, and is a measure of the potential rainfall retention on the surface. Crust resistance measures the degree to which the soil crust, in this case biological or physical, can be mechanically disturbed to yield sediment. It is measured on a dry soil. Crust brokenness measures the percentage of the surface covered with cracks and relates to the capacity of the surface to disintegrate and erode. In addition, degree of cracking may be indicative of potential microsites for seeds to settle. Crust stability is the degree to which surface soil aggregates maintain their stability when wetted and is measured using the Emerson slake test (Tongway & Hindley 2004). The type and severity of erosion is assessed in terms of erosional features such as rilling, sheeting, scalding, terracettes and pedestals, and the cover of deposited materials assesses the nature and amount of alluvium transported to and deposited on the surface. Projected foliage cover of vascular plants was measured to estimate the capacity of the vegetation to intercept raindrops, and basal cover of perennial long-lived plants and other permanent cover components such as rocks and logs estimated in order to examine the effect of cover on overland flow processes. Soil texture is assessed using the bolus technique (McDonald et al. 1990) on surface soils. Litter cover, assesses the percentage cover, origin (transported from the site or deposited locally) and degree of incorporation in the soil and therefore decomposition of plant material (Tongway & Hindley 2004).

Using the measurements described above, we derived

**Table 1.** Surface features measured during the soil surface condition assessment, and indexes derived from these scores (from Tongway & Hindley 2004). Stability index\* =  $(B+C+D+E+F+G+J) / 0.36$ ; Infiltration index\*\* =  $(A+B+D+H+I+(J*K*L)) / 0.57$ ; Nutrient index =  $(A+H+(J*K*L)) / 0.39$ . \*Cryptogam cover (scores 0 - 4) omitted; \*\*Resistance score adjusted for calculating infiltration index (see Tongway & Hindley 2004 for explanation).

Surface feature	Classes
A. Surface roughness	1 = < 3 mm, 2 = 3-8 mm, 3 = 8-25 mm, 4 = large depressions with base, 5 = very large depressions > 100 mm
B. Crust resistance	1 = sandy, non-coherent, 2 = easily broken, 3 = moderately hard, 4 = very hard and brittle, 5 = flexible or self-mulching
C. Crust brokenness	0 = no crust, 1 = extensively broken, 2 = moderately broken, 3 = slightly broken, 4 = intact crust
D. Crust stability	0 = not applicable, 1 = very unstable, 2 = unstable, 3 = moderately stable, 4 = very stable
E. Erosion cover	1 = >50 %, 2 = 25-50 %, 3 = 10-25 %, 4 = <10 %
F. Cover of deposited material	1 = >50% cover, 2 = 20-50% cover, 3 = 5-20% cover, 4 = 0-5% cover
G. Projected foliage cover	1 = < 1 %, 2 = 1-10 %, 3 = 10-25 %, 4 = 25-50 %, 5 = > 50 %
H. Basal cover	1 = <1%, 2 = 1-10%, 3 = 10-20%, 4 = >20%
I. Soil texture	1 = silty to heavy clay, 2 = sandy clay loam to sandy clay, 3 = sandy to silty loam, 4 = sand to clayey sand
J. Litter cover	1 = < 10 %, 2 = 10-25 %, 3 = 25-50 %, 4 = 50-75 %, 5 = 75-100 %, 6 = 100 % < 21 mm thick, 7 = 100% 21-70 mm thick, 8 = 100% 70-120 mm thick, 9 = 100% 120-170 mm thick, 10 = 100% >170 mm thick
K. Litter origin	1.5 = local, 1 = transported
L. Litter incorporation	1 = nil, 1.3 = slight, 1.7 = moderate, 2 = extensive

three indices of soil surface condition which give a measure of the health of the soil surface. These are: (1) stability, a measure of how the soil withstands erosive forces or reforms after erosion; (2) infiltration, which indicates how soil water is partitioned between infiltration and runoff; and (3) nutrients which provides a measure of how efficiently organic material is recycled into the soil (Tongway 1995). The surface features used in the calculation of the three indices are shown in Table 1. The score for each surface feature described above was used in the calculation of the three indices using data for each of the five quadrats separately. A site score was then derived as the average score across all quadrats. While the original measurements included a score for the cover of biological soil crusts, this surface feature was not included in the calculations as we were interested in relating these scores to the cover of biological soil crusts.

#### *Soil crust floristics*

Soil surface samples were sieved to remove any loose soil and examined under a 10× binocular dissection microscope. Soil crust taxa were identified, where possible, to species level, but the lack of reproductive structures such as capsules limited the identification of some specimens to genus level. Moss identification followed the taxonomic keys and descriptions in Scott & Stone (1976) and Catcheside (1980). Liverwort identification and nomenclature follows Scott (1985). There remains inconclusive separation of *Crossidium davidai* and *Tortula atrovirens*; all specimens were classified as *Tortula atrovirens*.

#### *Statistical analyses*

Each taxon was assigned an abundance score where 1 = < 10 individuals, 2 = 10-100 individuals, 3 = 101-1000 individuals and 4 = > 1000 individuals. Mean species abundance was calculated as the sum of mid-points of the classes shown above for each species. Accordingly, percent species abundance was calculated as the sum of mid-points of individual species at all sites divided by the sum of mid-points for all species at all sites. A matrix of the original four class scores for each of the 86 columns (species or taxa) by 83 rows (sites) was converted to a similarity matrix using the Bray Curtis similarity coefficients contained within the PRIMER (Version 5.2.9) statistical package (Clarke & Warwick 2001) with no transformation. This similarity matrix was subjected to Non-metric Multi-Dimensional Scaling (MDS). Hypothesis tests of differences in the pattern of species abundance in relation to soil texture, rainfall class or forestry treatment, defined a priori, were performed using ANOSIM which derives a test statistic

(Global *R*) and a significance level. The degree of association of individual crust species with soil texture class, rainfall class or forestry practice was measured using Indicator-Species Analysis using PC-ORD (McCune & Mefford 1999). Indicator values combine information on relative abundance and frequency of species. For example, when all individuals of a given species are restricted to a particular class, and all samples from the particular class contain an occurrence of that species, then the indicator value is maximal ( $IV = 100$ ). Species data were randomized among the soil texture, rainfall and forestry practice classes, and a Monte Carlo randomization procedure performed with 1000 iterations in order to determine the statistical significance of the indicator values.

Relationships between non-vascular and vascular plants, and the environmental variables were examined using linear and non-linear regressions, Student *t*-tests and the non-parametric Kruskal-Wallis tests with Minitab (1997) and S-PLUS (MathSoft Inc., Seattle, WA). Curvilinear models were fitted to the data where we felt that the underlying ecological relationship was best represented, *a priori*, by a non-linear relationship.

## **Results**

#### *Crust floristics and cover*

We recorded a total of 86 soil crust species comprising 53 bryophyte (39 mosses, 14 liverworts) and 33 soil lichen species across all sites (Table 2). Biological soil crust taxa were found at all sites, and the number of species per site varied from 3 to 33 (mean = 20.0 + 0.88 SE). Species from the family *Pottiaceae* were the most abundant (Table 2). The most common mosses, in terms of the number of sites at which they were found, were *Barbula calycina* (67 sites), *Didymodon torquatus* (61), *Gemmabryum pachytheca* (58), *Fissidens megalotis* (55), and *Tortula atrovirens* (49). The most common liverwort taxa were *Fossombronia* spp. (64), *Asterella drummondii* (56) and *Cephaloziella arctica* ssp. *antarctica* (40), while the most common soil lichens were *Cladonia* spp. (72), *Collema coccophorum* (59), *Endocarpon pusillum* (55) and *Endocarpon simplicatum* var. *biosporum* (54). The cover of biological soil crusts averaged 12.2 + 1.2 % (range 1 - 55%) and was significantly greater on loamy soils (13.2 + 1.4%) compared with sandy soils (7.8 + 1.5%;  $t = 2.58$ ,  $df = 45$ ,  $P = 0.013$ ).

Of all sites 56% contained 20 or more species, 30% of sites contained 10-19 species, and 13% of sites had < 10 species; 45 species (52%) occurred at ten or fewer sites, and six species accounted for over half of the total abundance across all sites.

**Table 2.** Abundance (abund) of biological soil crust taxa found in *Callitris glaucophylla* woodlands in eastern Australia.

Biological soil crust species	Family	No. of sites	% abund
<b>Mosses</b>			
<i>Barbula calycina</i>	Pottiaceae	67	12.89
<i>Triquetrella papillata</i>	Pottiaceae	39	8.38
<i>Didymodon torquatus</i>	Pottiaceae	61	6.55
<i>Fissidens megalotis</i>	Fissidentaceae	55	5.74
<i>Barbula crinita</i>	Pottiaceae	40	3.56
<i>Rosulabryum billarderi</i>	Bryaceae	15	2.51
<i>Tortula atrovirens</i>	Pottiaceae	49	1.63
<i>Gemmabryum pachytheca</i>	Bryaceae	58	1.60
<i>Bryum argenteum</i>	Bryaceae	35	1.57
<i>Eccleridium arcuatum</i>	Ditrichaceae	45	1.57
<i>Pottia</i> spp.	Pottiaceae	30	1.29
<i>Ceratodon purpureus</i>	Ditrichaceae	5	1.14
<i>Rosulabryum campylotheicum</i>	Bryaceae	34	0.96
<i>Gigaspermum repens</i>	Gigaspermaceae	44	0.93
<i>Trichostomum brachydontium</i>	Pottiaceae	8	0.78
<i>Bryum caespiticum</i>	Bryaceae	4	0.66
<i>Weissia controversa</i>	Pottiaceae	2	0.42
<i>Campylopus introflexus</i>	Dicranaceae	10	0.39
<i>Stonea oleaginoso</i>	Pottiaceae	36	0.30
<i>Archidium stellatum</i>	Archidiaceae	3	0.27
<i>Ditrichum difficile</i>	Ditrichaceae	11	0.27
<i>Eccleridium pulchellum</i>	Ditrichaceae	24	0.26
<i>Entosthodon muhlenbergii</i>	Funariaceae	1	0.21
<i>Barbula hornschiuchiana</i>	Pottiaceae	7	0.19
<i>Rosulabryum capillare</i>	Bryaceae	8	0.18
<i>Fissidens taylorii</i>	Fissidentaceae	28	0.14
<i>Goniomitrium acuminatum</i> ssp. <i>nerve</i>	Funariaceae	23	0.10
<i>Phascum robustum</i>	Pottiaceae	16	0.09
<i>Acaulon sullivaniana</i>	Pottiaceae	3	0.07
<i>Acaulon mediterraneum</i>	Pottiaceae	12	0.06
<i>Tortula pagorum</i>	Pottiaceae	3	0.06
<i>Tetrapterum cylindricum</i>	Pottiaceae	3	0.04
<i>Polytrichum juniperinum</i>	Polytrichaceae	2	0.04
<i>Crossidium geheebii</i>	Pottiaceae	3	0.02
<i>Rosulabryum torquescens</i>	Bryaceae	3	0.02
<i>Gemmabryum eremaicum</i>	Bryaceae	2	0.02
<i>Tortella</i> spp.	Pottiaceae	1	0.02
<i>Ephemerum cristatum</i>	Ephemereaeae	1	0.00
<i>Gemmabryum dichotomum</i>	Bryaceae	1	0.00
<b>Liverworts</b>			
<i>Cephaloziella artica</i>	Cephaloziellaceae	40	2.62
<i>Fossombronia</i> spp.	Cosoniaceae	64	2.26
<i>Asterella drummondii</i>	Aytoniaceae	56	1.13
<i>Lophocolea semiteres</i>	Geocalycaceae	2	0.44
<i>Plagiochasma rupestre</i>	Aytoniaceae	10	0.16
<i>Riccia limbata</i>	Ricciaceae	25	0.13
<i>Riccia lamellosa</i>	Ricciaceae	27	0.06
<i>Riccia crinita</i>	Ricciaceae	19	0.06
<i>Riccia nigrella</i>	Ricciaceae	6	0.03
<i>Lunularia cruciata</i>	Lunulariaceae	1	0.02
<i>Riccia</i> spp.	Ricciaceae	8	0.02
<i>Riccia sorocarpa</i>	Ricciaceae	2	0.00
<i>Riccia cartillaginosa</i>	Ricciaceae	1	0.00
<i>Riccia crystallina</i>	Ricciaceae	1	0.00
<b>Lichens</b>			
<i>Diploschistes</i> spp.	Thelotremaataceae	32	8.85
<i>Cladonia</i> spp.	Cladoniaceae	72	8.74
<i>Cladia aggregata</i>	Cladiaceae	19	3.06
<i>Lecidea</i> spp.	Lecideaceae	24	3.05
<i>Collema coccophorum</i>	Collemaataceae	59	1.85
<i>Endocarpon simplicatum bisporum</i>	Verrucariaceae	54	1.82
<i>Psora decipiens</i>	Psoraceae	26	1.75
<i>Cladia corallaizon</i>	Cladiaceae	8	1.58

Biological soil crust species	Family	No. of sites	% abund
<i>Trapelia coarctata</i>	Trapeliaceae	24	1.22
<i>Endocarpon pusillum</i>	Verrucariaceae	55	1.14
<i>Heterodea muelleri</i>	Heterodeaceae	34	1.12
<i>Peltula</i> spp.	Peltulaceae	48	1.01
<i>Xanthoparmelia bellatula</i>	Parmeliaceae	34	0.67
<i>Heterodea beaugleholei</i>	Heterodeaceae	39	0.35
<i>Placydium squamulosum</i>	Verrucariaceae	11	0.35
<i>Psora crystallifera</i>	Psoraceae	4	0.26
<i>Buellia subcoronata</i>	Physciaceae	3	0.25
<i>Toninia sedifolia</i>	Lecideaceae	1	0.21
<i>Xanthoparmelia reptans</i>	Parmeliaceae	7	0.19
<i>Placydium lacinulatum</i>	Verrucariaceae	10	0.12
<i>Xanthoparmelia pseudoamphixantha maculata</i>	Parmeliaceae	3	0.09
<i>Endocarpon pallidum</i>	Verrucariaceae	11	0.08
<i>Chondropsis semiviridis</i>	Parmeliaceae	2	0.06
<i>Xanthoparmelia pseudoamphixantha</i>	Parmeliaceae	3	0.04
<i>Lecanora</i> spp.	Lecanoraceae	2	0.04
<i>Endocarpon rogersii</i>	Verrucariaceae	7	0.03
<i>Leptogium</i> spp.	Collemaataceae	5	0.03
<i>Xanthoparmelia flavescentireagens</i>	Parmeliaceae	2	0.02
<i>Neofuscelia</i> spec.	Parmeliaceae	1	0.02
<i>Placydium pilosellum</i>	Verrucariaceae	1	0.02
Unknown crustose lichen		1	0.02
<i>Xanthoparmelia taractica</i>	Parmeliaceae	1	0.02
<i>Heppia despreuxii</i>	Heppiaceae	2	0.00

### Biological soil crust community structure

The first dimension of the MDS biplot was negatively correlated with mean annual rainfall ( $F_{1;81} = 52.8$ ,  $P < 0.001$ ,  $R^2 = 0.39$ ) and cover of vascular plants ( $F_{1;81} = 116.2$ ,  $P < 0.001$ ,  $R^2 = 0.58$ ), and positively correlated with the proportion of native vascular plants at a site ( $F_{1;81} = 21.4$ ,  $P < 0.001$ ,  $R^2 = 0.20$ ) and the proportion of perennial vascular plants ( $F_{1;81} = 32.3$ ,  $P < 0.001$ ,  $R^2 = 0.28$ ). The second dimension of the MDS biplot was negatively correlated with the diversity of mosses ( $F_{1;81} = 29.6$ ,  $P < 0.001$ ,  $R^2 = 0.26$ ), diversity of lichens ( $F_{1;81} = 17.6$ ,  $P < 0.001$ ,  $R^2 = 0.17$ ) and the derived score for stability ( $F_{1;81} = 12.9$ ,  $P = 0.001$ ,  $R^2 = 0.13$ ). These relationships were best described by linear models.

Analysis of similarities (ANOSIM) indicated a highly significant difference in crust composition between sandy and loamy soils (Global  $R = 0.420$ ,  $P = 0.001$ ). More species were recorded from the loamy soils (22.0 + 0.84 species) compared with the sandy soils (12.0 + 1.93 species; Kruskal-Wallis  $H = 16.19$ ,  $P < 0.001$ ). Some species exhibited strong preferences for the loamy soils (Table 3). Six species, all bryophytes, (*Fissidens megalotis*,  $IV = 75.6\%$ ,  $P < 0.001$ ; *Asterella drummondii*  $IV = 69.5\%$ ,  $P < 0.001$ ; *Barbula calycina*,  $IV = 67.9\%$ ,  $P < 0.001$ ; *Fossombronia* spec.,  $IV = 64.8\%$ ,  $P = 0.012$ ; *Riccia lamellosa*,  $IV = 40.3\%$ ,  $P = 0.009$  and *Fissidens taylorii*,  $IV = 38.1\%$ ,  $P = 0.037$ ) were important indicators of loamy-textured soils. There were no strong indicators of sandy soils ( $P > 0.05$ ).

**Table 3.** Mean abundance of biological soil crust species differing significantly in relation to soil texture and logging. Within a soil texture class or logging class, different letters between factors within a row indicate a significant difference in that species at  $P < 0.05$  using the Kruskal-Wallis test.

	Sand	Loam	Logged	Unlogged
<i>Cladonia</i> spp.	162.5 a	302.2 b	259.5 a	280.2 a
<i>Barbula calycina</i>	158.1 a	465.2 b	288.8 a	443.3 a
<i>Fossombronia</i> spp.	25.6 a	81.9 b	65.5 a	72.9 a
<i>Collema coccophorum</i>	31.9 a	64.4 b	56.3 a	58.7 b
<i>Gemmabryum pachytheca</i>	28.1 a	55.5 a	24.3 a	58.5 b
<i>Asterella drummondii</i>	5.0 a	42.9 b	43.8 a	33.0 a
<i>Fissidens megalotis</i>	10.3 a	221.6 b	195.5 a	176.3 a
<i>Endocarpon simplicatum</i> var. <i>bisporum</i>	27.8 a	64.3 a	14.8 a	70.8 b
<i>Peltula</i> spp.	5.3 a	38.2 a	4.0 a	40.7 b
<i>Eccremidium arcuatum</i>	17.5 a	57.2 b	30.8 a	55.5 a
<i>Goniomitrium acuminatum</i> ssp. <i>enerve</i>	7.5 a	34.3 b	37.3 a	26.6 b
<i>Cephaloziella arctica</i>	70.0 a	85.4 b	20.3 a	102.1 a
<i>Triquetrella papillata</i>	343.0 a	245.1 a	363.0 a	232.5 b
<i>Stonea oleaginosa</i>	4.7 a	10.8 a	3.8 a	11.4 b
<i>Gemmabryum argenteum</i>	4.7 a	60.3 a	95.5 a	35.0 b

We found no significant relationships between mean annual rainfall and either the abundance or diversity (species richness) of biological soil crust taxa ( $P > 0.34$ ). However the diversity of lichens was negatively correlated with average annual rainfall ( $F_{1,81} = 13.5$ ,  $P < 0.001$ ,  $R^2 = 0.13$ ). There were no significant correlations for liverworts ( $P > 0.69$ ).

Significant differences in species composition were detected between the three rainfall classes (Global  $R = 0.16$ ,  $P < 0.01$ ). For several species (*Didymodon torquatus*, *Gemmabryum pachytheca*, *Endocarpon pusillum*, *Heterodea beagleholei* and *Stonea oleaginosa*) the most significant differences occurred between the moderate (350–450 mm) and high (> 450 mm) rainfall classes. As with soil texture, there were some strong links between individual species and particular rainfall classes. Four species (*Pottia* spp.  $IV = 55.2\%$ ,  $P < 0.001$ ; *Endocarpon simplicatum* var. *bisporum*  $IV = 47.2\%$ ,  $P = 0.023$ ; *Psora decipiens*,  $IV = 41.7\%$ ,  $P = 0.006$  and *Heterodea beagleholei*,  $IV = 40.0\%$ ,  $P = 0.024$ ) were associated with lower rainfall areas (< 350 mm) while *Triquetrella papillata* ( $IV = 50.9\%$ ,  $P = 0.005$ ), *Heterodea muelleri* ( $IV = 40.9\%$ ,  $P = 0.037$ ) and *Rosulabryum billardieri* ( $IV = 37.4\%$ ,  $P = 0.006$ ) were associated with higher rainfall areas (> 450 mm).

#### Biological soil crusts and vascular plant cover

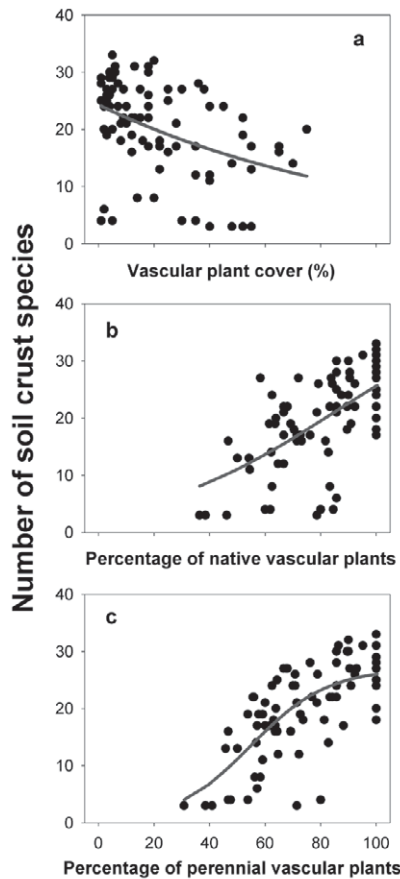
We detected no meaningful relationship between soil crust diversity and tree canopy cover ( $P = 0.08$ ). However, there was a significant, though weak, positive relationship between canopy cover and abundance of soil crust taxa ( $F_{1,81} = 9.93$ ,  $R^2 = 0.10$ ,  $P < 0.002$ ). There were no significant relationships between canopy cover and abundance of any individual biological soil crust group i.e. lichens, liverworts or mosses ( $P = 0.17$ ,  $P = 0.83$ , and  $P = 0.14$ , respectively).

The diversity of crust taxa declined exponentially with increases in vascular plant cover ( $F_{1,81} = 16.6$ ,  $P = 0.001$ ,  $R^2 = 0.15$ , Fig. 1a). However, when we considered only native species, crust diversity increased with increases in the proportion of native plant cover ( $F_{2,80} = 26.5$ ,  $P < 0.001$ ,  $R^2 = 0.38$ , Fig. 1b). Further, there was a positive relationship between perennial plant cover as a proportion of total cover, and crust diversity, and this was best described as a sigmoidal model ( $F_{2,80} = 42.3$ ,  $P < 0.001$ ,  $R^2 = 0.50$ , Fig. 1c). The relationship between the cover of vascular plants and the percentage of taxa at a site dominated by moss species followed a Gaussian function, with maximum percent moss cover at vascular cover of about 40% ( $F_{2,80} = 16.4$ ,  $P < 0.001$ ,  $R^2 = 0.26$ , Fig. 2a). The percentage of lichen species in the crust declined exponentially with increases in the percent cover of vascular plants ( $F_{1,81} = 13.1$ ,  $P < 0.001$ ,  $R^2 = 0.12$ , Fig. 2b).

Litter cover at the sites ranged from <10% to 100%. Increasing cover of litter did not correspond with a decline in either diversity nor abundance of taxa in the biological soil crust. There were weak positive relationships, best described by linear models, between litter cover and both biological soil crust species diversity ( $F_{1,81} = 6.4$ ,  $P = 0.014$ ,  $R^2 = 0.06$ ) and abundance ( $F_{1,81} = 5.1$ ,  $P = 0.027$ ,  $R^2 = 0.05$ ).

#### Biological soil crusts, soil stability and disturbance

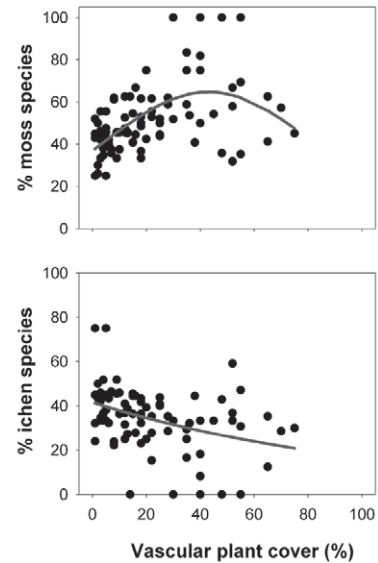
The soil surface at *Callitris glaucophylla* sites had moderate scores for the derived stability index (62.4 + 0.5%, mean + SD), but generally low scores for infiltration (38.2 + 0.7%) and nutrients (31.8 + 0.7%). There were some highly significant positive linear relationships between the diversity of biological soil crusts and the average scores for both stability and infiltration ( $F_{1,81} = 23.5$ ,  $P < 0.001$ ,  $R^2 = 0.22$  and  $F_{1,81} = 7.6$ ,  $P <$



**Fig. 1.** Relationships between the number of soil crust species and (a) vascular plant cover; (b) percentage of native plants only; (c) percentage of perennial plants only.

0.007,  $R^2 = 0.07$ , respectively), but the predictive power was low. There were also significant positive associations between abundance of soil crust taxa and average stability ( $F_{1,81} = 96$ ,  $P < 0.003$ ,  $R^2 = 0.06$ ), but no relationships between nutrient indices and either crust diversity or abundance ( $P > 0.42$ ).

We did not detect any relationships between biological soil crust diversity or abundance and any of the measures of site disturbance i.e. overstorey thinning or stock grazing. However, ANOSIM indicated that there were statistically significant differences in species composition in the soil crust communities between logged and unlogged sites (Global  $R = 0.208$ ,  $P = 0.005$ ). More species occurred on unlogged compared with logged sites (Kruskal-Wallis,  $H = 8.48$ ,  $P < 0.004$ , Table 3). Two species (*Endocarpon simplicatum* var. *bisporum*,  $IV = 63.1\%$ ,  $P = 0.005$ , *Peltula* spp.  $IV = 62.1\%$ ,  $P = 0.017$ ) showed a strong preference for unlogged sites while *Rosulabryum billardieri*, *Cladia aggregata* and *Cladia corallaizon* were weak indicators ( $IV < 30\%$ ) of logged sites.



**Fig. 2.** Relationships between vascular plant cover and percentage of (a) moss species at a site; (b) lichen species at a site.

## Discussion

The aim of our study was to examine changes in the diversity, cover and community structure of biological soil crusts at *Callitris glaucophylla*-dominated woodland sites of varying cover and density. These sites were located along a gradient of declining average annual rainfall, and with land uses ranging from grazing leases to conservation reserves. Our results indicated clearly-defined effects of rainfall and soil texture, weak effects of logging, but no effects of grazing or tree thinning. Together the results suggest that biological soil crust taxa are responding to influences that are largely independent of the structure of *Callitris glaucophylla* woodland communities. We conclude that the notion that dense *Callitris glaucophylla* woodlands are suppressing the cover and diversity of biological soil crust taxa is not well founded, over a large area of eastern Australia.

The first result of the study supports the first hypothesis that loamy soils supported significantly more species than sandy soils. Soil texture had major effects on diversity and abundance, but also had effects at the species level. Soil texture is known to be a major driver of biological soil crust communities (West 1990; Metting 1991; Downing 1992), and soils with a high silt and clay content typically support a greater diversity and cover of biological soil crust species compared with coarser-textured soils (Anderson et al. 1982; Rogers & Lange 1972; Eldridge 2001). Increased clay content could be related to the greater adsorption of micronutrients such as Ca, Mg and K required by some lichens and cyanobacteria (e.g. Davidson et al. 2002). Cyanolichens, in

particular, are known to have a high requirement for P, which is necessary for nitrogen fixation (Kershaw 1985); hence soils with a higher clay content would be preferred substrates for lichens. In the present study, sandy soils did support biological soil crust taxa, but they were mainly dominated by the mosses *Triquetrella papillata* and *Barbula calycina*. Notwithstanding the links between micronutrients, texture and lichens, taxa showing the strongest preferences for loamy soils (Indicator Values > 50%) were all bryophytes (*Fissidens megalotis*, *Asterella drummondii*, *Barbula calycina* and *Fossombronia* spp.). The mechanisms for this are poorly understood, but may relate to complex interactions with other factors such as topography, soil chemistry, aspect, light levels and previous levels of soil degradation.

The composition of biological soil crusts tended to vary with differences in rainfall, partly supporting our second hypothesis. However, the results were not as predictable as we expected. We did not detect major differences in either species abundance or diversity with declining average annual rainfall, although clear differences in species assemblages were apparent between the low rainfall (< 350 mm mean annual rainfall) and higher rainfall (> 600 mm) sites. The distribution of bryophytes, in particular, is largely driven by rainfall (and soil pH; Downing & Selkirk 1993). In Australia, bryophyte diversity typically declines with declining rainfall and increases with increasing summer rainfall (Eldridge 2001). Many bryophytes in harsh, water-limited environments have developed desiccation-tolerant morphologies such as highly papillose leaf surfaces, recurved leaf margins and hyaline hair points (Bell 1982), while others such as the ephemerals, are essentially drought evaders (Longton 1992).

Predictably, in the present study, moss species abundance and diversity declined, and lichen increased, along a gradient in declining annual rainfall. The positive relationship between the soil lichen abundance and declining rainfall suggests a number of possibilities. Lichens could be competitively inferior to mosses, particularly in areas of denser cover of vascular plants, or in areas of moderate litter cover where litter could preferentially enhance the nutrient status of soils and hence moss growth (e.g. Rincón 1988). However, high litter cover has the potential to limit the growth of moss, especially within broad-leaved forests and woodlands (B. McCune pers. comm. 2005). Declines in rainfall westward are associated with increases in soil pH resulting from increasing marine-derived aeolian calcium carbonate in arid soils. Soil lichens are also known to tolerate higher surface temperatures and more extreme conditions than most bryophytes (Rogers 1972) but to be limited by summer rainfall. The absence of well-developed lichen-dominated crusts in areas of summer

rainfall results from a suppression of photosynthesis at high temperatures when lichen thalli are hydrated (Lange et al. 1996).

Contrary to our expectation, we found no linear relationships between crust diversity, and the density or cover of the overstorey *Callitris glaucophylla*, and only weak linear relationships for soil crust abundance, providing no support for our third hypothesis. The weak linear relationship between tree canopy cover and crust abundance could have been related to the impact of trees on shade levels, or their effect on the morphology of the soil surface. Shading is known to affect biological soil crust species, and lichens are more favourably associated with higher light intensities (i.e. reduced shade) than moss communities (Sedia & Ehrenfeld 2003). Mosses however will persist in shaded environments, and in *Callitris glaucophylla* woodlands, two moss species, *Fissidens vitattus* and *Barbula hornschurchiana*, have been identified as being 'shade tolerators' under dense tree canopies (Eldridge 1999). However both moss and lichen species within woodland communities can persist under varying conditions of light and moisture (e.g. Frego & Carleton 1994; Sedia & Ehrenfeld 2003) but the quality of their habitat is suboptimal.

*Callitris glaucophylla* produces large amounts of litter which is known to be hydrophobic (Lacey 1972; Harris et al. 2003). We expected therefore that increasing levels of litter cover would be associated with reduced cover and diversity of soil crust organisms. Contrary to our expectations however, there were no clear trends between diversity and abundance, and cover of litter ( $R^2 = 0.02$ ). Although litter may have restricted the availability of some microsites for establishment, it clearly did not have a major impact on the structure of the crust community. We attribute this in part to the geometry of the leaf litter, as needle-shaped leaf litter is less likely to completely block light from the crust colonies compared with broad-leaf litter (Sveinbjörnsson & Oechel 1992). Further, litter is known to have a negative effect on the growth of vascular plants (e.g. Wilsey & Polley 2003), potentially reducing competition on soil crust organisms from vascular plants. As indicated above, litter could also have a positive effect on mosses by increasing the availability of some nutrients (Rincón 1988, 1990).

In the present study, at a given level of vascular plant cover, sites with a greater proportion of perennial and/or native plants in the ground-storey layer also supported a substantially greater diversity of non-vascular species (Fig. 1), supporting our fourth hypothesis. The cover of perennial native grasses generally declines with prolonged grazing (e.g. McIntyre & Tongway 2005) and therefore would be expected to reflect greater diversity of non-vascular plants. Reduced levels of disturbance



would potentially allow for establishment of a greater diversity of crust species by providing them with a greater variety of regenerative niches (*sensu* Grubb 1977; Slack 1990).

Grazing, logging and fire are the major disturbances in *Callitris glaucophylla* woodlands (Thompson & Eldridge 2005). Although we have no data on fire frequency at the sites, some data were available for grazing and logging. Grazing-induced trampling by domestic livestock is known to be highly detrimental to biological soil crust species (e.g. Rogers & Lange 1971; Memmott et al. 1998), reducing cover and diversity, and destabilizing the soil surface (Eldridge 1999). Although we found no significant difference in diversity and abundance between sites classified as grazed and ungrazed, the categorization of grazing was based solely on indicators present at the time of survey and did not reflect the extent or intensity of previous or long-term grazing events. Had we been able to quantify actual stocking rates, we believe that more realistic grazing effects might have been detected.

The diversity or abundance of soil crust taxa did not change between thinned and unthinned sites, but logged sites had significantly greater diversity and abundance compared with unlogged sites (Table 3). Apart from the ubiquitous matt-forming moss *Triquetrella papillata* and the cosmopolitan moss *Gemabryum argenteum*, logging was associated with reduced abundance of soil crust taxa (Table 3). Logging operations involve substantial soil surface disturbance, which is likely to reduce soil roughness; silvicultural activities in boreal forest significantly reduced soil crust diversity (Newmaster & Bell 2002).

## Conclusions

*Callitris glaucophylla*-dominated woodlands support a relatively rich community of biological soil crust organisms. However, the impact of current land management practices such as logging and grazing on crust communities is not well known. The high-density and closed canopies of *Callitris glaucophylla* woodlands, which are thought to have a deleterious effect on vascular plants, do not appear to have a major influence on the structure of biological crust communities. The implication of our study is that, in terms of soil crust conservation, most sites were moderate repositories of soil crust taxa, and most species could therefore be reserved with relatively few woodland areas. This varies from other vegetation communities where a large number of sites is required to adequately ensure a high diversity (see Margules et al. 1988; Eldridge et al. 2006).

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