Impact of disturbance on above-ground water storage capacity of bryophytes in New Zealand indigenous tussock grassland ecosystems

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Abstract: Bryophytes are widespread in many plant communities and can attain cover and biomass levels that influence ecosystem processes. We investigated the impact of disturbance (fire, topsoil removal) on the composition, biomass, and water storage capacity of bryophytes in indigenous temperate tall-tussock grasslands managed to sustain an ecosystem service (regular provision of water) to nearby urban areas. We surveyed bryophyte composition, structure and water-related traits 9 years after experimental fires and topsoil removal. Total water storage capacity of non-epiphytic bryophytes in control grassland sites was estimated at 4.3 mm, a value similar to that found in temperate New Zealand forests. Total biomass, species composition, and water-related traits were the main drivers of water storage potential from bryophytes. A major shift in bryophyte species composition following disturbances reduced this potential by over 80%. Bryophyte community changed from a dense ground cover (71%) of the pleurocarpous moss *Hypnum cupressiforme* with high water holding capacity (c. 1400% of dry mass) in control plots, to low frequency of the colonist moss *Polytrichum juniperinum* in burned plots, and two *Campylopus* species in areas with topsoil removed for firebreaks (all three displaying a low water holding capacity of less than 800% dry mass). We concluded that despite their low species diversity (12 species in total in undisturbed sites), bryophytes form a major, previously unrecognised, component of indigenous tall-tussock grasslands in New Zealand, and contribute towards sustaining the valued water holding capacity of these systems. Like the tussock dominants, bryophytes and their associated ecological functions are highly susceptible to long-term impacts from burning and vegetation clearance. It is therefore critical to account for the recovery of bryophytes in the management of indigenous tall-tussock grasslands to maintain healthy ecosystems.

Keywords: ecosystem functions; fire; hydrology; mosses; species composition; successional communities; water-related traits

Introduction

Terricolous bryophytes (species of mosses, liverworts and hornworts that grow exclusively on the ground) play important roles in many ecosystems (Lindo & Gonzalez 2010), including in grasslands (Keizer et al. 1985; van Tooren et al. 1985; van Tooren 1990; Zamfir 2000); and shifts in their composition and relative abundance can lead to substantial changes in, for example, soil respiration, N input and community assembly (Zaady et al. 2000; Maestre et al. 2005; Michel et al. 2011). Water storage in bryophytes appears to be the most critical factor for ecosystem functioning, as many cryptogam species (bryophytes and lichens) can enhance water capture and retention, thereby controlling water availability to roots of vascular plants (Belnap 2006). For this reason, area-based water storage capacity is increasingly considered an important trait of bryophytic communities (Bowker et al. 2010). However, the relative contribution of terricolous bryophytes to the water holding capacity of ecosystems is poorly known, especially for non-forest successional communities where disturbances are frequently used to maintain the seral status of the vegetation.

Due to their structure, bryophytes have a higher water holding capacity (up to 1400% of their dry mass) than many other plant groups (Glime 2007; Proctor 2008). Unlike vascular plants, bryophytes obtain moisture directly by absorbing atmospheric water (dew, fog or rainfall) and condensed water vapour from the ground through cell surfaces, or externally by transport from wet to dry zones via capillary channels (Anderson & Bourdeau 1955; Proctor 2000a). In the majority of mosses and leafy liverworts, external capillary water can exceed the symplast water within the cells (water that freely diffuses within the inner side of the plasma membrane) (Proctor 2000b). Terricolous bryophytes can thus regulate water availability from precipitation and dew by acting as a store for intercepted water and by re-delivering it to the environment (Schulten 1985; Belnap 2006). Bryophytes are estimated to contribute up to 5 mm of water storage capacity in forest ecosystems, with terricolous species showing greater capacity (2–5 mm) than epiphytic species (0.8–1.3 mm) (Llorens & Gallart 2000; DeLucia et al. 2003; Hölscher et al. 2004; Pypker et al. 2006a).

Unlike water flux in vascular plants, which is controlled physiologically by opening and closing of stomata, water loss from most bryophytes is determined by the size and structural properties of the individual shoots and the cushion canopy. Variations in individual plant measures (e.g. size and cell walls) dictate the relative proportion of organs and tissues that control fluxes in and storage of water in bryophytes (Proctor 2008). Shoot and canopy architecture also influences the development of boundary layers adjacent to plant surfaces, altering wind turbulence and governing the rate of evaporation (Proctor 1980; Zotz et al. 2000; Rice et al. 2001; Rice & Schneider 2004). Water relationships (water holding capacity, evaporation rate, and desiccation tolerance) in bryophytes are highly variable among species (Glime 2007; Elumeeva et al. 2011), and communities (Rixen & Mulder 2005; Michel et al. 2012). Spatial or temporal shifts in the composition and structure of bryophyte communities following environmental changes (e.g. disturbance) can therefore be expected to affect the hydrological regime by altering the plant community's capacity to intercept, retain, and release atmospheric water (Chang et al. 2002; Llevia & Frost 2003; Tobón et al. 2011).

Temperate grassland ecosystems in human-managed landscapes are maintained by regular disturbances, especially fire and mammalian grazing. Composition and cover of terricolous bryophytes are often altered by intense and repeated disturbance (e.g. burning, mowing) (Faust et al. 2011). In the short term (2–8 years post-fire), the ability of spores of a few bryophyte species (e.g. *Funaria hygrometrica*, *Ceratodon purpureus* and *Polytrichum juniperinum* in Australia) to germinate on burned substrates facilitates the establishment of these fast-growing colonists (Duncan & Dalton 1982). In the longer term (>20 years post-fire), perennial pleurocarpous (horizontal growth form) mosses (e.g. *Hypnum cupressiforme* in Australia and New Zealand) dominate the bryoflora (Mark & Dickinson 2003; Morgan 2004). The turnover in bryophyte species following fire generally is influenced by the physical loss of the species, change in substrate suitability (rich humus layer or soil stability and humidity) and species' life strategies (During 1990; Thomas et al. 1994).

This study investigates shifts in the bryophyte communities of a temperate tall-tussock grassland (managed to sustain an urban water supply) after fire and soil disturbance, and estimates the associated impact on above-ground water storage capacity. More specifically, in a large-scale field experiment, we monitored the recovery of bryophyte communities in terms of species growth form and life strategies (During 1990, 1992) and water-related traits (water holding capacity and evaporation rate). We also estimated the water holding capacity for individual species that contributed significantly to the total bryophyte biomass in each treatment plot. By doing so, we aimed to establish whether patterns of bryophyte recolonisation in tall-tussock grassland ecosystems after disturbance influence total water storage by the above-ground vegetation. We predicted that the dense cover of perennial pleurocarpous mosses in these indigenous grassland ecosystems would enhance water storage capacity through their potential to store large quantities of water (over 1000% dry mass); and dominance of colonist species following disturbance (fire or soil removal) would lead to a reduction in this capacity.

Materials and methods

Study area

An upland indigenous tall-tussock grassland dominated by *Chionochloa rigida* (Poaceae) was investigated at Deep Stream (45°2′10″ S, 170°15′50″ E), at 600–700 m altitude on the Lammerlaw Range, south-eastern South Island, New Zealand. In this area, annual temperature averages 6.8°C and rainfall 993 mm; and rainfall is lower than the potential evapotranspiration for up to 7 months (September–March) of the year (Payton & Pearce 2009). The extensive grassland vegetation at the site was derived from a mosaic of natural forest, scrublands and grasslands following Polynesian fires in the 15th century, and maintained after European settlement, in c. 1850, by regular fire and stock (sheep and cattle) grazing (Molloy et al. 1963; Stevens et al. 1988; Mark 1993). The site was withdrawn from pastoral farming in the 1970s, and has remained unburned since the 1980s. The area is currently managed by the Dunedin City Council (DCC) as a water supply catchment.

We investigated the effect of disturbance on bryophyte composition and water-related function in tall-tussock grassland communities using a field experiment established by Payton and Pearce (2009). Nine 1-ha (100 × 100 m) plots were allocated randomly to be either unburned (control), burned in the spring (October), or burned in the summer (March) of 2000, giving three replicates for each treatment. To form firebreak zones the vegetation and topsoil (c. 10–15 cm depth) were removed from an area 2–5 m wide surrounding each 1-ha plot. These firebreaks allowed us to examine the recovery and role of bryophytes on sites where topsoil had been removed. Although it is unlikely that the burning treatment (unburned, burned in spring, burned in summer) induced inside each 1-ha plot influenced the surrounding fire break areas, the firebreak areas for each burning treatment were considered separately. Plant nomenclature in this study follows Allan Herbarium (2000).

Changes in bryophyte communities

Bryophyte composition

We estimated the post-fire recovery of bryophyte species in April 2010, 9 years after the experimental treatments were established. The frequency of species occurrence and biomass of bryophytes were recorded in each 1-ha plot (n = 9) and firebreak areas (n = 9) using 10 50 × 50 cm quadrats, subdivided into 5 × 5 cm grid cells and placed every 10 m along a 100-m transect line (18 transects and 180 quadrats in total). In each 1-ha plot, transects were placed randomly along a north to south direction. In the narrower firebreak areas, transects were placed at the centre of the break areas along the southern boundary of each 1-ha plot. Species' local frequency was determined by counting the number of 5 × 5 cm cells in which a species was present (100 cells per quadrat), and was expressed as a percentage. To understand the distributional patterns of bryophytes across treatments, we classified species according to their life strategies as described by During (1992). In this study, we mainly identified (1) colonists with long-distance spore dispersal and short lifespan (2–5 years) and (2) perennial stayers with long-distance spore or vegetative dispersal and a very long lifespan.

Bryophyte biomass

To estimate biomass of each bryophyte species in each 1-ha plot and firebreak areas, all bryophytes (above-ground live materials) were harvested in a 50-cm^2 area within each 50 × 50 cm quadrat. Biomass samples included five moss species. Due to their small size and biomass, and to the fact that they often grow intertwined, species of liverworts were sampled as a group. Bryophyte samples ($n = 180$) were cleaned of soil and other organic material in the laboratory, separated by species, oven-dried at 60°C for 72 h, and weighed for dry mass.

Measurements of bryophyte water-related traits

Water holding capacity

Bryophyte water holding capacity was estimated using methods described in Pypker et al. (2006a). Ten shoots of each bryophyte species were collected in the field. Individual shoots were left in 2 mm of water in sealed plastic containers for 12 h to rehydrate, blotted dry, and weighed for maximum wet mass. To estimate rate of external water loss, shoots were then air-dried at room temperature and weighed every 20 min until 50% water loss was reached (T_{50}) (Michel et al. 2012). They were finally oven-dried at 60°C for 72 h and weighed for dry mass.

Maximum water holding capacity of each species ($f_{(x)\max}$)[1] and at each site ($m_{(n)\max}$) were calculated using formulas adapted from Pypker et al. (2006a):

$$f_{(x)\max} = (\mathrm{WM}_x - \mathrm{DM}_x)/\mathrm{DM}_x, \qquad (1)$$

where WM_x was the maximum wet mass (g) of species x after rehydration and DM_x was the shoot dry mass (g) after 72 h at 60°C in a drying oven; and

$$m_{(n)\max} = \Sigma_i \, \mathrm{TDM}_{in} \times f_{(i)\max}, \qquad (2)$$

where TDM_{xn} and TDM_{yn} were the total dry mass (g) of species x and y, respectively, at site n, and $f_{(x)\max}$ and $f_{(y)\max}$ the maximum water holding capacity of species x and y, respectively. Values for $f_{(x)\max}$ (g) were expressed as percentage dry mass and $m_{(n)\max}$ (g m^{-2}) as in a millimetre of rainfall.

Destructive harvesting for measurements of vascular plant biomass was not possible in the ongoing burning experiment at the Deep Stream site, thus we alternatively extracted the pre-burn total biomass values of vascular vegetation in the undisturbed (control) plots from Payton and Pearce (2009), and used equation 2 above to estimate maximum water storage of the vascular vegetation. To assess the bryophyte contribution to total water storage capacity of above-ground vegetation in a New Zealand tussock grassland, we also obtained measurements of water holding capacity (% water content to dry mass) for each of the five vascular vegetation categories used by Payton and Pearce (2009): 1. Grasses, rushes and sedges, 2. Shrubs, 3. Forbs, 4. Lower plants, and 5. Litter. Litter included dead vascular and non-vascular plant materials. Ten subsamples of each plant category were brought fresh from the field, saturated with deionised water using the spraying method described in Wohlfahrt et al. (2006), and blotted dry before being weighed for maximum wet weight. Samples were then dried at 60°C for 72 h and weighed for dry mass.

Shoot morphology and species growth form

Individual shoots of each bryophyte species were measured to the nearest 1.0 mm. To describe structural form of bryophyte cushions, we used species' growth form categories as defined by Mägdefrau (1982). In this study we mainly identified: (1) small cushions: plants with short erect shoots radiating in more or less dome shaped groups, reaching heights of a few centimetres with high shoot density; (2) rough mats: plants forming dense and interwoven mats adhering to the substrate and extending horizontally over the substrates with branches growing in oblique and vertical directions; (3) wefts: plants with robust shoots, laterals often arching and ascending, and straggling shoots and branches loosely interwoven; and (4) tall turfs: plants with parallel upright shoots with some, usually subapical, branching (During 1990). All liverworts recorded were leafy species growing in a mat form.

Soil moisture

To determine the effect of disturbance on moisture levels in the soil, we measured the volumetric soil moisture in the upper soil column in each quadrat along the 18 transect lines ($n = 180$), using a ThetaProbe (Delta-T Devices, Cambridge, UK) vertically inserted to a depth of 10 cm. Three readings were taken randomly within each quadrat during the drier period of the year, in February 2011, and were averaged for statistical analysis.

Statistical analyses

To test for differences in bryophyte composition between sites we used non-parametric multivariate analysis in the computer software package PRIMER. We first plotted Bray–Curtis similarity distances in species frequency between treatment plots, using non-parametric multidimensional scaling (NMDS) to identify plots of similar bryophyte assemblages (species' local frequency). On an ordination, the closer the points were to each other, the more similar their vegetation composition, and at a stress level < 0.2 the ordination gives a two-dimensional representation of the data. One-way analysis of similarities (ANOSIM; 999 permutations) was used to test for significance. We estimated the contribution (in percent) of each bryophyte species to the 90% dissimilarity among and within plots, using a SIMPER analysis (Clarke & Warwick 2001). When required, data were normalised by square-root transformations (Clarke & Warwick 2001). We also applied additive partitioning to plant species data, to analyse the observed local patterns of additive species diversity components in respect to disturbance treatments (Klimek et al. 2008). Thus, we calculated γ_r diversity: $\gamma_r = \alpha_l + \beta_l + \beta_r$ where α_l = diversity within and β_l = among quadrats, and β_r = among treatment blocks (α- and β- diversity being expressed as number of species).

To determine the effect of disturbance (fire, topsoil and vegetation removal) on bryophyte communities and their contribution to above-ground water storage capacity, we tested for differences in (1) bryophyte local frequency and maximum potential water storage among treatment plots and (2) water holding and retention capacity (water-related shoot traits) among bryophyte species, using one-way analysis of variance (ANOVA; with Tukey post hoc comparison). Homogeneity of variance was checked with Levene's test, and if significant, data were square-root transformed. If Levene's test remained significant after transformation, the non-parametric Kruskal–Wallis test was used, with the Mann–Whitney U-test used for post hoc comparisons. To examine the relationship between bryophyte water storage capability and moisture content in the soil, we tested non-parametrically for relationships between soil humidity and (1) bryophyte biomass and (2) potential

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[1] $f_{(x)\max}$ (maximum water fraction) = maximum mass of internal and external water stored divided by tissue dry mass (Pypker et al. 2006a, p. 810).

water storage from bryophytes, using the Spearman rank correlation coefficient.

Results

Variations in bryophyte cover and biomass following disturbance

In a New Zealand indigenous tussock grassland at Deep Stream, bryophyte cushions were found to occupy up to 71 ± 4% of the inter-tussock space prior to disturbances (control) and their biomass to average 3330 ± 605 kg ha^{-1}. Both the local frequency and biomass of bryophyte cushions were greatly reduced (by over 80%) following disturbance (Fig. 1).

Following burning

Total mean frequency of bryophytes, particularly of mosses, was on average greater inside control than in burned plots (reductions of 37% following summer burns and 19% following spring burns) ($F_{2,87}$ = 30.672, P = 0.001) (Appendix 1, Fig. 1a). Burning did not reduce the local frequency of liverworts ($F_{2,87}$ = 0.497, P = 0.610). Total bryophyte biomass was also lower in burned than control plots ($\chi^2_{2,89}$ = 34.211, $P < 0.001$), and season of burns did not affect this result ($t_{1,58}$ = 1.287, P = 0.203) (Fig. 1b). Burning severely reduced bryophyte biomass accumulation, which, after 9 years, remained 69.8% (spring-burned) to 82.3% (summer-burned) below values of control areas, but did not affect bryophyte local species richness α_l ($F_{2,89}$ = 0.321, P = 0.726), which in general remained low (α_l averaged 2 species and γ_l ranged between 5 and 8 species) (Fig. 2).

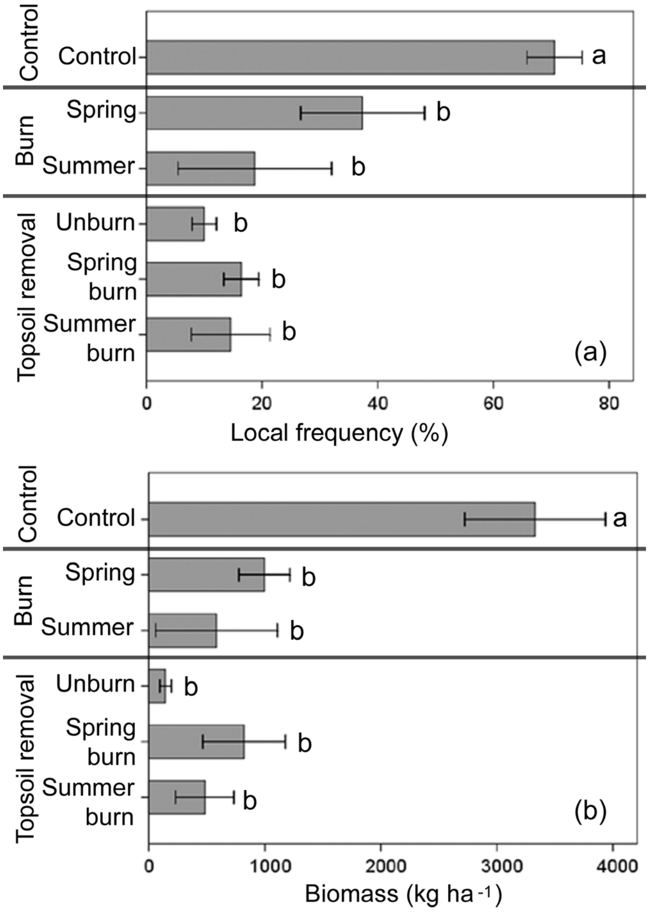

Figure 1. Effect of disturbances (fire, and topsoil and vegetation removal) on: (a) local bryophyte frequency (%), and (b) bryophyte biomass (kg ha^{-1}). Different letters within each panel indicate significance at $P < 0.05$ (one-way ANOVA, Tukey), n = 180.

Following topsoil and vegetation removal

The removal of topsoil and vegetation in firebreak areas reduced the biomass and cover of bryophytes by c. 80% in comparison with undisturbed plots (control) (Fig. 1). Bryophyte species diversity remained poor in the firebreak areas with α_l = 1 species and γ_l = 6 species (Fig. 2). Firebreak areas appeared unaffected by different nearby burning treatments (mean frequency: $F_{2,87}$ = 0.731, P = 0.484; species richness: $F_{2,87}$ = 0.569, P = 0.568).

Changes in bryophyte composition following disturbance

At the Deep Stream site 29 bryophyte species (Gamma diversity) were recorded, comprising 17 species of mosses and 12 liverworts (Appendix 1). Of these, *Hypnum cupressiforme*, *Polytrichum juniperinum* and *Campylopus clavatus* were the most common mosses (present in 26.1%, 39.4% and 27.2% of the plots, respectively), while *Lepidozia laevifolia* and *Kurzia hippuroides* were the most common liverworts (present in 10% and 3% of the plots, respectively). In control plots, bryophyte communities were dominated by the perennial-stayer *Hypnum cupressiforme* (Appendix 1). Seven other moss species and three liverworts were also present at low frequencies (<4%).

Our first non-parametric multidimensional scaling (NMDS) ordination distinguished three quadrats in the firebreak

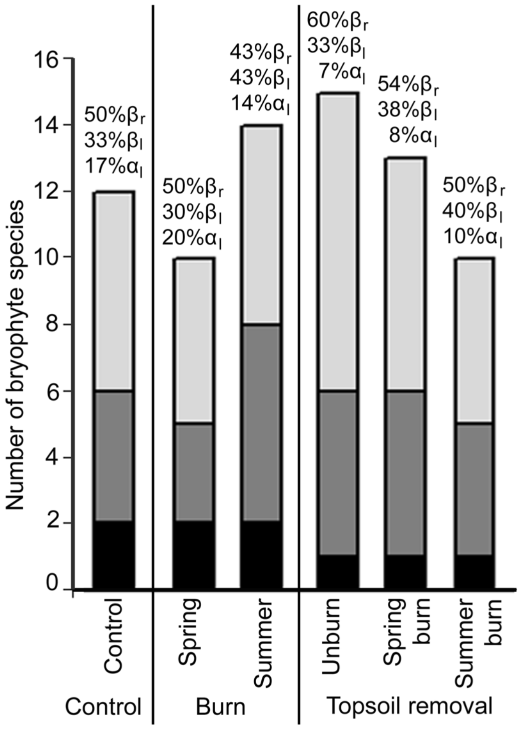

Figure 2. Effect of disturbances (fire, and topsoil and vegetation removal) on total observed regional diversity (γ_r) using the additive partitioning method for three replicates of each treatment block. Percentage contribution of species richness within (α_l in black) and among quadrats (β_l in dark grey) and among plots (β_r in light grey) are given above each bar.

around control plots from the composition of all other quadrats. These quadrats were characterised by a dense cover of the moss *Racomitrium crispulum,* a species not recorded in any other treatment, and therefore were treated as outliers. After removing outliers from the analysis, the NMDS ordination clearly separated (stress = 0.08) treatment plots [burned and firebreaks (spring and summer)] from control plots (Fig. 3), and ANOSIM analysis confirmed differences in species composition being greater among treatment blocks than within (R_{anosim} = 0.636, P = 0.01).

Following burning

Burned plots differed greatly from control plots (averaged dissimilarity > 85%) in bryophyte species composition (Table 1). Two species (*Hypnum cupressiforme* and *Polytrichum juniperinum)* contributed to more than 30% of this dissimilarity, with cover of perennial-stayer *H. cupressiforme* being lower and the colonist *P. juniperinum* greater following a burn (Table 1); cover of *P. juniperinum* was greatest following spring burns. The colonist moss *Bryum billardieri* and the liverwort *Kurzia hippuroides* contributed another 30% to this dissimilarity, the cover of both species being greater following burning and in particular after a summer burn. Contributing somewhat less to site dissimilarities (2%), the liverwort *Lepidozia laevifolia,* usually common in forest habitats, was more abundant in control plots (average abundance 1.7 in controls and 0.1 in burned sites) (Appendix 1). Although at very low frequency, a few opportunistic species (*Chiloscyphus subporosus, Telaranea herzogii, T. patentissima* and *Solenostoma inundatum*) occurred following the summer burn only.

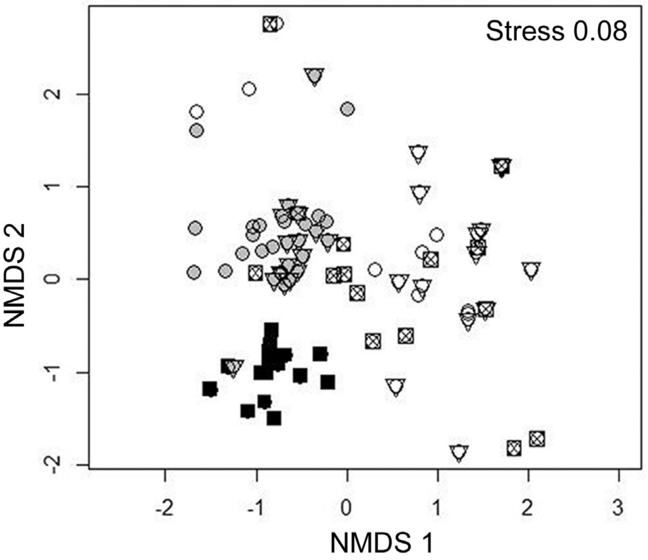

Figure 3. Non-parametric multidimensional scaling ordination representing similarity in bryophyte species composition (shoot frequency) between treatment plots (burning, and topsoil and vegetation removal). Black squares represent undisturbed plots [control]; grey symbols burned plots (grey triangles = spring-burned plots and grey circles = summer-burned plots); and white symbols firebreak plots (white crossed squares = adjoining unburned plots, white triangles = adjoining spring-burned plots and white circles = adjoining summer-burned plots) (n = 177).

Table 1. Summary results from SIMPER and ANOSIM analyses testing the effects of disturbance (burning, and topsoil and vegetation removal (firebreaks)) on bryophyte species composition (shoot frequency). Results are given for bryophyte species that contributed >10% to the dissimilarity between treatments.

Effect of burning	Control (n =30)	Spring-burned (n =30)	Control/ Spring-burned	Summer-burned (n =30)	Control/ Summer-burned	Spring/ Summer-burned
	Average dissimilarity = 85.75% R_{anosim} = 0.895, P = 0.001			Average dissimilarity = 90.05% R_{anosim} = 0.949, P = 0.001		Average dissimilarity = 43.20% R_{anosim} = 0.161, P = 0.005
Species	Average abundance	Average abundance	Contribution (%)	Average abundance	Contribution (%)	Contribution (%)
Hypnum cupressiforme	61.3	0.7	42.2	0.2	37.3	-
Polytrichum juniperinum	2.2	32.2	39.2	22.4	30.5	20.8
Bryum billardieri	-	0.0	-	2.6	-	18.6
Kurzia hippuroides	-	0.1	-	1.2	-	13.1

Effect of topsoil and vegetation removal	Control (n =30)	Firebreak Unburned (n =30)		Firebreak Spring-burned (n =30)	Control/ Firebreak Spring-burned	Firebreak Summer-burned (n =30)	Control/ Firebreak Summer-burned
	Average dissimilarity = 91.61% R_{anosim} = 0.805 P = 0.001			Average dissimilarity = 99.00% R_{anosim} = 0.850, P = 0.001		Average dissimilarity = 99.10% R_{anosim} = 0.948, P = 0.001	
Species	Average abundance	Average abundance	Contribution (%)	Average abundance	Contribution (%)	Average abundance	Contribution (%)
Hypnum cupressiforme	61.3	0.4	38.8	0.0	39.7	0.0	39.6
Polytrichum juniperinum	2.2	3.1	17.2	-	-	-	-
Campylopus clavatus	0.0	4.7	14.4	10.0	27.2	21.2	35.2
Ditrichum punctulatum	0.1	-	-	7.9	12.5	-	-

Following topsoil and vegetation removal

The dissimilarity between control plots and the firebreak areas averaged more than 90%, and was best explained by differences in the cover of four moss species, *Hypnum cupressiforme, Polytrichum juniperinum, Campylopus clavatus*, and *Ditrichum punctulatum* (Table 1). The cover of *Hypnum cupressiforme* decreased to zero in the firebreak area around spring- and summer-burned plots. In contrast, the colonist cushion-forming moss *Campylopus clavatus* increased in local frequency and dominated the bryophyte contribution in these two treatments (Table 1, Appendix 1). The early-coloniser moss *Polytrichum juniperinum* and the short turf-forming moss *Ditrichum punctulatum* were respectively the second and third most important species in explaining this dissimilarity, being more abundant in the disturbed area. Opportunistic species of liverworts (*Kurzia* and *Telaranea* species) were recorded on the firebreaks of summer-burned plots. The perennial-stayer liverwort *Lepidozia laevifolia* also occurred in lower frequency to the control and often was absent in the firebreak area.

Variations in water holding capacity among species

Of the bryophytes, *Hypnum cupressiforme* showed the greatest water holding capability, being able to hold more than 1470% of dry mass, and *Polytrichum juniperinum* and *Campylopus clavatus* the lowest (665% and 823%, respectively) (Table 2). The pleurocarpous species *Hypnum cupressiforme* and *Racomitrium pruinosum* exhibited the highest lengths, a characteristic that enabled them to cover large areas. Although, the water holding capacity of *Racomitrium pruinosum* shoots (c. 1090%) was close to average (c. 1043%), the water retention (i.e. time for this species to lose external water) was the greatest. In general, with the lowest water holding capacity and size, and fastest external evaporation rate, *Campylopus clavatus* had a lower water storage potential than all other studied species, and *Hypnum cupressiforme* and *Racomitrium pruinosum* the greatest.

Potential water storage capacity of bryophytes

From measurements of biomass and water holding capacity, we estimated the maximum potential water storage of bryophytes in the indigenous tall-tussock grassland, prior to disturbances (control), to be 4.3 ± 0.6 mm. Bryophytes displayed greater water holding capacity (1043.4 ± 25.4% to dry mass) than other plant groups (*Chionochloa rigida* 174.2 ± 6.2%, other graminoids 393.9 ± 16.3%, shrubs 279.9 ± 11.2%, forbs 467.4 ± 65.4%, lichens and *Lycopodium* spp. 348.0 ± 16.3%, and litter 266.3 ± 18.9%). Based on the data in Payton & Pearce (2009), bryophytes contributed c. 4% to the total above-ground plant biomass (live and dead materials) of this grassland (Fig.4). Our study shows they were the second most important contributor (15.5%) to the total water storage capacity held in above-ground vegetative materials of the grassland (externally on leaves and branches, and internal water held in plant tissues); litter being the primary contributor (56.2%) (Fig. 4).

The estimates of potential water storage by bryophytes were significantly lower (< 1 mm) in all disturbed sites (i.e. in burned and in firebreak areas) than in the control, suggesting these disturbances reduce the above-ground water storage capability from bryophytes by 81–97% (Fig. 5) for at least 9 years after the initial disturbance. Estimates of water storage capacity from bryophytes did not differ significantly among disturbed sites ($F_{4,\,145} = 2.111$, $P = 0.082$).

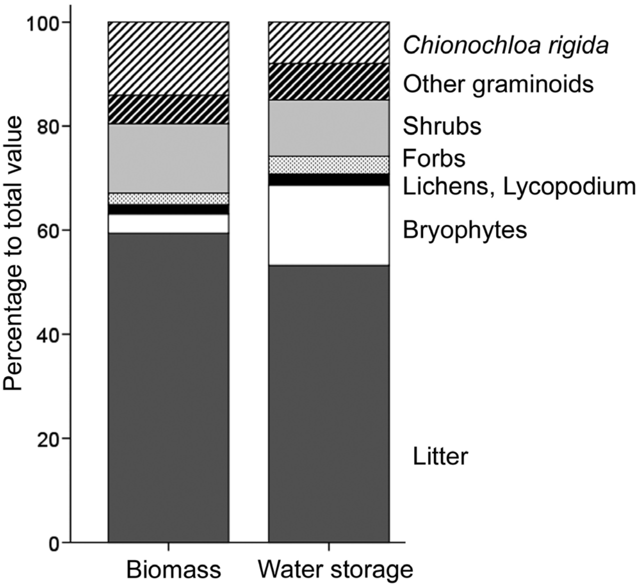

Figure 4. Estimates of percentage contribution to the total above-ground vegetative biomass and maximum water storage potential for all plant groups in a New Zealand indigenous tall-tussock grassland.

Table 2. Description of life form and water-related shoot traits for bryophyte species that contributed to the total bryophyte biomass of each sampled quadrat.

Species	Life form	Water-related shoot traits			
		Max. water holding capacity (%) (*n* = 180)	T_{50} (min) (*n* = 180)	Dry mass (mg) (*n* = 60)	Vertical length (mm) (*n* = 60)
Campylopus clavatus	Small cushions	822.8 ± 47.0 (a)	64 ± 5 (a)	2.7 ± 0.4 (a)	13.1 ± 0.7 (a)
Hypnum cupressiforme	Rough mats	1469.6 ± 35.8 (c)	117 ± 5 (b)	50.6 ± 5.6 (b)	60.6 ± 2.7 (b,d)
Leptotheca gaudichaudii	Wefts	1135.1 ± 29.4 (b)	86 ± 5 (c)	7.6 ± 1.0 (a)	41.4 ± 1.6 (c,b)
Polytrichum juniperinum	Tall turfs	664.7 ± 39.2 (a)	113 ± 5 (b)	27.3 ± 3.5 (c)	53.9 ± 8.7 (b)
Racomitrium pruinosum	Rough mats	1090.5 ± 28.6 (b)	185 ± 6 (d)	11.2 ± 0.5 (a)	77.6 ± 5.1 (d)
Liverworts	Leafy mats/wefts	1077.5 ± 61.9 (b)	32 ± 2 (e)	3.1 ± 0.2 (a)	38.2 ± 3.5 (c)
Total bryophyte		1043.4 ± 25.4	100 ± 4	17.1 ± 2.5	47.5 ± 3.2

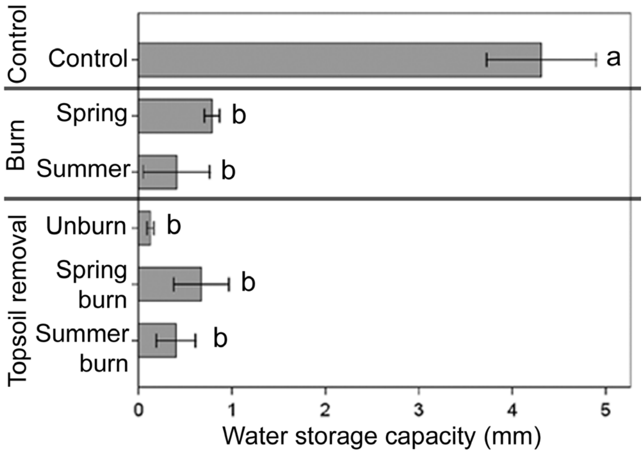

Figure 5. Effect of disturbances (burning, and topsoil and vegetation removal) on above-ground water storage capacity from bryophytes. Different letters indicate significance at $P < 0.05$ (one-way ANOVA, Tukey), $n = 180$.

Variation in soil moisture following disturbance

Soil moisture level in the upper 10 cm of the soil column was higher (44%) in control sites and did not differ between disturbed sites (c. 36%) (Fig. 6a). Significant positive correlations were obtained between soil moisture and (1) total bryophyte biomass ($R_{\mathrm{Spearman}} = 0.264$, $P < 0.001$) and (2) maximum water storage in bryophytes ($R_{\mathrm{Spearman}} = 0.324$, $P < 0.001$) (Fig. 6b and c). Results suggested increasing soil moisture with both increasing above-ground bryophyte biomass and increasing water holding capacity of individual bryophyte species.

Discussion

This study presents the first demonstration of reduced above-ground water storage capacity associated with a shift in bryophyte community composition following disturbances in indigenous temperate tall-tussock grassland systems. At the Deep Stream site, bryophytes are a major component of the vegetation, contributing up to 71% of the inter-tussock ground cover and representing 4% of the above-ground vegetative biomass. This inter-tussock bryophyte carpet contributed on average 4.3 mm (15%) to the potential water storage capacity (combined external and internal water) of above-ground vegetation. Species' biomass, composition, and water-related traits, combined, were the main drivers of water storage from bryophytes. A major shift in bryophyte species composition following disturbances, from a dense ground cover of pleurocarpous mosses with high water holding capacity (c. 1400% of dry mass) to low frequency of colonist short-lived species with low water holding capacity (< 800% dry mass), contributed to an average loss of 81% in water storage capacity.

Our results suggest that non-epiphytic bryophytes are as important in New Zealand indigenous tall-tussock grasslands as they are in forested habitats. Bryophytes can cover up to 95% of the forest floor (Pfeiffer 2003) and contribute to 4.4 mm of storage water capacity (DeLucia et al. 2003). Our value for water storage capacity is also comparative with that for a range of ecosystems: 1.5 – 5 mm can be derived from the data of Pócs (1980) for epiphytes in two rainforest types in Tanzania, and from Pypker et al. (2006b) for western North America.

The reduced values of water storage capability from bryophytes following experimental burning and soil removal resulted primarily from the loss of bryophytic cover and biomass, and were further exacerbated by compositional changes. Less than 20% of the original bryophyte biomass was recovered 9 years after the disturbance was induced, and colonisation patterns described in this study are similar to post-disturbance successions elsewhere (Duncan & Dalton 1982; Delach & Kimmerer 2002: O'Bryan et al. 2009). More specifically, the bryophytic assemblage of undisturbed indigenous tall-tussock grassland observed at Deep Stream (Lammerlaw Range, south-eastern New Zealand) appeared to be widespread in the area c. 30 years after cessation of burning and grazing (Mark & Dickinson 2003). It was poor in species and largely dominated by the pleurocarpous moss *Hypnum cupressiforme*, with lesser contributions from two other mosses, *Leptotheca gaudichaudii* and *Polytrichum juniperinum*. Dominant liverworts in this grassland were species of shady and moist habitats, usually found in forested habitats (e.g. *Chiloscyphus lentus, Lepidozia laevifolia, Telaranea hergozii*, and *T. pratentissima*) (Engel & Glenny 2008).

The presence of these forest bryophyte species supports the pollen evidence that this area was previously discontinuous broadleaved forest (McGlone 2001). The removal of vegetation and topsoil or burning have altered the physico-chemical

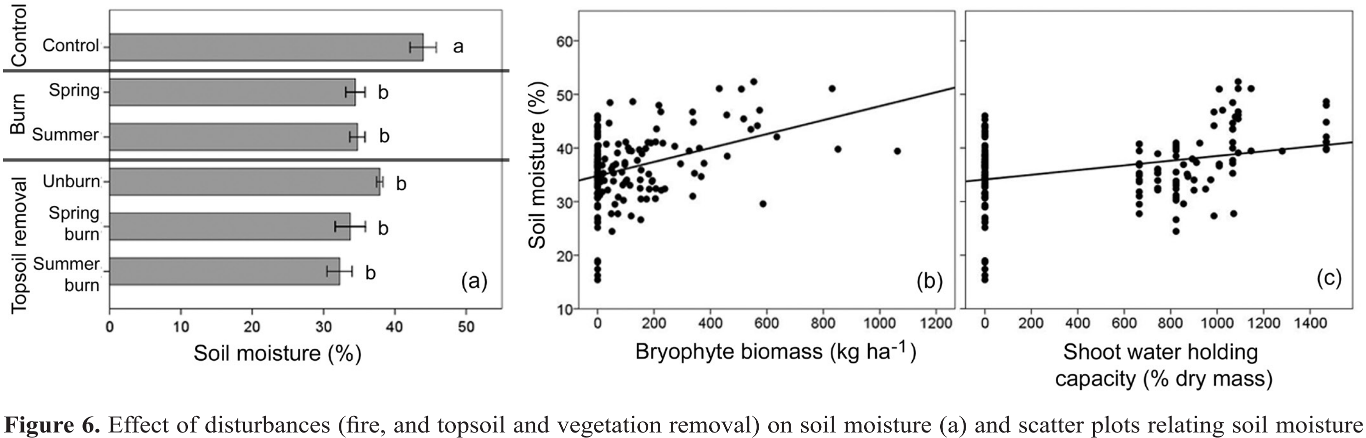

Figure 6. Effect of disturbances (fire, and topsoil and vegetation removal) on soil moisture (a) and scatter plots relating soil moisture (%) to (b) bryophyte biomass (kg ha^{-1}) and (c) shoot water holding capacity (% to dry mass).

environment (e.g. substrate type, pH, UV-B radiation), thus facilitating the establishment of bryophyte species with adaptive strategies to successfully colonise and survive in these new habitats (Clément & Touffet 1990; During 1992; Hedderson & Longton 1996; Åström et al. 2005; Dynesius & Hylander 2007; Bates 2008). In this study, four species of mosses (*Dicranum robustum, Pohlia nutans, Ptychomnion aciculare and Thuidium furfurosum*), all but one (*P. nutans*) perennial stayers, disappeared after disturbances. *Polytrichum juniperinum* became the dominant species on the burned sites. Several *Polytrichum* species are generally associated with primary succession in dry habitats, being drought-tolerant and a colonist-pioneer on disturbed areas (e.g. following mining or burning) (Delach & Kimmerer 2002; Fenton & Frego 2005). *Polytrichum* species have a rhizome system and central nerve allowing for the transport of moisture from soil and wet humus (Glime 2007). Many short-lived colonising liverwort species also colonised burned areas, in particular following a summer burn, suggesting ongoing dynamic processes during post-fire recovery, as described in Australian systems (Duncan & Dalton 1982; Morgan 2004; Ferguson et al. 2009; O'Bryan et al. 2009). In contrast, the removal of topsoil during construction of the fire breaks around treatment blocks contributed to the establishment of a different bryophyte community dominated by species typical of exposed mineral soil elsewhere. For example, both the aggressive small turf- and cushion-forming colonists *Campylopus* spp. (*C. clavatus* and *C. introflexus*) and *Ditrichum difficile* are common species of mineral substrates and open exposed environments, often found on roadside banks or rocks (Blöcher & Frahm 2002).

The variation in life form among bryophyte species always determines their ability to take up and retain water. Our results show similar trends to other studies with water holding capacity being double in weft life forms compared with tall-turf species (Dilks & Proctor 1979; Skre et al. 1983; Proctor 2000b). Mosses with an internal conduction system, such as *Polytrichum*, rely largely on external water transport from moist humus and thus can sustain dry conditions and large variation in moisture (Anderson & Bourdeau 1955; Proctor 2000a; Glime 2007). Consequently, these species often have the lowest water storage capacity (95–125% of dry mass at full turgor) of all bryophytes (Skre et al. 1983) and the fastest rate of evaporation (Elumeeva et al. 2011; Michel et al. 2012). In contrast, later-successional pleurocarpous mosses (weft or mat growth forms) obtain moisture exclusively through their cell membrane, holding water to 485–625% of their dry mass, and thus require relatively wet conditions. Persistent species (*Hypnum cupressiforme* and *Racomitrium pruinosum* in particular), in our study, displayed water-related traits that are best adapted to store (water holding capacity, dry mass to area) and retain water. However, they did not always display lower evaporation rates than *Polytrichum* species (Elumeeva et al. 2011; Michel et al. 2012), likely reflecting species-dependent differences based on subtle variations in shoot and cushion morphometry (Michel et al. 2012). The bryoflora at Deep Stream shifted following disturbances, from large cushions of high water storage capacity and low evaporation rates to small cushions of low water storage capacity and high evaporation rates. This shift led to at least a 76% loss of the total potential water storage from bryophytes.

The successional pattern of the above-ground vegetation, including bryophyte communities, following disturbance is likely to influence below-ground soil humidity. In this study, a strong linear relationship was observed between biomass and water-related traits of bryophytes and moisture content in the soil. Areas of greatest soil moisture coincided with areas of densest moss cover with greatest water holding capacity. In general, the initial colonisers of de-vegetated areas contribute to the build-up of soil moisture and humus to allow vascular plant to recover (Longton 1992; Delach & Kimmerer 2002). When canopy cover of vascular plants is dense enough to provide a large amount of moist litter and shade for less-light-tolerant species, persistent perennial species with greater water holding capacity can re-establish. In comparison with vascular plants, bryophytes intercept more water in relation to their dry mass (in this study: bryophytes = 600–1700%; vascular plants = 150–470%). In this study, the tall-tussock species *Chionochloa rigida* had the lowest capacity to hold water (174.2% dry mass). In contrast, other studies have shown that tall-tussock grasses collect water (up to 0.5 L h^{-1}) from rain, fog and snow via their diffuse finely elongated leaves to the base of the tillers, contributing substantially to high water yield (up to 80% of the measured 1372 mm annual rainfall) (Ingraham & Mark 2000; Mark & Dickinson 2008). The loss of above-ground vegetation following fire influences water yield and stream flow at the catchment level (Bosch & Hewlett 1982; McGlone 2009) through the alteration of evapotranspiration and interception processes (Duncan & Thomas 2004; Davie et al. 2006). Our results suggest that bryophyte cover plays an important role in the hydrological recovery of the grassland after disturbance. Over time the increasing cover of pleurocarpous mosses in recovering grassland systems can increase the interception of atmospheric water (by up to 20% of total above-ground vegetal interception), while also contributing to the stabilisation of mineral soils and the improvement of water quality by reducing soil erosion and sediment transport by heavy rainfall to wetlands, rivers and streams (Hallingbäck & Hodgetts 2000; Dojani et al. 2011). Furthermore, by intercepting rain, fog and snow, bryophytes help maintain high soil humidity and facilitate infiltration into the soil (Graetz & Tongway 1986; Maestre et al. 2002; Belnap 2006); particularly in highly degraded areas (Eldridge et al. 1997). Through these processes terrestrial bryophytes are known to aid erosion control and facilitate above-ground primary production (Scott 2000; Zamfir 2000; Belnap 2006).

In conclusion, terricolous bryophytes have historically been overlooked in New Zealand indigenous tall-tussock grasslands. Despite low species diversity, bryophytes form a major component of the vegetation (particularly in terms of cover) and contribute towards sustaining the valued water holding capacity of these systems. Like the tussock dominants, bryophytes and their associated ecological functions are highly susceptible to long-term impacts from burning and vegetation clearance and slower to recover than vascular plants (Morgan 2004). In respect to biodiversity effects on ecosystem functions, this study highlights the importance of weighing the functional role of individual species against the species richness of ecosystems (Bowker et al. 2010). Furthermore, in this study, the two species that contributed most to the hydrological functioning of the ecosystem required habitat conditions that are provided in mature tussock landscapes only. It is therefore critical to account for the recovery of bryophyte species and their associated ecosystem functions in the management of temperate indigenous tall-tussock grasslands to allow the maintaining of healthy ecosystems.

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Appendix 1. Bryophyte species composition (mean shoot frequency (% ± SE)), species richness (number of species), and total bryophyte cover 9 years after a fire experiment at the Deep Stream catchment, Lammerlaw Range, south-eastern New Zealand. Abbreviations for the life strategies of recorded bryophyte species at Deep Stream are colonists (C) and perennial stayers (PS).

	Life	Control/	Fire		Topsoil and vegetation removal		
Species	strategies	Undisturbed	Spring-burned	Summer-burned	Unburned	Spring-burned	Summer-burned
Mosses							
Bartramia papillata	C	-	0.1 ± 0.1	< 0.1	< 0.01	0.8 ± 0.1	0.1 ± 0.1
Bryum billardieri	C	-	-	1.7 ± 0.6	0.1 ± 0.1	-	< 0.1
Campylopus clavatus	C	-	-	-	2.8 ± 1.7	8.3 ± 2.7	13.4 ± 4.0
Campylopus introflexus	C	-	-	-	0.4 ± 0.3	< 0.1	-
Ceratodon purpureus	C	-	0.2 ± 0.1	-	-	-	-
Dicranum robustum	PS	0.5 ± 0.3	-	-	-	-	-
Ditrichum difficile	C	-	-	0.1 ± 0.1	-	-	-
Ditrichum punctulatum	C	0.1 ± 0.1	-	0.1 ± 0.1	2.1 ± 1.7	6.6 ± 3.3	0.2 ± 0.2
Hypnum cupressiforme	PS	61.3 ± 4.2	0.6 ± 0.2	0.2 ± 0.1	0.2 ± 0.2	-	-
Leptotheca gaudichaudii	C-PS	3.6 ± 1.4	4.9 ± 2.4	< 0.1	0.1 ± 0.1	0.1 ± 0.1	-
Pohlia nutans	C	0.1 ± 0.1	-	-	-	-	-
Polytrichum commune	PS	-	-	-	-	< 0.1	-
Polytrichum juniperinum	C-PS	2.2 ± 0.8	31.1 ± 3.8	14.9 ± 4.2	1.8 ± 0.8	0.2 ± 0.1	0.1 ± 0.1
Ptychomnion aciculare	PS	< 0.1	-	-	-	-	-
Racomitrium crispulum	PS	-	-	-	2.0 ± 1.4	-	-
Racomitrium pruinosum	PS	1.1 ± 1.1	-	-	-	< 0.1	-
Thuidium furfurosum	PS	< 0.1	-	-	-	-	-
Total mosses		68.8 ± 4.3	36.9 ± 5.2	17.1 ± 4.4	9.7 ± 3.7	15.8 ± 3.9	13.9 ± 4.0
Liverworts							
Austrolophozia paradoxa	C	-	-	-	< 0.1	-	-
Chiloscyphus lentus	PS	< 0.1	0.1 ± 0.1	0.1 ± 0.1	< 0.1	0.1 ± 0.1	-
Chiloscyphus subporosus	PS	-	-	0.1 ± 0.1	-	-	-
Kurzia compacta	C	-	-	-	< 0.1	-	-
Kurzia helophila	C	0.1 ± 0.1	0.1 ± 0.1	-	0.1 ± 0.1	< 0.1	0.1 ± 0.1
Kurzia hippuroides	C	-	0.1 ± 0.1	0.8 ± 0.4	0.1 ± 0.1	-	0.3 ± 0.2
Lepidozia laevifolia	PS	1.7 ± 1.7	0.1 ± 0.1	< 0.1	-	-	0.1 ± 0.1
Riccardia aequicellularis	C	-	< 0.1	-	-	-	-
Solenostoma inundatum	C	-	-	< 0.1	0.1 ± 0.1	0.2 ± 0.2	< 0.1
Telaranea herzogii	C	-	-	0.2 ± 0.1	-	0.1 ± 0.1	0.1 ± 0.1
Telaranea pallescens	C	-	-	-	-	0.2 ± 0.2	-
Telaranea patentissima	C	-	-	0.4 ± 0.3	-	-	-
Total liverworts		1.8 ± 1.7	0.4 ± 0.2	1.6 ± 0.6	0.3 ± 0.1	0.6 ± 0.4	0.6 ± 0.3
Total bryophytes local frequency		70.6 ± 4.3	37.4 ± 5.2	18.7 ± 4.6	10.0 ± 3.3	16.4 ± 3.9	14.5 ± 4.0
Species richness (α_l)		2.2 ± 0.2	1.9 ± 0.2	2.2 ± 0.4	1.5 ± 0.3	1.37 ± 0.19	1.1 ± 0.2
Number of quadrats with no bryophytes		0.0 ± 0.0	0.3 ± 0.3	3.3 ± 2.4	2.7 ± 0.7	1.3 ± 0.3	3.3 ± 1.5

Appendix 2. Species percentage contribution (% ± SE) to total bryophyte biomass (*n* = 18).

	Control/	Fire		Topsoil and vegetation removal		
Species	Undisturbed	Spring-burned	Summer-burned	Unburned	Spring-burned	Summer-burned
Mosses						
Bryum billardieri	3.9 ± 2.8	4.2 ± 4.2	5.0 ± 0.9	-	-	-
Campylopus clavatus	-	-	-	-	30.1 ± 30.1	96.8 ± 3.2
Campylopus introflexus	-	-	-	12.8 ±12.8	33.3 ± 33.3	-
Ditrichum punctulatum	1.1 ± 1.1	-	1.6 ± 1.6	33.3 ± 33.3	33.3 ± 33.3	-
Hypnum cupressiforme	69.4 ± 14.3	20.2 ± 20.2	<0.1	0.24 ± 0.24	-	-
Leptotheca gaudichaudii	10.1 ± 5.9	5.17 ± 2.8	<0.1	-	-	-
Polytrichum juniperinum	5.7 ± 4.8	70.4 ± 21.1	65.9 ± 26.1	5.9 ± 5.9	3.2 ± 3.2	0.07 ± 0.07
Racomitrium crispulum	-	-	-	33.4 ± 33.4	-	-
Racomitrium pruinosum	7.2 ± 7.2	-	-	-	-	-
Total mosses	97.4 ± 2.6	100.0 ± 0.0	72.7 ± 25.4	85.7 ± 14.4	100.0 ± 0.0	96.8 ± 3.2
Liverworts						
Chiloscyphus lentus	-	0.01 ± 0.01	12.7 ± 12.7	-	-	-
Kurzia hippuroides	-	-	13.3 ± 13.0	14.4 ± 14.4	-	-
Lepidozia laevifolia	2.6 ± 2.6	-	-	-	-	-
Solenostoma inundatum	-	-	-	-	<0.1	3.2 ± 3.2
Telaranea hergozii	-	-	0.8 ± 0.8	-	-	-
Telaranea patentissima	-	-	0.4 ± 0.4	-	-	-
Total liverworts	2.6 ± 2.6	<0.1	27.3 ± 25.4	14.4 ± 14.4	<0.1	3.2 ± 3.2
Total bryophytes biomass (kg ha^{-1})	3330.3 ± 605.5	995.0 ± 219.6	584.3 ± 524.3	143.8 ± 49.6	821.5 ± 357.0	482.8 ± 252.2