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RESEARCH ARTICLE

Post-fire restoration of *Sphagnum* bogs in the Tasmanian Wilderness World Heritage Area, Australia

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Sphagnum bogs in Australia are small, with a limited distribution, but of high conservation value. They are restricted to cool, wet environments that are typically fire free and are poorly adapted to recover from fire disturbance, unlike most Australian flora. Increased fire activity due to anthropogenic climate change is threatening _Sphagnum_ bogs. This increased threat has stimulated interest in their restoration. Compared with the northern hemisphere, there have been few studies of the ecology of _Sphagnum_ restoration in the southern hemisphere. Here, we report on a field experiment in Tasmania, in an area burned by an extensive fire in 2016. We investigated the role of shade, fertilizer and transplants, factors demonstrated to be important in the restoration of burnt bogs on the Australian mainland. Treatments commenced three to 4 years after the fire. Overall, we found that fire-damaged _Sphagnum_ recovers very slowly, and that there was no recovery in severely burned areas. The addition of shade increased recovery of damaged _Sphagnum_, but fertilizer was harmful, even to healthy _Sphagnum_. Transplants in fire-killed _Sphagnum_ grew poorly in both moderately and severely burnt _Sphagnum_ areas. Our findings support the use of shading in post-fire _Sphagnum_ recovery projects, although further work is required to determine the optimal approach and duration of providing shade.

Key words: bryophytes, fertilizer, fire severity, peatland, shading, transplanting

Implications for Practice

- Fire severity should be assessed as soon as possible after fire, to allow mapping of moderate severity (*Sphagnum* damaged but shows signs of life), and severely burned (*Sphagnum* killed) areas, and early implementation of treatments.
- Post-fire recovery of surviving *Sphagnum* can be improved by applying shadecloth to areas damaged by moderate severity fire.
- Standard fertilizer doses appear harmful; detailed experiments are required to identify if any nutrient additions can improve *Sphagnum* recovery.
- Further research is needed into techniques to improve success of *Sphagnum* transplants in key areas where *Sphagnum* is killed by severe fire.
- Climate change-induced droughts, and the associated increased fire risk, threatens persistence of *Sphagnum* bogs in Australia. Potential hydrological interventions need to be explored.

Introduction

The Tasmanian Wilderness World Heritage Area (TWWHA), covering 15,800 km^2, is one of the largest temperate natural areas in the southern hemisphere (DPIPWE 2016). The cool, maritime climate of the TWWHA contrasts with the drier, hotter and more seasonal climates that characterize eastern Tasmania and most of the Australian mainland, and favors mesic vegetation such as rainforest and sedgelands underlain by organic soils. The TWWHA is a global center of plant paleoendemism as a result of its geologically old, climatically buffered and infertile landscape, which allowed long-term persistence of many ancient, geographically restricted clades (Jordan et al. 2016). Despite the humid climate, landscape fires occur periodically during unusually dry conditions, and Tasmanian Aboriginal people used fire to maintain wildlife habitat for millennia (Bowman et al. 2021). The paleoendemic taxa, which have a Gondwanan heritage, are more vulnerable to fire than the more fire tolerant species, such as *Eucalyptus* species, which have radiated to dominate Australian woody vegetation (Bowman 2000). This has resulted in complex vegetation patterns, with small fire refugia rich in fire-sensitive Gondwanan species embedded in characteristically

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Australian, fire-adapted vegetation (Jordan et al. 2016; Bowman et al. 2021). A consequence of these interplays of climate, biogeographic history, and fire frequency is that the Gondwanan refugia hang in a delicate balance, which is being upset by the drying and warming trends of anthropogenic climate change and associated increases in area burnt (Styger et al. 2018; Bowman et al. 2021). This is exemplified by the 2016 wilderness bushfires ignited by lightning storms after an anomalous drought, which burnt about 20,000 ha of the TWWHA, threatening core refugia of fire-sensitive Gondwanan vegetation (Senate ECRC 2016; Harris et al. 2018).

Among the vegetation communities burnt by the 2016 fires was alpine peatland dominated by *Sphagnum cristatum*, the most common *Sphagnum* species in both Australia and New Zealand (Whinam et al. 2003). *Sphagnum* peatlands in Australasia are near their climatic limit, and occur in small, permanently wet sites in high rainfall alpine and montane areas (Whinam et al. 2003; DEWHA 2009). Despite the small area they occupy, alpine *Sphagnum* bogs play an important role in maintaining catchment hydrology and water quality, preventing erosion and supporting a rich endemic flora and fauna that require year-round moisture (DEWHA 2009). On a national level, "alpine *Sphagnum* bogs and associated fens" are listed as a threatened ecological community, due to their small size and restricted geographic distribution and threats they are facing, especially from fire and the ongoing effects of anthropogenic climate change, and trampling by feral animals (DEWHA 2009; French et al. 2016). Alpine *Sphagnum* bogs and associated fens occupy an estimated 3,100 ha in Tasmania, mainly in the Tasmanian Central Highlands and Tasmanian Southern Ranges bioregions, and "*Sphagnum* peatlands" are listed as rare in Tasmania (Threatened Species Scientific Committee 2009).

Sphagnum is considered particularly vulnerable to the effects of fire, the frequency and severity of which are increasing due to climate change (Threatened Species Scientific Committee 2009; French et al. 2016; Camac et al. 2021). Fire can immediately kill *Sphagnum* and other peatland species if they are sufficiently dry. Burning of *Sphagnum* can also have enduring indirect effects on peatland hydrology (Whinam et al. 2001). For example, fire decreases moisture retention and increases water repellency of the peat substrate (Kettridge et al. 2014; Lukenbach et al. 2016; Moore et al. 2017), which in turn can change whole-of-bog drainage patterns. When *Sphagnum* is burned, it also changes the albedo of bogs, increasing daytime surface temperatures and exacerbating hydrological changes (Kettridge et al. 2012).

In 2003, fires burned large areas of the Australian Alps in mainland Australia, including Namadgi and Kosciuszko National Parks, damaging *Sphagnum* bogs (Hope et al. 2005; Good et al. 2010) and this stimulated interest in *Sphagnum* bog restoration ecology in Australia (Clarkson et al. 2017). Studies following the 2003 fires found that fire immediately caused a marked reduction in *Sphagnum* cover, which had not recovered fully after a decade, despite localized recolonization (Whinam et al. 2010; McDougall et al. 2015). The poor recovery was related to the limited ability of *Sphagnum* mosses to recolonize bare organic soils after fire or mechanical disturbance (Groeneveld et al. 2007). Water tables near the soil surface are critical in allowing reestablishment of *Sphagnum* after wildfire (Lukenbach et al. 2015; Chimner et al. 2017). Another important factor for *Sphagnum* regeneration is shade, which protects against high ultraviolet light levels, high temperatures, and desiccation (Good et al. 2010; Graf & Rochefort 2010); shade nets in the greenhouse, and overtopping plant canopies in the field, were shown to be beneficial for *Sphagnum* and most other bryophyte species (Graf & Rochefort 2010). This shade effect was apparent in the Australian Alps, where *Sphagnum* regenerated fastest where there was free-standing water and shade from bog plants such as *Carex* and *Empodisma* species (Good et al. 2010). Such observations indicate the potential for applying ecological restoration interventions to accelerate the natural recovery of fire-affected *Sphagnum* communities (Gann et al. 2019).

Until the 2003 fires, there had been limited understanding of the post-fire recovery of *Sphagnum* species in Australia, as fires have been historically infrequent because *Sphagnum* occurs in fire refugia. There had also been little experience with *Sphagnum* restoration, given the rarity of fires and limited extent of peat mining. Many studies of *Sphagnum* restoration ecology have been conducted in the Northern Hemisphere (Rochefort et al. 2003; Caporn et al. 2017; Clarkson et al. 2017), but these largely focus on restoration following peat extraction, in areas accessible to heavy equipment. Because of environmental differences and differing effects of peat extraction and wildfire, it is not easy to transfer the proven *Sphagnum* bog restoration approaches developed in the northern hemisphere to Australia, especially as Australian *Sphagnum* communities are comparatively small and occur in fragile, remote alpine environments typically accessible only on foot or by helicopter. Therefore, Australian approaches developed after the 2003 fires involved simple treatments including various combinations of shading, rewetting, and transplantation of healthy *Sphagnum* blocks into fire-affected hummocks (Hope et al. 2005; Whinam et al. 2010). The recovery of *Sphagnum* observed in these trials was described as slow and complex, but results indicated that some interventions, particularly shading and combined transplant and fertilizer treatments, increased recovery rates to at least twice that of no treatment during the 4 years post-fire (Whinam et al. 2010).

In Tasmania, there has been little experience in rehabilitating *Sphagnum* bogs despite the conservation significance of this plant community. However, the damage caused to them by the 2016 Tasmanian Wilderness fires, and the likelihood of more frequent fires in the future due to anthropogenic climate change provided an impetus for research into methods to promote recovery, restoration, and maintenance of fire-damaged *Sphagnum* communities in the TWWHA. We therefore established a trial of the interventions found most promising in encouraging post-fire recovery of *Sphagnum* bogs in the Australian Alps. Specifically, we established a highly replicated field experiment to statistically evaluate the effect of shadecloth, fertilizer, and *Sphagnum* transplants treatments, alone and in combination, on the cover of healthy, damaged, and killed *Sphagnum* in eight environmentally similar bogs, six of which were burnt in the 2016 wildfires. We use the findings of this study to inform future *Sphagnum* bog restoration in Tasmania, and then discuss *Sphagnum* bog post-fire recovery more generally to contribute to understanding the restoration ecology of *Sphagnum* communities globally.

Methods

Geographic Context

The eight *Sphagnum* bogs selected as study sites in the field experiment were near the edge of Tasmania's Central Plateau at approximately 1,200 m above sea level, in the far north of the TWWHA (Fig. 1). The sites were situated within 8 km of Lake Mackenzie (41.67°S, 146.37°E), an impounded lake managed by Hydro Tasmania. The research sites were accessible only on foot from the Lake Mackenzie Road or by helicopter. Key geographic attributes of the study sites and survey dates are summarized in Table S1. Figure S1 shows photos of some of these bogs.

The vegetation of the area is a mosaic of subalpine woodlands, shrubland, and grasslands, and in fire refugia there are small patches of paleoendemic species, such as the long-lived conifer *Athrotaxis cupressoides* (Bowman et al. 2019). The soils are skeletal on ridges and organic on drainage lines and their slopes. The area was extensively burned by the January 2016 fires, which were ignited by dry lightning storms after an anomalously dry spring (Bowman et al. 2021).

Temperatures at Liawenee, the nearest high-elevation weather station, range from a mean monthly minimum of −1.6°C in July to a mean monthly maximum of 19.1°C in January, with a mean annual temperature of 6.9°C (Bureau of Meteorology 2022). Mean annual precipitation at Lake Mackenzie is 1985 mm. Although the study area was exceptionally dry at the time of the fire, near record rain fell during the following winter (Fig. S2). Precipitation was close to average in the lead up to the establishment of the first quadrats in autumn (March–May) 2019, but was well below average in the spring and summer of 2019/2020 after the second set of quadrats were established, and again in the winter and spring of 2020 after the final set of quadrats were established (Fig. S2), as well as the summer of 2021/2022, immediately before the final survey. The summer of 2021/2022 was also very much hotter than average across Tasmania (Bureau of Meteorology 2022; Fig. S3), intensifying the effects of the dry summer.

Of the eight study *Sphagnum* bogs, six were burnt and two unburnt, in *Sphagnum* heath complexes in which the principal *Sphagnum* species is *Sphagnum cristatum* (Whinam et al. 2001). These bogs were selected using high-resolution aerial photography collected from specially chartered fixed-wing manned aircraft in March 2018. The extent of *Sphagnum* cover and the area burnt for the six burned bogs was subsequently evaluated using high-resolution imagery acquired from an unmanned aerial vehicle (UAV) in 2019 and 2020 (Harding et al. 2022). The UAV imagery captured all *Sphagnum* patches within a contiguous area of the bog, and included a narrow buffer of non-*Sphagnum* vegetation (>1 m). A geographic information system was used to create a polygon to define the perimeter of the bog, ensuring that all *Sphagnum* patches apparent on

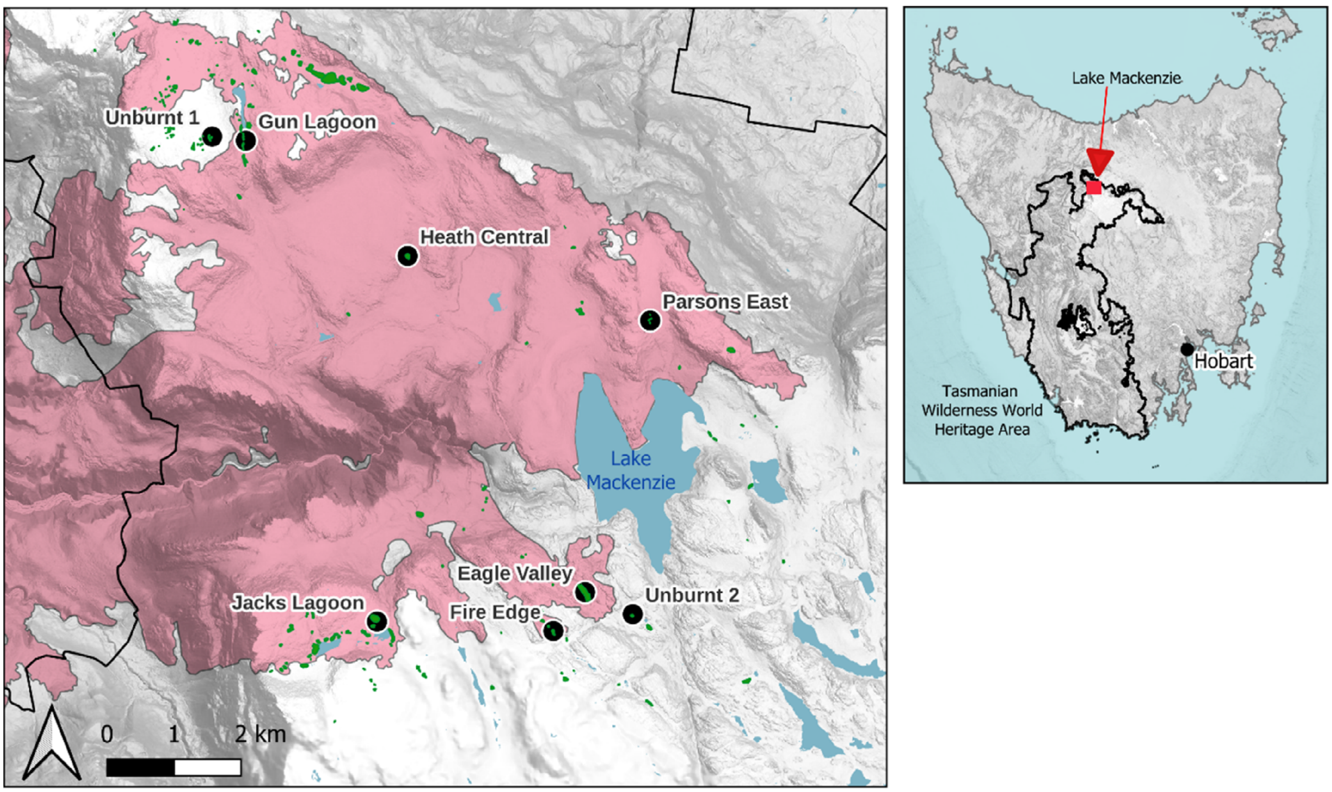

Figure 1. Location of the six burnt and two unburnt bogs used as study sites in the Lake Mackenzie *Sphagnum* restoration trials. The 2016 Lake Mackenzie fire footprint is shown in pink, with bogs shown in green and the black line indicating the boundary of the TWWHA. The small map shows the study location in Tasmania.

the imagery were included (Fig. S4). The delimitation of the bogs was based on vegetation boundaries apparent in the UAV imagery, noting this boundary sometimes arbitrarily segmented homogeneous tracts of non-*Sphagnum* vegetation. Analysis of the mapping based on the UAV imagery showed that 20–84% of the area of the six burnt bogs had been covered in *Sphagnum* before the fire, and that more than 90% of the *Sphagnum* cover had been burned by the 2016 fire (Table S1; Fig. S4). *Sphagnum* cover in the unburnt bogs, which was subjectively assessed during field surveys, was approximately 10% (Unburnt 1) and 5% (Unburnt 2) *Sphagnum* cover, with the remainder comprised of other unburnt vegetation.

Field Assessment of Study Quadrats

The study sites were established between March 2019 and March 2020, 3–4 years after the fire (Table S1). Delays in obtaining funding and permits precluded an earlier response. We used a stratified study design, in which we assigned six treatments, including a control, to quadrats in areas burnt at moderate severity (visually assessed as <75% *Sphagnum* killed) or high severity (≥75% killed) in each of the six burnt bogs (Table 1). We also applied four of these treatments to quadrats in the two unburnt bogs. At each burnt bog we established a total of 84 quadrats, allocated evenly between areas burnt at moderate and high severity (Table S2). In the two unburnt bogs, we established 20 quadrats which were located haphazardly, but at least 5 m distant from any neighboring quadrat. In total, 544 permanent quadrats were established to assess the initial vegetation cover in the various bogs and severity classes, and measure how it changed with time. Our focus was on the *Sphagnum*, but we also measured cover of other vegetation, as described below.

Quadrats (1 × 1 m) were positioned to overlay *Sphagnum* hummocks, using stratified sampling based on visually assessed *Sphagnum* burn severity (moderate, severe, or unburnt). Cover was assessed on the central 0.5 × 0.5 m (0.25 m^2), with the outer quadrat constituting a buffer (Fig. S6a). Within each quadrat, we visually assessed the percentage cover of healthy, damaged, and killed *Sphagnum*. Healthy *Sphagnum* was alive, with no apparent fire damage. Damaged *Sphagnum* was singed at the surface, but with evidence of life. Killed *Sphagnum* was deeply combusted, with no evidence of life. Examples of healthy *Sphagnum* in unburnt quadrats, damaged *Sphagnum* in moderate severity quadrats and killed *Sphagnum* in severely burnt quadrats are shown in Figure S5. In addition, we visually assessed the percentage cover of other lifeforms and species growing above the *Sphagnum* layer in the inner 0.25-m^2 quadrat (Table S3). We also counted the number of marsupial scats present in each quadrat as an indication of herbivory, removing them after the initial assessment to ensure that scats present at the final assessment had been deposited during the treatment period. Stems of the conifer *A. cupressoides* (alive and dead) were counted within a 5-m radius of the quadrat center.

Treatments

Three interventions, shade, fertilizer, and transplants, which have been shown elsewhere in Australasia to promote post-fire recovery of *Sphagnum* (Whinam et al. 2010; Clarkson et al. 2017), were tested at Lake Mackenzie. These three interventions were combined in an incomplete factorial design to give a total of six treatments, as follows. We applied all four combinations of shade and fertilizer to all burnt and unburnt sites. However, we minimized the number of quadrats receiving *Sphagnum* transplants because of the likely adverse effects on donor sites. Therefore, we did not transplant *Sphagnum* into unburnt quadrats. We also omitted the treatments without fertilizer, given expert advice based on experience in mainland Australia suggesting that all transplants should receive fertilizer (J. Whinam, personal communication, 2018). Thus, two transplant treatments were applied to only the burnt sites: Transplant + Fertilizer and Transplant + Fertilizer + Shade.

Shade. We used 1 × 1–m shadecloth squares, which allowed us to maximize replication by targeting small areas, and also to make it practical to carry materials several kilometers from the road to the study sites. Shadecloth squares were constructed off site from beige 70% block out shadecloth material (Whinam et al. 2010). Squares of 1.2 × 1.2 m were cut, and then the four edges were folded and creased at 0.1 m, and held together by 20-mm stainless steel eyelets at each corner, forming a total shade square of 1 m^2 (Fig. S6b). Lightweight 10-mm diameter aluminum stakes provided secure anchors against high winds. The outer quadrat aluminum marker stakes, plus two additional corner stakes were threaded through the eyelets and into the ground surface, then cinched and fixed securely with plastic cable ties (Fig. S6b).

Fertilizer. Fertilizer was used in all multi-factorial treatments, because it was believed to improve recovery of *Sphagnum* after fire in the Australian Alps, is inexpensive, simple to apply, and low doses are considered to have minimal adverse effects (Whinam et al. 2010). We applied slow-release fertilizer (Scotts Osmocote Native Gardens: Evergreen Garden Care, Bella Vista, New South Wales) specially formulated for phosphorus-sensitive plants (23% N, 0.49% P, 6.3% K, and 11% S with additional minor and trace elements) at a rate of

Table 1. Study design showing the number of study quadrats according to treatments and burn classes.

Burn Class	*Control*	*Shade*	*Fertilizer*	*Shade and Fertilizer*	*Transplant and Fertilizer*	*Shade, Transplant, and Fertilizer*
Unburnt	10	10	10	10	0	0
Moderate	42	42	42	42	42	42
Severe	42	42	42	42	42	42

80 g/m^2, as used by Whinam et al. (2010) and recommended after consultation with staff at the Royal Tasmanian Botanical Gardens.

Transplants. *Sphagnum* transplants potentially offer a way of reestablishing *Sphagnum* into sites where fire is so intense it is lethal to the *Sphagnum*. Transplant techniques were modeled on those described by Whinam et al. (2010). Transplant material was sourced from remnant healthy patches within each bog, typically within 200 m of the receiving plot (Fig. S6c). Blocks (20 × 20 × 20 cm) of live *Sphagnum* and underlying dead and humified material were cut using a bread knife and relocated to a cavity cut from the center of the burnt quadrat (Fig. S6d). Donor site locations were recorded to enable future monitoring of recovery (Fig. S6e).

Data Analyses

Data exploration and all statistical analyses were undertaken using statistical software R (R Core Team 2020). Our statistical approach was based on generalized linear modeling and model selection based on AICc a form of Akaike's information criterion corrected to accommodate small sample size. AICc balances model bias and parsimony, and lower values indicate greater support for the model relative to the others in the candidate set. We considered a difference in AICc of more than 2 indicating a difference in the level of support between two models (Burnham & Anderson 2001). The package lme4 was used for linear mixed effects models (Bates et al. 2014).

We tested for influences of site and fire history on initial cover of *Sphagnum* and other vegetation.

Our potential predictors of initial cover, the variables "Burnt" (binomial variable describing whether or not the site was burnt), "Burn Class" (unburnt, moderate, and high severity) and "Site" were all confounded: e.g. all sites were either burnt or not. Therefore, for each cover variable we constructed a candidate set of three models with a single predictor (Burnt, Burn Class, or Site), in addition to the intercept only model, and tested which had the strongest statistical support. Note that the variable "Site" includes the effects of fire, as well as differences among sites that are unrelated to burning, such as differences in geophysical attributes, initial vegetation, and intervention timing. It is not possible to attribute differences in vegetation recovery among bogs to these causes, given there were only six burnt bogs. However, the environmental variation makes any treatment effects detected more robust and generally applicable.

We then tested for preexisting differences in initial *Sphagnum* cover among the six treatments in quadrats at the burnt sites. To do this, we used linear mixed effects models with Treatment as a fixed effect and Site as random, to account for the spatial autocorrelation in the data. These showed no important differences in cover of healthy, damaged or killed *Sphagnum* among the burnt sites, with the intercept only models receiving more support than the corresponding models containing the term Treatment. Similarly, there were no initial differences between the two unburnt sites in *Sphagnum* cover in the study quadrats.

To analyze the effects of Burn Class and Treatment on *Sphagnum* cover change, for each *Sphagnum* response variable we constructed a candidate set of linear mixed effects models with a global model containing the terms Burn Class, Treatment and their interaction. Site was a random effect in this model set. There were also four reduced models containing all combinations of Burn Class and Treatment. Because we found important interactions between Burn Class and Treatment, we then examined the effects of Treatment within each Burn Class. For the burnt quadrats we used Site as a random effect to account for spatial autocorrelation, but for the unburnt quadrats, we used Site as a fixed effect, because there were only two sites. There were no obvious interactions between the three interventions (although we could not check interactions involving transplanting, because of the incomplete factorial design), so we estimated their effect size and statistical significance using a linear model containing the three binary variables shade, fertilizer, and transplant (present or absent). This model was fitted separately for the three Burn Classes. Again, Site was used as a random effect for the burnt quadrats, but had to be used as a fixed effect with unburnt quadrats. Effects of the interventions were considered significant if their confidence interval did not include zero.

For analysis of change in cover of vegetation other than *Sphagnum*, for simplicity we used "Burnt" as the fire-related explanatory variable, because there was similar statistical support for the "Burnt" and the "Burn Class" models. We used linear mixed effects models with all combinations of the terms "Burnt" and "Treatment," including the interactive one, and used Site as a random effect in all models. For these analyses, we used only quadrats where the relevant vegetation type was present at either the initial and/or final measurement.

Nonmetric multidimensional scaling (NMDS) ordination was used to explore aggregated dissimilarities in cover of different ground covers among the burned bogs using the R package "vegan" (Oksanen et al. 2022).

Results

Initial Vegetation Cover of Study Quadrats

Study quadrats intentionally targeted areas with high *Sphagnum* cover. Accordingly, total *Sphagnum* cover in individual study quadrats averaged 97% (range 70–100%), although in the burnt sites, much was damaged or killed. Moderate burn severity quadrats had on average 41% killed, 51% damaged, and 4% healthy *Sphagnum* cover (Fig. 2). By comparison, severely burnt quadrats averaged 97% killed, 0.6% damaged, and 0.1% healthy *Sphagnum* cover. Validating our quadrat selection, the strongest predictor of healthy, damaged, and killed *Sphagnum* cover was the Burn Class assigned to that quadrat, which received far more statistical support than simply whether a quadrat was burnt or not, and overwhelmed any effect of site (Table S3).

Because quadrats deliberately targeted areas that were predominantly *Sphagnum*, cover of other vegetation was generally low. In most bogs, there was substantial cover of Restionaceae and grasses that had rapidly reestablished after the fire, and several bogs also had moderate cover of other bryophytes and herbs

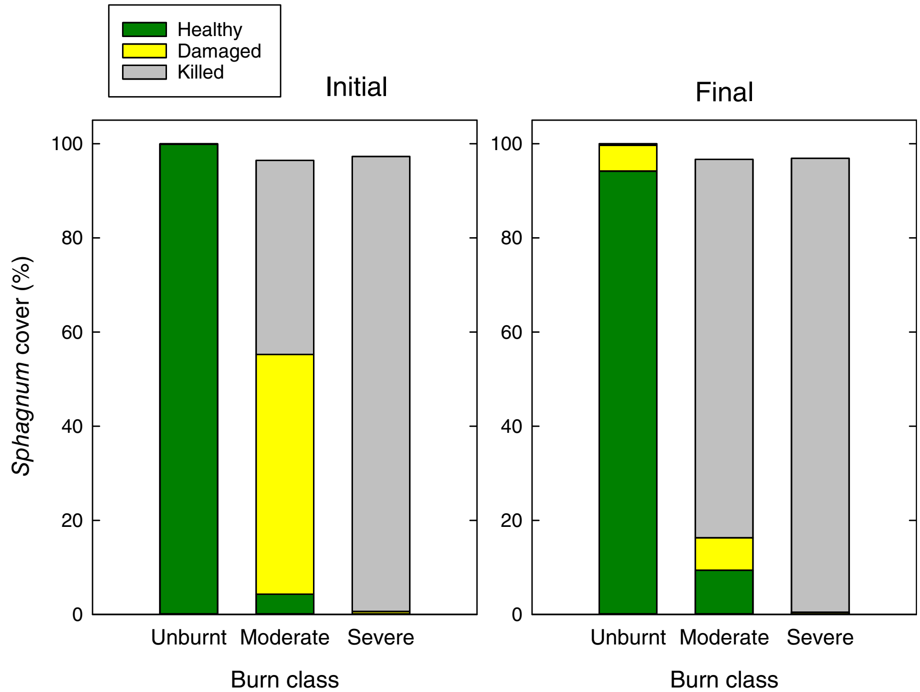

Figure 2. Cover of healthy, damaged, and killed *Sphagnum* in relation to Burn Class when quadrats were established (initial). Remeasured cover (final) is for the untreated control quadrats. All differences in cover among Burn Classes were significant, except for final cover of damaged *Sphagnum* between unburnt and moderately burnt quadrats.

(Table S2). Cover of most vegetation other than *Sphagnum* was more strongly correlated with Site than burning, suggesting pre-existing site attributes were dominant (Tables S2 & S3). The exception was that burnt quadrats had very little cover of *Richea scoparia* or other shrubs (Fig. S7), with no additional effect of fire severity. *Richea scoparia* cover was also strongly influenced by Site (Table S3). The most striking difference in vegetation among the sites was that *Gleichenia alpina* cover averaged 35% in quadrats at one unburnt site, but it was <2% at all other sites (Table S2). Other ferns were found only at Parsons East. Live *Athrotaxis cupressoides* trees were found only at Eagle Valley and Unburnt 2, and dead ones at Eagle Valley and Fire Edge. Overall, NMDS revealed there were minor differences among burnt sites in cover of vegetation other than *Sphagnum* (Fig. S8).

Change in Sphagnum Cover Between Initial and Final Assessments

In the absence of any interventions, there were substantial changes in *Sphagnum* health between the initial and final measurements. The changes were largest in the moderately burnt quadrats, where most damaged *Sphagnum* either died or recovered between the initial and final assessments (Fig. 2). By contrast, there was little change in *Sphagnum* health in the severely burnt control quadrats because, by design, most of the *Sphagnum* was already dead when the quadrats were established, and very little recovery occurred. In unburnt quadrats all *Sphagnum* was initially healthy, but 6% was classed as damaged in the final assessment.

Modeling showed that Burn Class had the strongest influence on the change in *Sphagnum* cover, but Treatments and their interaction with Burn Class were also important (Table 2; Fig. 3). As for the untreated quadrats, overall the changes were largest in moderately burnt quadrats. Shade was strongly beneficial to *Sphagnum* health (Figs. 3, 4, & S9). The three treatments that included shade (on its own, or in combination with fertilizer or fertilizer and transplants) all had substantially higher cover of healthy *Sphagnum*, and lower cover of killed *Sphagnum*, than the corresponding treatments without shade, especially in the moderate Burn Class. On average, in moderately burnt quadrats, the change in healthy *Sphagnum* was 14% higher, and dead *Sphagnum* 16% lower, in quadrats with shadecloth than those without it (Fig. 4). By contrast, fertilizer was detrimental to *Sphagnum* health, with significant or near-significant declines in cover of healthy *Sphagnum*, and increases in killed *Sphagnum* (Figs. 3 & 4). In unburnt and moderately burnt areas, healthy *Sphagnum* cover declined about 10% more in fertilized compared with unfertilized quadrats (Figs. 3 & 4). There was no gain to transplanting healthy *Sphagnum* into the moderately burnt *Sphagnum*, but in the severely burnt quadrats, transplanting led to a small (2.5%) increase in the cover of healthy *Sphagnum*, and a decrease (5%) in killed *Sphagnum* (Fig. 4). Note that the gain in healthy *Sphagnum* was much less than the 16% of the area of the inner quadrat filled by the transplanted *Sphagnum*.

Change in Cover of Other Vegetation Between Initial and Final Assessments

Change in shrub cover was affected by burning but not by treatment, with an increase in the burnt but not the unburnt quadrats (Table S4; Fig. 5). For other types of vegetation, the reverse

Table 2. Comparison of support (AICc) for generalized linear models describing change in cover of healthy, damaged, and killed *Sphagnum* between the initial and final measurements, with site as a random effect. The "*" symbol indicates the model that includes the additive effects and the interaction. The best-supported models (delta AICc <2) are shown in bold. Values should only be compared within rows. Lower values indicate more statistical support, with "0" representing the "best" model. Models with delta AICc <2 are regarded as having substantial support, those with delta AIC between 4 and 7 have considerably less support, while those with delta AICc >10 have essentially no support (Burnham & Anderson 2001).

	Model				
Response Variable	*Burn Class * Treatment*	*Burn Class + Treatment*	*Burn Class*	*Treatment*	*Intercept Only*
Healthy *Sphagnum*	**0**	84	140	161	208
Damaged *Sphagnum*	5.8	**0**	**1.1**	819	811
Killed *Sphagnum*	**0**	28	74	526	537

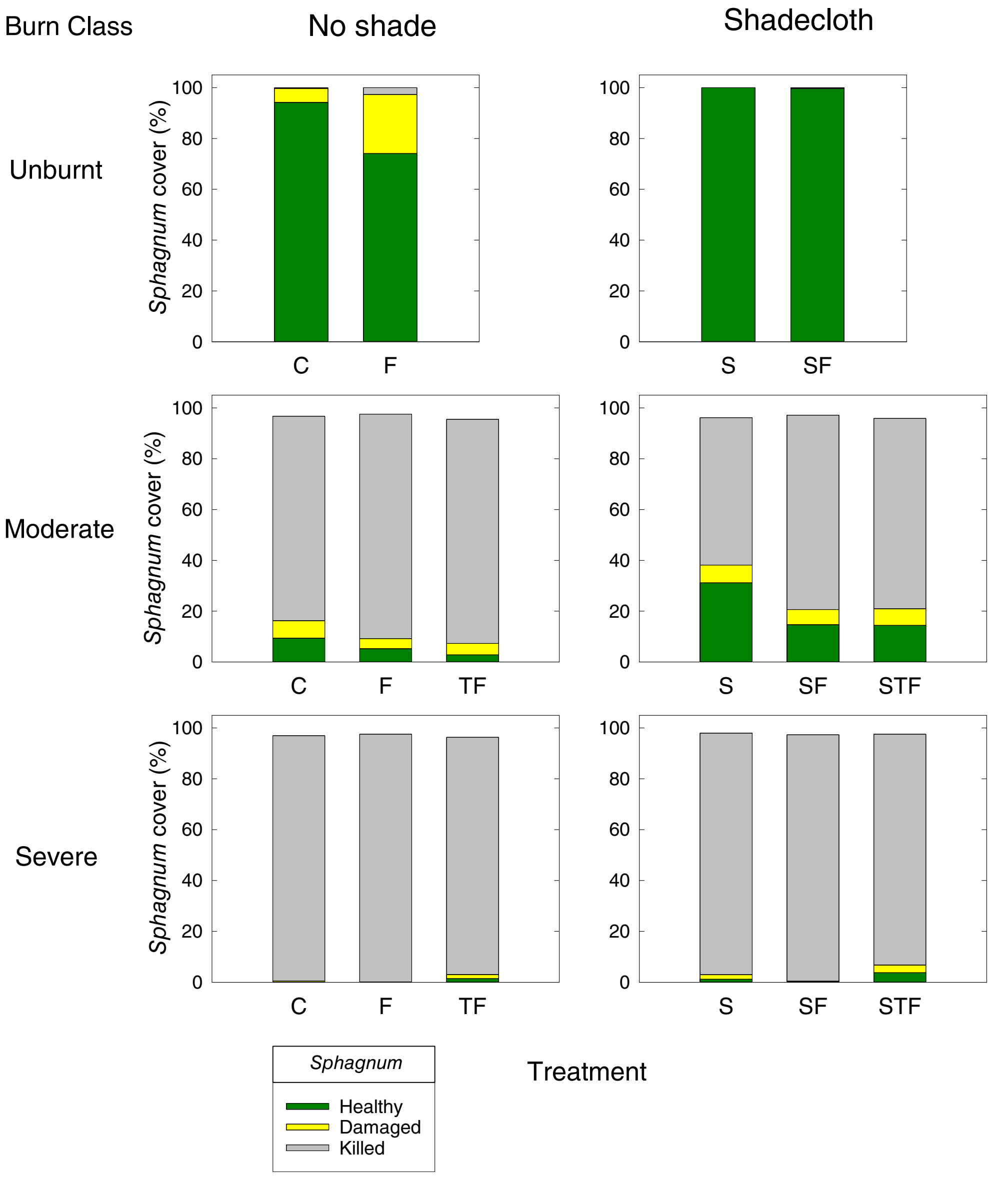

Figure 3. Cover of healthy, damaged, and killed *Sphagnum* at the end of the experiment, in relation to Burn Class (unburnt, damaged, and killed) and treatment. Left-hand panels are unshaded, those on the right, the corresponding shaded treatment. C is the untreated control, S is shade, F is fertilizer, and T is transplant. Transplant quadrats received 16% cover of healthy *Sphagnum*, but little survived. Box plots showing treatment variability are in Figure S9.

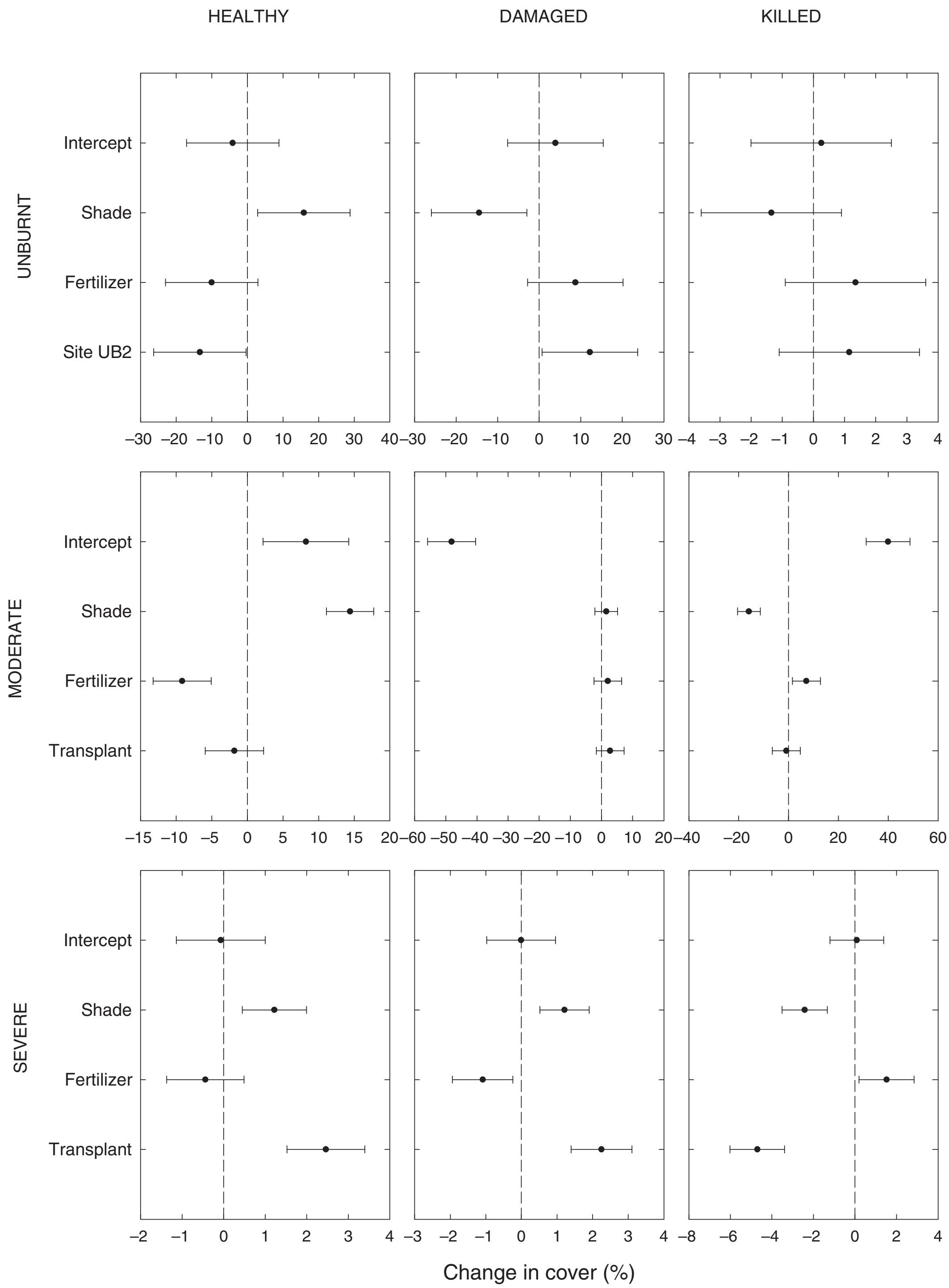

Figure 4. Change in cover of healthy, damaged, and killed *Sphagnum*, estimated using linear models containing the three variables shade, fertilizer and transplants, all binary (present or absent). Bars indicate 95% CI. The intercept applies to the change in cover of untreated control quadrats, and the other coefficients show change relative to the control. Site was a random effect in the models for the moderate and severely burnt quadrats. There were only two unburnt sites, insufficient to use as a random effect, so site was a fixed effect in the models for the unburnt quadrats, with the intercept applying to untreated control quadrats at unburnt site 1. Site UB2 is the second unburnt site.

applied, with a strong treatment effect but little or no effect of burning (Table S4). The cover of Restionaceae, grasses, herbs and *Gleichenia* were all favored by shadecloth. There were also very few scats in quadrats covered by shadecloth (Fig. 5). Other bryophytes were the only vegetation type that responded positively to fertilizer (Fig. 5), and their increase was greater in burnt quadrats.

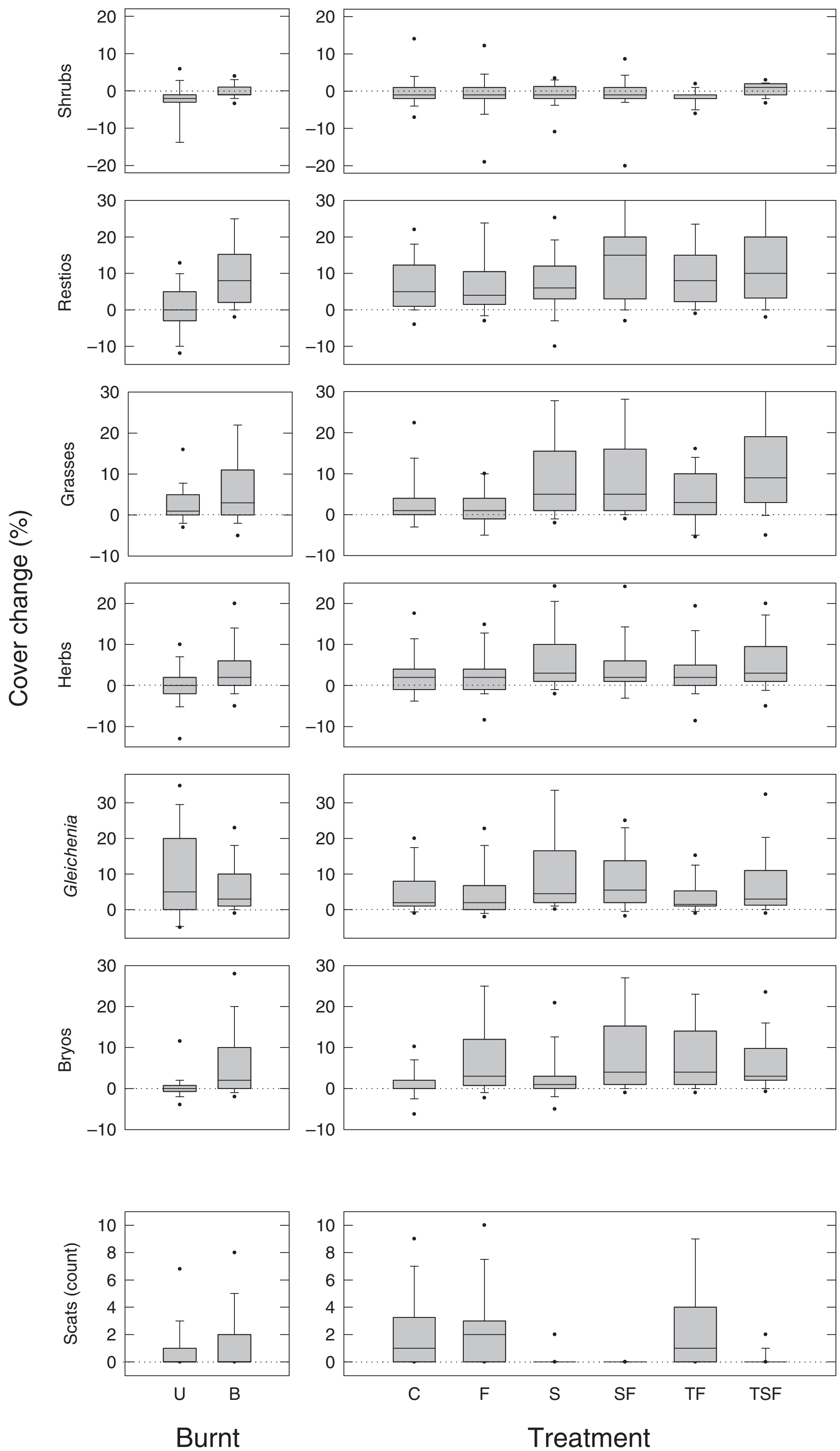

Figure 5. Change in cover, and the final scat count, in relation to whether the site was burnt and treatment. U is unburnt and B is burnt. Only quadrats with that vegetation type present at the initial and/or final measurement are included. C is untreated control, F is fertilizer, S is shadecloth, SF is shadecloth and fertilizer, TF is transplant and fertilizer, and TSF is transplant, shadecloth, and fertilizer.

Discussion

Our field experiment has illuminated important constraints on the post-fire recovery of *Sphagnum* bogs in Tasmania. We have demonstrated that natural post-fire recovery is highly dependent on the presence of some surviving *Sphagnum*, and the rate of recovery can be increased through the provision of shade. We found that fertilizer adversely affected *Sphagnum* recovery, while increasing the abundance of other bryophyte species. As discussed below, these finding harmonize with previous understanding of the ecology and restoration of *Sphagnum* bogs. Based on these findings, we make recommendations for *Sphagnum* restoration interventions and discuss their constraints.

Like other mosses, *Sphagnum* species do not have a seedbank and lack any adaptation to protect themselves from fire damage, a disturbance they are usually protected from because of the saturated habitat they favor. Our study concords with previous studies showing that *Sphagnum* recovers from living fragments that survived the fire (McDougall 2007), with limited recovery when cover is below 10% (Clarkson et al. 2017). A consistent finding of this and earlier Australasian studies is that if there is no surviving *Sphagnum*, then vegetative recovery does not occur and eventual return of *Sphagnum* cover depends on recolonization from spores (Johnson 2001; McDougall 2007). Typical of many growth processes, post-fire recovery is very slow initially, but it accelerates until full cover is regained. For instance, McDougall et al. (2015), working in the Australian Alps, observed poor recovery of *Sphagnum* cover in the first decade following a fire, but that 14 years after the fire it had returned to pre-fire levels. Similarly, Johnson (2001) reported that in New Zealand, in favorable areas *Sphagnum* was only 2 cm tall 15 months post-fire, 18 cm tall after 6 years, and 30 cm tall after 10 years. Based on these studies, and our own observations, we surmise that in the Lake Mackenzie area, full recovery of moderately burned areas is likely to take decades, and severely burned patches are unlikely to recover without massive and sustained restoration effort.

A robust finding of our experiment is that shade can increase the rate of post-fire recovery of *Sphagnum*, aligning with previous studies such as one in North America, showing *Sphagnum* species regenerated best under shade nets in the greenhouse, or in harvested peatland, under a dense canopy of herbaceous plants (Graf & Rochefort 2010). The beneficial effect of shading is likely related to protection from high ultraviolet light levels, high temperatures, and desiccation (Good et al. 2010; Graf & Rochefort 2010). We have shown that shading also benefits growth of plants such as Restionaceae, grasses, herbs, and *Gleichenia*. Whether these will act as competitors or serve as nurse crops for *Sphagnum* is unknown. Additionally, increased grass cover could elevate fire risk (Prior et al. 2017).

Based on this experiment, we can endorse shadecloth for restoration programs. Shadecloth has also been used in Australian Alps, where it was shown to benefit the recovery of *Sphagnum* bogs. An important difference between this study's shadecloth interventions and those used in the Australian Alps relates to the scale. We applied shadecloth to 1-m^2 quadrats, but in the Australian Alps it was rolled out post-fire in 20 m lengths to cover a total of 6,000 m^2 (Good et al. 2010; Whinam et al. 2010). The use of small areas of shadecloth is likely a more practical approach in Tasmania given the high cover of shrubs in these communities, and it could also allow more shrubs to establish adjacent to shaded areas to possibly act as nurse plants for *Sphagnum*. Shadecloth has other ecological effects which we have not investigated. For example, it is likely to protect from browsing and trampling of herbivores, as shown by the very few scats being present in quadrats covered by shadecloth. Shadecloth could also inhibit the establishment of shrubs if it remained in place for years, and whether this would affect the long-term persistence of *Sphagnum* is unclear, noting unburnt Tasmanian *Sphagnum* bogs have a characteristically well-developed shrub layer, which provides some natural protection against direct solar radiation. It is not known how long the beneficial effects of shadecloth persist after removal, nor the optimal duration for keeping cover in place. In our experiment we removed all shadecloth after the final survey in March 2022, to avoid contaminating the TWWHA study sites with degraded shade material.

The very slow natural recovery in fire-killed *Sphagnum* patches is a strong argument for transplanting *Sphagnum*, an approach that was very effective the Australian Alps (Whinam et al. 2010). However, we found that transplants did not significantly accelerate post-fire recovery. It is unclear why severely burnt peat is a poor substrate for *Sphagnum* establishment and growth in the Tasmanian bogs we studied, but it may be related to changes in water holding capacity and repellency, soil chemistry and microbiota, as well as microtopographic changes. Resolution of this problem requires greenhouse trials that separate these likely interacting soil characteristics. Even if the success of transplants can be enhanced, the approach is problematic in Australia because the restricted occurrence and high conservation values of *Sphagnum* make it difficult to find enough donor material at the scale that might be necessary after extensive wildfire. Micro-propagation could offer an alternative source of *Sphagnum* to reintroduce to degraded peatlands (Caporn et al. 2017).

The detrimental effect of fertilizer on *Sphagnum* cover found in our trial is counter to study expectations. Whinam et al. (2010) considered that the same fertilizer applied at the same rate as in our study was beneficial for post-fire *Sphagnum* recovery in the Australian Alps, but their study design did not allow this to be rigorously tested. In our study, the fertilizer enhanced the cover of bryophytes other than *Sphagnum*. A positive effect of P on *Sphagnum* and other wetland species has been reported in North America (Ferland & Rochefort 1997; Rochefort et al. 2003). However, a large meta-analysis found high N loading depresses *Sphagnum* production relative to untreated controls (Limpens et al. 2012). Higher summer temperatures can intensify the negative effects of N (Limpens et al. 2011). Thus, the hotter than average summer of 2021/2022 could plausibly have contributed to the damage to *Sphagnum* we observed in some unburnt quadrats and fertilized quadrats. Further work is required on dosages, composition and timing of fertilizer applications to determine if nutrient additions can improve *Sphagnum* recovery.

In this study, because of permitting and funding constraints, treatments were applied 3–4 years after the fire, compared with the 3–10 months in the Australian Alps study (Whinam et al. 2010). It is possible that application of shadecloth immediately after a fire could have giving even larger benefits than we found, by both reducing delayed mortality and accelerating recovery of damaged *Sphagnum*. The delay in applying treatments could also have reduced the success of the transplants, through hydrological or other effects (Lukenbach et al. 2016; Moore et al. 2017). We consider it less likely that earlier application would have improved the response to fertilizer, given that fire quickly releases a pulse of nutrients into the system (Van Beest et al. 2019). We recommend that fire severity should be assessed as soon as possible after fire (Harding et al. 2022), to map and identify moderately burnt *Sphagnum* areas, which are most likely to respond to treatments. The optimal timing of interventions needs investigation, but we consider early interventions are likely to be most successful.

It is not possible to attribute differences in vegetation recovery among bogs to any particular cause, because there were only six burnt bogs, which differed in position, initial vegetation, and timing of the interventions. We made several observations that could warrant further investigation. In the moderately burnt bogs, the largest increase in healthy *Sphagnum* cover occurred in the two bogs where the quadrats were established in spring (compared with autumn in the other four bogs), but there were slight differences in other vegetation cover in these bogs, so other factors could be responsible. We also found that Gun Lagoon, the site where quadrats were established at least one summer later than the other burnt sites, showed the smallest response to shading, although the difference was significant only compared to Eagle Valley, and then only in moderately burnt quadrats. Importantly, the environmental and floristic variability among bogs, and the different seasons and years when transplanting occurred, introduces experimental variation that strengthens our findings.

Importantly, *Sphagnum* bogs are likely affected by the "press" of climate change and "pulse" of drought-initiated fire disturbance that is threatening other fire-sensitive Gondwanan vegetation (Harris et al. 2018). These stressors of climate change not only threaten healthy *Sphagnum* bogs, but affect post-fire recovery of burned bogs, which takes decades because of the slow dispersal and growth of the moss. Unfortunately, it is likely that near-term future climates are going to be less favorable for *Sphagnum* growth, with conditions being hot, drier, and more fire prone. As in most of the world, temperatures in Tasmania are already rising, and are projected to rise by 1.6 to 2.9°C during the 21st century (ACE CRC 2010). Rainfall is projected to decline in central and north west Tasmania, with seasonal changes being more pronounced than annual totals (ACE CRC 2010). In the TWWHA, both the number of fires following lightning storms, and the area burnt by these fires have increased since the year 2000, with these increases attributed to more lightning strikes occurring in dry conditions (Styger et al. 2018). It is also possible that as bogs become drier they will be colonized by woody vegetation, further changing hydrology and fire risk (Heijmans et al. 2013). Maintaining a suitable hydrological regime is key to retaining peatlands in the landscape (Chimner et al. 2017), and especially critical for Australasian peatlands, given they are already near their climatic limits (Whinam et al. 2003; French et al. 2016). Therefore, potential hydrological interventions to aid the longer-term survival of *Sphagnum* bogs need to be explored.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Photos of study bogs.
Figure S2. Precipitation at Lake Mackenzie from the lead up to the fire to the end of the trials.
Figure S3. Mean temperature deciles during summer 2021/22 and the trend in anomalies in mean annual temperature relative to the 1961–1990 baseline.
Figure S4. Classification of UAV-derived images of each burnt bog.
Figure S5. Examples of healthy, damaged and killed *Sphagnum*.

Figure S6. Photos of quadrats showing experimental treatments.
Figure S7. The cover of *Richea* and other shrubs according to whether the quadrat had burned or not.
Figure S8. Site differences in the change in healthy *Sphagnum* cover in the moderate burn class and initial differences among sites revealed by NMDS.
Figure S9. Change in cover between establishment and the final measurements in relation to burn class and treatments of (a) healthy *Sphagnum*, (b) damaged *Sphagnum*, and (c) killed *Sphagnum*.
Table S1. Summary of geophysical and vegetation cover attributes for the eight *Sphagnum* bogs.
Table S2. (a) Characteristics of the study quadrats at all eight bogs, and (b) Explanations of the cover variables.
Table S3. Comparison of generalized linear models describing initial cover and scat counts
Table S4. Comparison of support (delta AICc) for generalized linear mixed effects models describing change in cover of other vegetation.

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