Post-grazing and post-fire vegetation dynamics: long-term changes in mountain bogs reveal community resilience

Peter J. Clarke, David A. Keith, Ben E. Vincent & Andrew D. Letten

Keith, D.A. (corresponding author, david. keith@unsw.edu.au)[2,3,4]
Clarke, P.J. (pclarke1@une.edu.au)[1],
Vincent, B.E. (bvincen3@myune.edu.au)[1],
Letten, A.D. (andrewletten@gmail.com)[2]

[1]Botany, School of Environmental and Rural Science, University of New England, Armidale, NSW 2351, Australia;
[2]Centre for Ecosystem Science, University of New South Wales, Sydney, NSW 2052, Australia;
[3]NSW Office of Environment and Heritage, Hurstville, NSW 2220, Australia;
[4]Australian Long Term Ecological Research Network, Canberra, ACT 2601, Australia

Abstract

Questions: Are Australian *Sphagnum* bogs compositionally stable or undergoing long-term change in response to grazing legacies or environmental change along a climatic gradient? Are these *Sphagnum* bogs resilient to discrete fire events, and over what time scales does recovery from disturbance take place? How does fire disturbance influence species composition in the assembly of fire-prone Australian bog communities?

Location: Alpine and subalpine bogs in mainland eastern Australia (Kosciuszko National Park).

Method: Full floristic sampling over ca. 50 yr (1960s, 1990, 2005, 2007, 2013) at 11 sites; each site sampled with 25 quadrats (0.1 m^2) haphazardly placed during each successive survey. Sites were stratified over alpine and subalpine elevations, in burned and unburned areas. Changes in species composition over space and time were examined with multivariate and univariate analyses.

Results: The *Sphagnum* bogs of the subalpine and alpine regions show progressive increases in cover of *Sphagnum* over the last 40–50 yr. Overall species richness and frequency of dominant woody species declined. These trends were not strongly related to the climate gradient. Fire temporarily reduced the frequency of most species but initial floristic composition was regained a decade after fire. There was fire-dependent variation related to regeneration of hygrophyllous woody species through seed germination and seedling growth in open ground.

Conclusion: Our results show a degree of community resilience to both grazing and fire, although some observed changes appear directional and the recovery time for grazing was much longer than that for fire. The increase in *Sphagnum* frequency across subalpine and alpine bogs is likely to reflect progressive recovery of *Sphagnum* from the grazing era, possibly enhanced by the changing atmosphere. Concurrently, there have been declines in species richness and woody species frequency. The bogs exhibited resilience to infrequent pulse disturbance related to fires, which appear to drive community assembly through cycles of compositional change.

Introduction

Plant communities exhibit two contrasting patterns of change. On the one hand, they undergo gradual change under the influence of persistent pressures (e.g., grazing regimes) or fluctuating resources (e.g., nutrients, water, light) and environmental conditions (e.g., temperature) because of high functional redundancy, strong feedback effects and positive neighbour effects (Frelich & Reich 1999). Alternatively, plant communities may respond rapidly to stochastic disturbance events, such as fire, if these are large enough to remove or reduce species that maintain stability, allowing different processes to govern community assembly, or if they create new niches (Scheffer & Carpenter 2003). Ecosystems dominated by mesic bryophytes, such as *Sphagnum* bogs, are potentially highly susceptible to environmental change because these organisms, unlike other bryophytes, have little tolerance

to prolonged desiccation (Proctor et al. 2007) and are mostly unable to store resources. Nevertheless, spores of *Sphagnum* and some other mesic bryophytes are able germinate after dry periods of at least 3 yr (Proctor et al. 2007), enabling them to recruit opportunistically and respond rapidly to new favourable environments. The potential resilience and stability through disturbance of *Sphagnum*-dominated communities, such as bogs, therefore warrants investigation (Turetsky et al. 2012).

Mosses, and in particular *Sphagnum* species, facilitate peat accumulation and development of moist soil microclimates, and are thought to regulate vascular plant demography in northern hemisphere bogs (Turetsky et al. 2012). Positive feedbacks are prominent in these systems, underpinning the function of bogs as carbon sinks because, for example, mosses develop hummock–hollow microtopography that, in turn, maintains access of mosses to a stable moisture supply (Benscoter & Wieder 2003; Belyea & Baird 2006). These positive feedbacks potentially make bog communities resilient to drought and wildfire, but may also promote regime changes between stable states. Conversely, negative feedbacks can occur through shading mechanisms in which vascular plant growth is favoured by climate warming and is postulated to reduce moss fitness (Turetsky et al. 2012).

Whilst the resilience and functional role of bogs and fens has been the focus of many studies and several reviews in the northern hemisphere (see Turetsky et al. 2012), the ecology of southern hemisphere bogs and fens is poorly understood (Whinam et al. 2003; Whinam & Hope 2005). In contrast to the boreal and arctic ecosystems, where moss-dominant communities occupy a significant area of the landscape, bogs and fens have very restricted occurrence in the temperate and mountain regions of Australia, where the total area of *Sphagnum*-dominated communities is less than a few thousand hectares (Whinam & Hope 2005). Stratigraphic reconstruction of vegetation change during the Holocene for Australian mountain bogs aligns with general models from the northern hemisphere, showing directional change from swamp and fen communities to *Sphagnum*-dominated hummock heath (e.g., Whinam & Kirkpatrick 1995; Martin 1999). As in some northern peatland systems (e.g., Hörnberg et al. 1995; Ohlson et al. 2006), these Holocene stratigraphic sequences are often interrupted by layers of charcoal, indicating regular disturbance by fire (McKenzie 1997, 2002; Martin 1999), and suggesting that gradual and episodic processes may both play roles in the structure and dynamics of Australian bog communities.

Long-term studies (>50 yr) are uncommon in both northern and southern hemisphere bogs, but provide important insights into mechanisms governing ecosystem change (e.g., Gunnarsson et al. 2000, 2002). In the moun-

tains of mainland Australia, much of the understanding of responses of mires to disturbance is based on studies over relatively short time frames (Wimbush & Costin 1979a,b; Clarke & Martin 1999; Wahren et al. 2001; McDougall 2005, 2007). In this paper, we use data from a long-term study of Australian *Sphagnum* bogs to explore patterns of ecosystem dynamics in response to gradual and episodic disturbance.

Alpine and sub-alpine bogs in Australia are subject to natural and anthropogenic disturbances including drought, fire, livestock grazing and snow skiing. Summer grazing by sheep and cattle commenced in the alpine and subalpine regions from about the 1830s (Costin et al. 2000), causing erosion (Bryant 1971) and changes in vegetation structure and composition (Costin 1954; Wimbush & Costin 1979a,b; Scherrer & Pickering 2005). Consequently, livestock grazing has been banned in the main alpine region of Kosciuszko since 1944 and in the subalpine zone since 1958. Since then, atmospheric CO_2 concentrations have risen from 316 to 396 ppm (Earth Systems Research Laboratory 2013) and mean global temperatures have risen by 0.6 °C (Hansen et al. 2010). Fires were thought to be frequent during the grazing period but since the 1950s only localized fires were recorded in the alpine or adjacent subalpine zone until an extensive wildfire in January 2003, which burned alpine and subalpine vegetation including *Sphagnum* bogs (Worboys 2003; Walsh & McDougall 2004). These fires partially or completely burned some *Sphagnum* bogs previously sampled for long-term study by Clarke & Martin (1999; see Table 1).

The effects of these mixed disturbance histories on *Sphagnum* bogs in space and time were fortuitously measured after baseline plots were established in the late 1950s, early 1960s and 1970s using a large number of haphazardly placed quadrats in each site/bog (see Table 1). Here we test whether the long-term floristic composition and growth form traits of southern hemisphere bog vegetation are: (i) compositionally stable or responding gradually to grazing removal or environmental change across an elevational gradient over decadal time scales; and (ii) resilient or sensitive to a discrete fire event in 2003.

Methods

Study sites and sampling

The study area was situated in the subalpine and alpine region of Kosciuszko National Park on the mainland of southeastern Australia. The mires in this area mostly occur as small (<1 ha) discrete patches with high groundwater levels interspersed in herbfields, heaths and woodlands (Costin 1954; Wimbush & Costin 1979a,b; Whinam & Hope 2005). Only a few of the mires are strictly

Table 1. Location of *Sphagnum* bog sampling sites and their attributes.

Sites	Type	Basal Date (yr BP)	m a.s.l.	Elevational Zone	Year Sampled	Recent Fire History
Wilson Valley[1]	Valley bog	1600 + 80	1498	Upper montane	1960, 1991, 2005, 2007, 2013	Unburned
Boggy Plain[1,2]	Valley bog	10410 + 210	1585	Subalpine	1959, 1991, 2005, 2007, 2013	Unburned
Boggy Plain[2]					2005, 2007, 2013	Burned 2003
Hydrology Bog[2]	Valley bog	n.d.	1650	Subalpine	1963, 1991, 2005, 2007, 2013	Burned 2003
Diggers Creek[1,2]	Raised bog	10170 + 150	1762	Subalpine	1960, 1991, 2005, 2007, 2013	Unburned
Diggers Creek[2]					2005, 2007, 2013	Burned 2003
Schlink Pass[1,2]	Raised bog	n.d.	1785	Subalpine	1973, 1991, 2005, 2007, 2013	Unburned
Charlotte Pass[1,2]	Raised bog	6870 + 160	1843	Approximately tree line, alpine	1959, 1991, 2005, 2007, 2013	Unburned
Wrights Creek[1]	Raised bog	7460 + 110	1866	Alpine	1963, 1991, 2005, 2007, 2013	Unburned
Lake Browne[1]	Raised bog	n.d.	1935	Alpine	1973, 1991, 2005, 2007, 2013	Unburned
Mt Stilwell[1]	Raised bog	1570 + 100	1996	Alpine	1960, 1991, 2005, 2007, 2013	Unburned

[1]Elevation × time analyses, [2]Burned × time analyses, Basal date, C^{14} date at the base of the sedimentary profile; n.d., No data.

ombrogenous: many receive some run-off or seepage waters from small catchments. Despite the input of run-off and seepage moisture, their acid waters and substrates (pH~4) and paucity of nutrients (including P and mineral cations) support vegetation dominated by shrubs, sedges and abundant *Sphagnum,* not unlike descriptions of 'bogs' from the northern hemisphere (Økland et al. 2001; Grover et al. 2005). These mires are sometimes described as 'valley bogs', although some are perched on upper slopes within seepage zones. In accordance with customary terminology, we will refer to these mires as (mountain) bogs. Their properties contrast with *Carex*-dominated fens in the same area, which lack *Sphagnum,* and many of the shrubs and sedges that characterize mountain bogs in Kosciuszko (Costin et al. 2000).

The alpine area is restricted to an undulating landscape of about 100 km², while the subalpine landscape has stronger relief. Both have snow cover during winter, but only the alpine area maintains isolated and small snow patches throughout summer (Edmonds et al. 2006). The 11 study sites (bogs) were located along an altitudinal transect (1500–2000 m a.s.l.) ascending the main alpine plateaux, mostly adjacent to the Kosciuszko summit road as described in Clarke & Martin (1999; see their Fig. 1; Table 1). All sites regularly receive snow that persists over winter and all are situated in small broad valleys or on seepage slopes (Table 1). In some subalpine locations (<1800 m a.s.l.), bogs are surrounded by thickets of snow gum (*Eucalyptus niphophila*). All bogs had common structural components of *Sphagnum cristatum* hummocks, prominence of sedges (*Carex*), chord rushes (*Empodisma, Baloskion*), hygrophilous shrubs (*Richea, Epacris, Baeckea*) and small open pools, but lack hummock–hollow transition patterns (Clarke & Martin 1999). When sites were originally selected for study (1959–1973, henceforth these samples are termed '1960s'), they were chosen on the basis
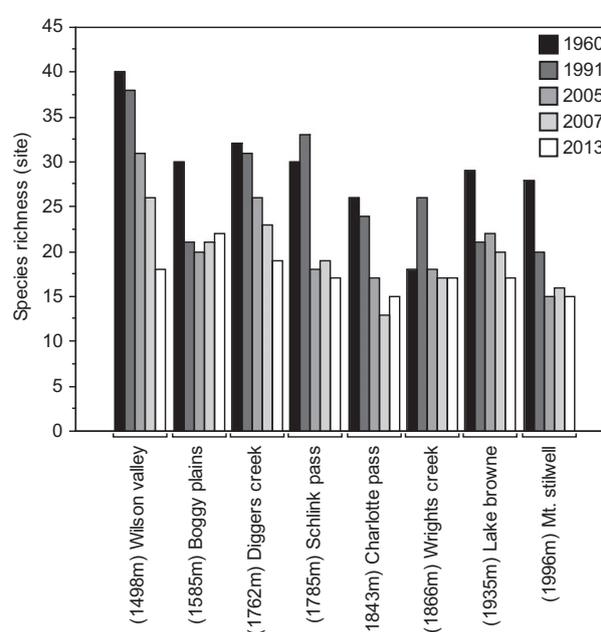
Fig. 1. Total species richness of vascular plants and bryophytes in each site (bog) that was not disturbed by fire over time. Note that the initial sampling date varied among sites, see Table 1.

of having minimal evidence of physical disturbance and all sites had an intact bog surface with little or no erosion. This contrasts with many subalpine and alpine bogs that were severely degraded through prior livestock grazing (see Wimbush & Costin 1979a). Thus, *a priori*, the trends described in this account are likely to represent less pronounced examples of vegetation change in Kosciuszko bogs.

Floristic composition was sampled in 0.1 m² (20 cm × 50 cm) quadrats that were haphazardly located (by blind throw) at 11 sites within the boundaries of nine

bogs, including two bogs with two sites (one burned and one unburned; Table 1). The original number of quadrats (20–30) was determined according to the approximate extent of the bogs, but over time this was standardized to 25 samples per bog. Frequency of occurrence out of the total number of quadrats was recorded for all bryophyte and vascular plant species at each of the 11 sites. A new set of 25 haphazardly located quadrats was recorded on each of the five sampling occasions. All sites were sampled during the late austral summer (late January or early February) to minimize seasonal effects, and the haphazardly located quadrats for each sampling occasion were constrained within the same area (<1 ha) of the respective bogs to minimize effects of fine-scale spatial variation.

Sites that were burned in 2003 were also revisited in 2007 to measure fire severity using the tip thickness method on a common shrub (Hammill & Bradstock 2006). The minimum diameter of twigs remaining on the terminal branches of burned *Richea continentis* was measured on 20–30 individuals on each of the three burned bogs. The resulting measurements served as an index of fire severity, with larger minimum twig diameters indicating higher fire severity in the bogs.

Design of data contrasts

The presence–absence records from quadrats within each site were used to calculate frequency scores for each species at each site, including all vascular and bryophyte taxa. Two subsets of the frequency data were established. First, to determine whether bogs were compositionally stable or responding gradually to environmental change across an elevational gradient, a site by species frequency matrix (the 'elevation' data set) was constructed for eight alpine, subalpine and montane bogs, each sampled on five occasions, thus 40 samples by 126 species, excluding the three sites burned in 2003 (Table 1). To assist interpretation of this first comparison, each site was classified as upper montane (1400–1500 m a.s.l.), subalpine (1500–1800 m a.s.l.) or alpine (>1800 m a.s.l.) and each species was labelled 'alpine', 'subalpine' or 'pan-altitidunal', depending on its occurrence across the sites. Second, to determine whether bogs were resilient or sensitive to discrete fire events, a site by species frequency matrix was constructed for bogs that were burned in 2003 with comparator unburned sites at similar altitudes (the 'fire' data set; Table 1). All seven sites included in this analysis were situated at subalpine elevations. Comparator sites were located within the same bogs at two locations (Boggy Plain, Diggers Creek). For the third burned site (Hydrology Bog), we included the other unburned subalpine site (Schlink Pass) and the unburned tree line site (Charlotte Pass) as comparators. The matrix for this second comparison thus included 35 samples (7 sites × 5 times) and 203 species. We also examined species richness and cover of bare ground (including both bare peat and exposed mineral soil) to assess vegetation stability in the comparisons.

Data analyses

Overall changes in the composition of vegetation were assessed over the five sample times by ordination of sites using the package *vegan* in R v 3.0.3 (R Foundation for Statistical Computing, Vienna, AT). Bray-Curtis dissimilarities were first calculated for each of the elevation and fire data sets described above, followed by a global non-metric multidimensional scaling (GNMDS) ordination in two, three and four dimensions. The Epsilon threshold was set at 0.8, to convert higher Bray-Curtis values to geodesic distances; however none of the dissimilarity values in our data sets exceeded 0.8. Optimum (lowest stress) configurations were selected from 100 runs derived from random initial configurations, with a maximum of 200 iterations for convergence. The convergence ratio for stress was 0.99999. The two ordinations with the lowest stress values were compared with a Procrustes test and were found to be identical ($r = 1$, $P = 0.001$, permutations = 999). The elevation analysis was repeated without the montane site, Wilson Valley, which was found to be an outlier in the analysis of 11 sites with potential impact on displayed relationships between other sites.

All ordination axes were subject to varimax rotation and were rescaled linearly into half-change (H-C) units. Covariables (time and elevation) were fitted to the ordination as both linear vectors (permuted 999 times to check goodness of fit) and as smooth non-linear surfaces using thin-plate splines splines, using in-built *vegan* functions.

To check for potential inconsistency in the ordination results (van Son & van Halvorsen 2014), a contrasting ordination procedure, detrended correspondence analysis (DCA), was used in parallel. Congruence between GNMDS and DCA was evaluated with the Procrustes correlation coefficient r and by calculating pair-wise Kendall's rank correlation coefficients (τ) between corresponding DCA and GNMDS axes.

Generalized linear models (GLMs) were used to further explore the influence of time, elevation and fire on frequencies of individual species that had a summed frequency of >100 in each data set. The data were well suited for use of a binomial error structure and a logit link function, where the binomial denominator was the number of samples (25 quadrats) for each site, and the y-variate for each species was its frequency score of 0–25. Plots of the residuals were examined and only those species that had

linear relationships with the respective covariates were included in the analyses. In addition, GLMs with normally distributed errors were fitted to species frequency scores averaged for each of five growth form groups: shrubs, mosses, grasses, forbs and sedges, as well as species richness and the cover of bare ground to explore their relationships with time, elevation and fire. Plots of the residuals confirmed that averaging of frequency scores for multiple species within these groups approximated normal distribution of the data.

For the elevation data set, the model comprised two fixed interactive factors, elevation (four alpine vs three subalpine sites) (Table 1) and time (1960s, 1991, 2005, 2007, 2013). Time was treated as a fixed factor because new plots were haphazardly placed at each sampling time, rather than repeatedly sampling fixed plots. Additionally, species richness was regressed against *Sphagnum* frequency to test for evidence of competitive effects and other potential interactions between the hummock moss and vascular plants.

For the fire data set, a two-factor BACI (Before fire/After fire vs Control/Impact) model was used with seven sites (Table 1). Time was divided into two periods: before fire (1960s, 1991) and after fire (2005, 2007, 2013). Even though this two-factor model was unbalanced, plots of the residuals showed linearity for all of the common species and growth form groups analysed.

Results

Stress values of GNMDS ordinations declined as their dimensionality increased. For the set of all unburned alpine, subalpine and montane sites (including Wilson Valley), stress values of the 2-D, 3-D and 4-D solutions were 0.158, 0.102 and 0.074, respectively. For unburned subalpine and alpine sites (excluding Wilson Valley), stress values were 0.155, 0.102 and 0.078, respectively. For burned vs unburned sites, stress values were 0.136, 0.088 and 0.067, respectively. In all cases, diagnostic values for the fit between compositional variation and explanatory variables indicated that the 2-D solution provided a parsimonious representation of relationships, despite the reduced stress at higher dimensions (Table S1).

There was comparatively strong congruence between GNMDS and DCA ordinations (Figs S1–S3): all unburned sites (including Wilson Valley) ($r = 0.76$, $\tau_1 = -0.59$, $\tau_1 = -0.54$); all unburned sites (excluding Wilson Valley) ($r = 0.91$, $\tau_1 = -0.67$, $\tau_1 = -0.61$); and burned vs unburned sites ($r = 0.96$, $\tau_1 = 0.86$, $\tau_1 = 0.68$). Linear vectors representing elevation and time were broadly in agreement with spline surfaces, except in the fire analysis when trends with time were conspicuously non-linear (Figs S4 and S5).

Vegetation change along the elevation gradient

The ordination of all unburned sites over time showed large directional change in the outlying montane bog (Wilson Valley) as a result of encroachment and shading by tall shrubs (*Leptospermum* spp.) in the bog over time (Fig. 2a). With this site removed (Fig. 2b), the other subalpine and alpine sites remained floristically distinct from one another through time, with few sites (e.g., Wrights Creek) overlapping in composition with other sites in time (Fig. 2b). There were relatively strong and statistically significant relationships between floristic composition and the elevation gradient ($R^2 = 0.63$) and between composition and time ($R^2 = 0.42$; Fig. 2b). For both explanatory variables, linear vectors were broadly in agreement with patterns represented by spline surfaces (Fig. S4). The temporal trajectories for each site were unrelated to the elevational gradient (indicated by contrasting directions of the elevation and time vectors in Fig. 2b). In particular, the alpine sites (Mount Stilwell, Lake Browne, Charlotte Pass) showed no trend of convergence toward the more subalpine sites (Fig. 2b). The magnitude of floristic changes in time did not reflect the intervals between sampling, as some sites underwent large floristic changes between 1959 and 1991 (Boggy Plain) but others (Diggers Creek) showed little difference over the same interval (Fig. 2b), suggesting site-specific floristic fluctuations at different times. Species plots on the ordination diagram show a general increase in *Sphagnum* over time and decreases in many of the vascular plant species (Fig. 2c).

Most tested species varied in frequency with elevation and time (Table 2). The most frequent species (*S. cristatum*) increased in frequency through time and then declined slightly in the latest sampling period. In contrast, most of the vascular plant species decreased in frequency through time, although this varied with elevation (Table 2). The exceptions were the shrub *Richea continentis*, which decreased in frequency in the alpine zone but increased in the subalpine zone (Table 2), and the sedge *Carex gaudichaudiana*, which fluctuated in the subalpine and increased in the alpine zone (Table 2). Several species exhibited strong interactions between time and elevation (Table 2), indicating that patterns of change differed between the alpine and subalpine zones. The shrub *Oxylobium ellipticum* increased in frequency in the subalpine zone, but overall shrub frequency was relatively constant through time (Table 2). The frequency of the most dominant grass (*Poa costiniana*) decreased over time, as did the mean cover of bare ground, from 18% to 6.5%. This corresponded with an increase in forb and graminoid frequency (Table 2). Mean species richness per site decreased progressively from 27 species to 17 species over time, with the lowest elevation site having the largest decrease through time
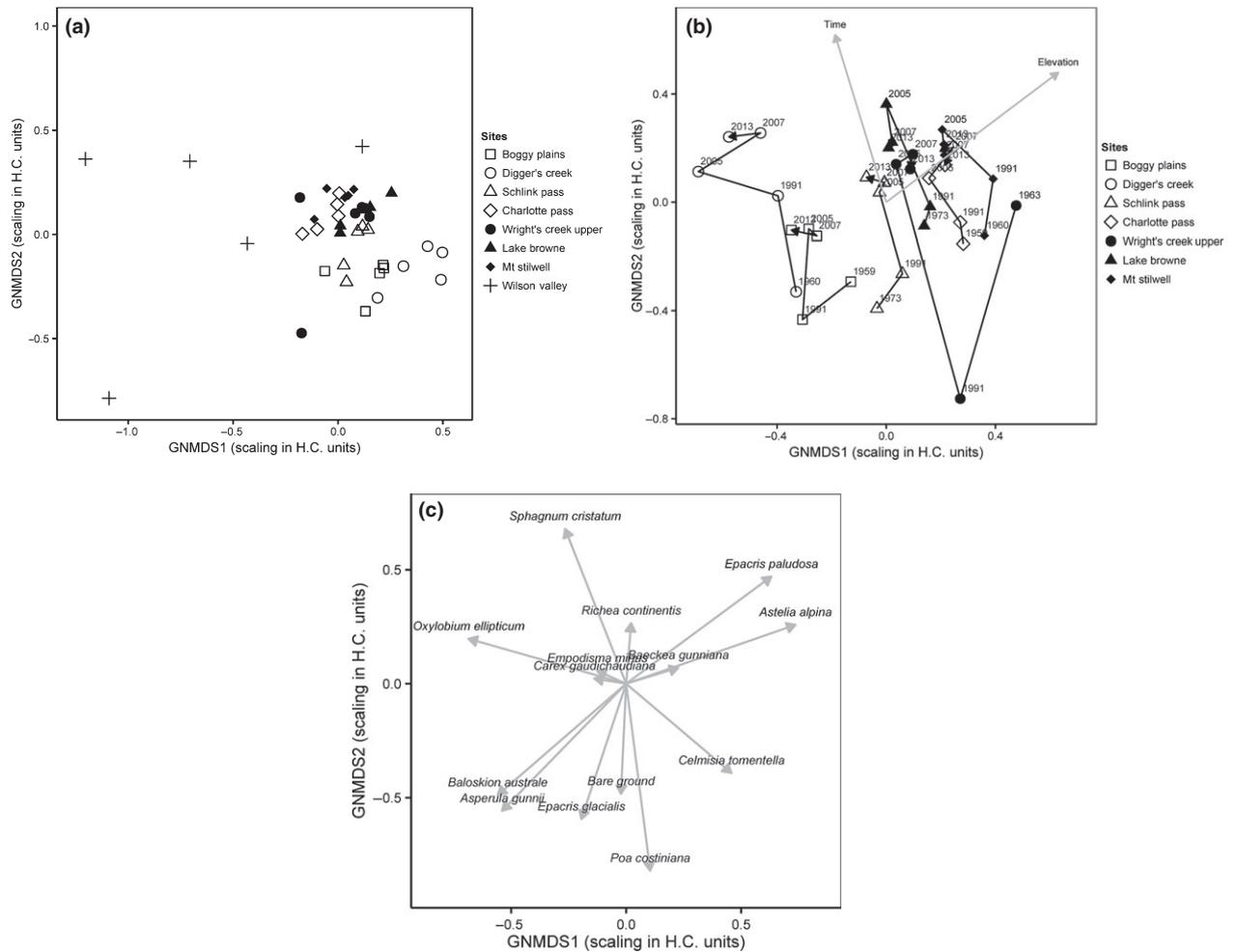
Fig. 2. GNMDS ordination of undisturbed sites over time. (**a**) All sites shown with the montane bog (Wilsons Valley included), (**b**) subalpine and alpine sites with temporal trajectory vectors (black lines) representing elevation ($R^2 = 0.63$) and time ($R^2 = 0.42$) (grey arrows; length proportional to the square-root of the correlation between variables and the ordination axes), (**c**) species vectors based on their distribution among site × time samples.

(Table 2, Fig. 1). Overall there was a weak but significant negative relationship ($R^2 = 0.33$, $P < 0.0001$, slope $= -0.58$) between *Sphagnum* frequency and total species richness per site.

Impact of the 2003 fire

The ordinations showed pronounced effects of the fire on floristic composition. A linear vector produced a reasonable representation of the elevational gradient ($R^2 = 0.47$), but not temporal trends ($R^2 = 0.07$, $P = 0.296$). Spline surfaces provided a more informative representation of temporal trends, indicating strongly nonlinear patterns of change (38% of the total deviance explained; Fig. S5). Prior to the fire, the amount of floristic variation was relatively small, with short temporal

trajectories, compared with the longer, more cyclical compositional trajectories in the bogs that burned in 2003 (Fig. 3). The trajectories of burned sites were longest between the 1991 and 2005 samples, the interval in which the 2003 fire occurred. Major change continued to occur between 2005 and 2013, although the 2013 samples are tracking back towards their pre-fire state in two of the sites (Diggers Creek and Hydrology Bog), but not at the burned Boggy Plain site (Fig. 3). This difference corresponds to the larger burned twig diameters measured on *Richea continentis* at Boggy Plain (mean ± SD, 11.3 ± 3.3 mm), compared with Hydrology Bog (5.7 ± 1.3 mm) and Diggers Creek (3.7 ± 0.8 mm), indicating a higher severity fire occurred at Boggy Plain relative to the other sites. The control sites (Boggy Plain unburned, Diggers Creeks unburned, Schlink Pass, Char-

Table 2. Summary results for GLM for the effects of elevation (E, subalpine vs alpine) and year of sampling (Y). The model was constructed from 35 observations [$df(E) = 1$, $df(Y) = 4$, $df(E \times Y) = 4$, df(residual) $= 25$].

Response Variable	Model Factor				Mean frequEncies ($n = 8$)				
Rank Order	Elevation	Year	$E \times Y$		1960s	1991	2005	2007	2013
Sphagnum cristatum (Sphagnaceae)	**	***	**	Subalpine	0.69	0.64	0.93	0.95	0.81
				Alpine	0.51	0.36	0.94	0.95	0.89
Empodisma minus (Restionaceae)	n.s.	***	***	Subalpine	0.89	0.88	0.86	0.95	0.83
				Alpine	0.62	0.91	0.94	0.99	0.82
Epacris paludosa (Ericaceae)	***	***	*	Subalpine	0.55	0.29	0.30	0.53	0.36
				Alpine	0.80	0.60	0.87	0.83	0.78
Richea continentis (Ericaceae)	n.s.	n.s.	***	Subalpine	0.37	0.66	0.67	0.68	0.68
				Alpine	0.76	0.63	0.68	0.56	0.54
Baeckea gunniana (Mytaceae)	n.s.	n.s.	n.s.	Subalpine	0.49	0.58	0.43	0.53	0.41
				Alpine	0.65	0.49	0.59	0.59	0.51
Poa costiniana (Poaceae)	***	***	*	Subalpine	0.70	0.63	0.31	0.27	0.19
				Alpine	0.38	0.61	0.15	0.09	0.13
Carex gaudichaudiana (Cyperaceae)	**	***	n.s.	Subalpine	0.50	0.26	0.46	0.51	0.40
				Alpine	0.19	0.20	0.42	0.40	0.36
Astelia alpina (Astelicaeae)	***	***	n.s.	Subalpine	0.01	0.03	0.00	0.01	0.00
				Alpine	0.48	0.46	0.24	0.52	0.42
Asperula gunnii (Rubiaceae)	***	***	***	Subalpine	0.37	0.41	0.38	0.40	0.32
				Alpine	0.48	0.14	0.00	0.00	0.00
Epacris glacialis (Ericaceae)	***	***	***	Subalpine	0.47	0.08	0.02	0.01	0.08
				Alpine	0.27	0.07	0.00	0.00	0.00
Celmisia tomentella (Asteraceae)	*	***	n.s.	Subalpine	0.32	0.22	0.22	0.20	0.12
				Alpine	0.44	0.34	0.21	0.23	0.21
Oxylobium ellipticum (Fabaceae)	***	*	*	Subalpine	0.12	0.25	0.33	0.32	0.36
				Alpine	0.01	0.03	0.00	0.00	0.00
Baloskion australe (Restionaceae)	***	**	n.s.	Subalpine	0.37	0.31	0.25	0.20	0.13
				Alpine	0.00	0.01	0.00	0.00	0.00
All Mosses	**	***	**	Subalpine	0.32	0.32	0.78	0.79	0.53
				Alpine	0.32	0.35	0.80	0.95	0.78
All Grasses	**	***	**	Subalpine	0.38	0.44	0.31	0.22	0.18
				Alpine	0.33	0.43	0.15	0.09	0.12
All Shrubs	***	***	***	Subalpine	0.40	0.32	0.40	0.50	0.39
				Alpine	0.44	0.34	0.66	0.66	0.49
All Forbs	***	***	n.s.	Subalpine	0.19	0.21	0.21	0.25	0.26
				Alpine	0.22	0.25	0.27	0.30	0.29
All Graminoids	n.s.	***	n.s.	Subalpine	0.19	0.16	0.23	0.23	0.19
				Alpine	0.11	0.16	0.25	0.23	0.22
Bare Ground	n.s.	**	n.s.	Subalpine	0.16	0.17	0.09	0.08	0.08
				Alpine	0.22	0.09	0.10	0.07	0.05
Species Richness	***	***	n.s.	Subalpine	25.3	22.8	18.0	16.5	16.0
				Alpine	30.3	28.3	21.3	21.0	10.3

*$P < 0.05$, **$P < 0.001$, ***$P < 0.0001$. Significant effects at $P < 0.05$ should be treated cautiously because of Type I errors associated with multiple tests. Taxa are listed in descending order of frequency across the whole data set.

lotte Pass) had small changes over the entire time interval, similar to pre-fire trajectories of the burned sites (Fig. 3).

The impact of the 2003 fire was most pronounced in the sampling of burned bogs in 2005 with a decrease in the frequency of most species, including mosses, grasses and shrubs, and an increase in a few ruderal forbs (*Asperula gunnii, Gonocarpus micranthus*) and graminoids (*Carex gaudichaudiana*). Subsequently, many species of moss, shrub,

forb and graminoid increased in frequency (Table 3). We observed strong colonization of a range of moss and liverwort species on mineral soil following fire (*Polytrichum juniperium, Bryum campylothecium, Ditrichum* spp. *Marchantia berteroana*), but these decreased in frequency over time as ground cover of other species increased (species-level data not shown). The dominant moss *S. cristatum* decreased in cover after the fire and then slowly recovered a decade after fire (Table 3). The dominant shrub species (*Epacris*
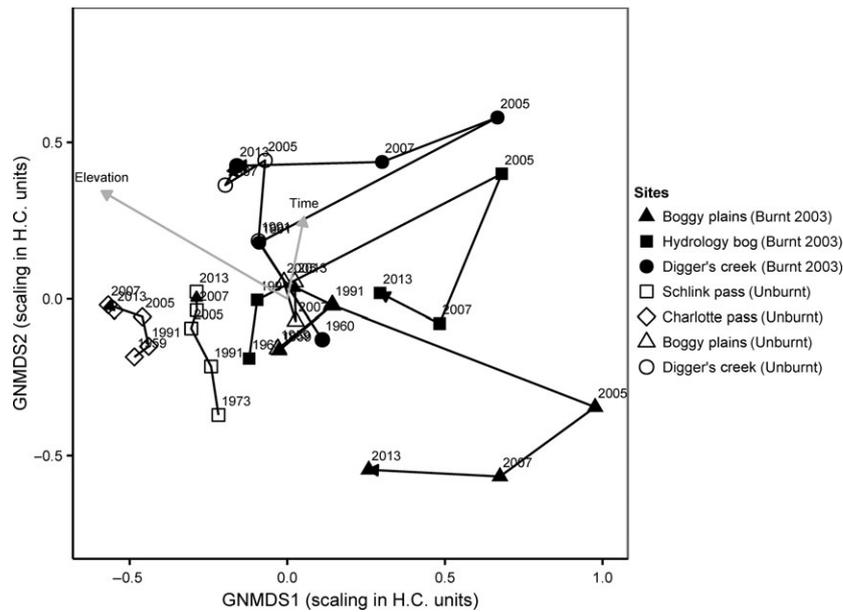
Fig. 3. Ordination (multi-dimensional scaling) of burned sites in 2003 (Diggers Creek, Hydrology Bog and Boggy Plain) and adjacent unburned sites (Boggy Plain, Diggers Creek, Schlink Pass, Charlotte Pass) over time. Open symbols unburned through time, closed symbols burned. Temporal trajectories over time (black lines) and vectors (grey arrows) representing elevation ($R^2 = 0.47$) and time ($R^2 = 0.07$; not significant at 95% confidence level). Length of vectors is proportional to the square root of the correlation between variables and the ordination.

glacialis and *Richea continentis*) were killed by fire and recovered only via seedling recruitment, hence their frequency values were slow to recover (Table 3); in contrast, their frequency in the control sites remained stable before and after fire. Resprouting graminoid species (*Carex gaudichaudiana, Empodisma minus, Baloskion australe*) recovered rapidly (Table 3).

There was a strong interactive effect on species richness in the BACI analysis (Fig. 4). Species richness before vs after in the control (unburned) sites decreased over time and, conversely, species richness increased in the impacted sites 2 yr after the fire (2005), then decreased over the 10 yr since fire (2013).

Discussion

Long-term change in the absence of disturbance

Overall, *Sphagnum* bogs exhibited considerable variability in patterns of species composition over the 50 yr since the 1960s; however, individual bogs changed more or less independently of one another and maintained their floristic distinctness despite the observed changes. Increasing frequency of *Sphagnum*, declining cover of bare ground and declining frequency of shrubs are general trends common to both alpine and subalpine bogs. These changes are consistent with long-term recovery of bog vegetation with time since the cessation of livestock grazing that took place in the region for more than a century prior to 1960. *Sphag-*

num is especially sensitive to trampling by livestock (Whinam et al. 2003), and its increase in frequency only began to abate in 2005–2007, suggesting that some 40–50 yr are required for recovery from grazing. The cover of bare ground took a similar length of time to stabilize, and the data suggest a slightly longer recovery time for alpine elevations than subalpine elevations. This difference may relate to frost heave on bare soils, as this has been shown to be a major factor inhibiting the restoration of bogs and mires (Groeneveld & Rochefort 2005). Frost heave may therefore prolong the legacy effect of grazing at higher elevations. We observed a coincident decline in mosses and herbaceous ground cover species that appear to exploit open space.

The attribution of our results primarily to lagged effects of grazing removal over half a century is consistent with several long-term studies that show slow recovery of alpine and subalpine plant communities after the exclusion of cattle grazing (Williams & Ashton 1987; Williams 1990; Wahren et al. 1994, 2001; McDougall 2007) and with controlled experiments in which grazing animals were removed (Wimbush & Costin 1979a,b; Clarke & Martin 1999; Scherrer & Pickering 2005). The longest study of *Sphagnum* peatlands in Australia documented slow recovery of *Sphagnum* in subalpine peatlands that were fenced in 1946 to exclude livestock, relative to peatlands that were grazed continuously until 2004 (McDougall 2007). Similarly, over a 15-yr period on the Bogong High Plains,

Table 3. Summary results for GLM for the effects of fire (control vs impact) and time (before 1960s, 1991 vs after fire, 2005, 2007, 2013) of sampling. The model was constructed from 35 observations [df(fire) = 1, df(time) = 1, df($E \times Y$) = 1, df(residual) = 31].

| Response Variable	Model Factor				Mean Frequencies ($n = 7$)				
	Fire	Time	$F \times T$		1960s	1991	2005	2007	2013
Sphagnum cristatum (Sphagnaceae)	***	n.s.	***	Control	0.76	0.52	0.98	0.98	0.94
				Impact	0.64	0.64	0.20	0.31	0.57
Empodisma minus (Restionaceae)	n.s.	n.s.	***	Control	0.68	0.84	0.92	1.00	0.82
				Impact	0.91	0.85	0.74	0.88	0.83
Epacris paludosa (Ericaceae)	***	n.s.	***	Control	0.54	0.58	0.80	0.98	0.88
				Impact	0.70	0.37	0.16	0.23	0.33
Richea continentis (Ericaceae)	***	***	***	Control	0.64	0.68	0.52	0.62	0.60
				Impact	0.46	0.67	0.02	0.13	0.28
Baeckea gunniana (Myrtaceae)	**	**	**	Control	0.44	0.68	0.62	0.62	0.54
				Impact	0.62	0.54	0.28	0.41	0.41
Poa costiniana (Poaceae)	n.s.	***	n.s.	Control	0.70	0.60	0.42	0.16	0.22
				Impact	0.60	0.61	0.23	0.23	0.20
Carex gaudichaudiana (Cyperaceae)	n.s.	n.s.	n.s.	Control	0.38	0.28	0.40	0.40	0.30
				Impact	0.51	0.19	0.31	0.39	0.28
Astelia alpina (Asteliaceae)	***	n.s.	*	Control	0.24	0.20	0.04	0.28	0.20
				Impact	0.04	0.00	0.00	0.00	0.00
Asperula gunnii (Rubiaceae)	***	*	***	Control	0.16	0.08	0.00	0.00	0.00
				Impact	0.42	0.48	0.78	0.79	0.41
Epacris glacialis (Ericaeae)	***	***	*	Control	0.10	0.00	0.00	0.00	0.00
				Impact	0.44	0.01	0.00	0.27	0.12
Celmisia tomentella (Asteraceae)	***	n.s.	n.s.	Control	0.44	0.48	0.52	0.38	0.34
				Impact	0.28	0.08	0.15	0.07	0.13
Oxylobium ellipticum (Fabaceae)	***	n.s.	***	Control	0.02	0.10	0.12	0.14	0.18
				Impact	0.20	0.29	0.19	0.21	0.27
Baloskion australe (Restionaceae)	***	**	n.s.	Control	0.00	0.00	0.00	0.00	0.00
				Impact	0.45	0.40	0.17	0.16	0.51
All Mosses	***	***	***	Control	0.30	0.37	0.98	0.98	0.94
				Impact	0.29	0.32	0.22	0.29	0.33
All Grasses	***	***	*	Control	0.47	0.28	0.42	0.11	0.22
				Impact	0.32	0.53	0.15	0.14	0.15
All Shrubs	***	n.s.	***	Control	0.26	0.34	0.59	0.67	0.47
				Impact	0.48	0.37	0.20	0.27	0.28
All Forbs	n.s.	***	n.s.	Control	0.19	0.19	0.22	0.29	0.27
				Impact	0.20	0.21	0.21	0.25	0.28
All Graminoids	*	**	n.s.	Control	0.18	0.17	0.27	0.18	0.23
				Impact	0.17	0.11	0.22	0.25	0.13
Bare Ground	*	n.s.	n.s.	Control	0.22	0.10	0.06	0.10	0.04
				Impact	0.19	0.18	0.06	0.36	0.05

*$P < 0.05$, **$P < 0.001$, ***$P < 0.0001$. Significant effects at $P < 0.05$ should be treated cautiously because of Type I errors associated with multiple tests. Taxa are listed in descending order of frequency across the whole data set.

Sphagnum was shown to increase in ungrazed plots while cover remained low in grazed plots (Wahren et al. 2001). Recent government decisions to implement short-term livestock grazing in the Victorian Alpine National Park seems to be at odds with this large and growing body of evidence.

Trends in shrub frequency are more complex than those observed for *Sphagnum* and bare ground, with some species apparently becoming more frequent soon after release from grazing, and gradually declining thereafter. Consistent with this interpretation, our observations of recent shrub decline follow on from documented historical increases in hygrophilous shrubs in alpine and subalpine bogs during the 1960s, soon after the removal of grazing livestock (Wimbush & Costin 1979a). We therefore interpret the long-term decline in shrub cover as gradual senescence after mass recruitment during the immediate post-grazing phase, while the increase in *Sphagnum* reflects the slow colonization of sites after grazing.

Floristic changes in the bogs since the 1960s are largely independent of the elevational gradient. Thus, if
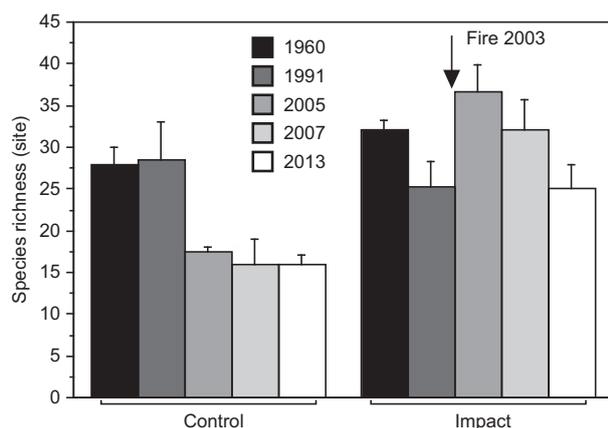
Fig. 4. Mean (±SE) species richness of vascular plants and bryophytes in control (unburned) sites vs sites impacted by fire in 2003.

vegetation dynamics were related to climate change, the data do not support a simple response model, whereby species simply migrate to higher elevations. It is possible that some of the observed changes, such as the increasing frequency of *Sphagnum*, could be partially attributed to atmospheric changes over the past 50 yr, such as increased atmospheric CO_2 concentration (Earth Systems Research Laboratory 2013) and/or reduced evapotranspiration (Berry & Roderick 2002). Increased water-use efficiency may result in less transpiration and increased retention of moisture, favouring *Sphagnum* growth and limiting shrub growth. However, the observed trends both in *Sphagnum* and woody species were opposite to those attributed to atmospheric changes in northern hemisphere bogs (Turetsky et al. 2012).

Response to fire event

Our results suggest that some *Sphagnum* bogs demonstrate a degree of resilience, as exemplified by the fire of 2003, which consumed the surface layer of vegetation but rarely burned more than 10 cm into the surface *Sphagnum* and peat in the sites sampled. Sites that were exposed to low-severity fire underwent a cyclical pattern of change that began to converge with the pre-fire compositional state a decade after the event. In contrast, a site exposed to higher-severity fire underwent a directional change that after 10 yr has not yet shown evidence of convergence. Fire is rarely considered an ecological factor in alpine regions of the world (Körner 2003), although it is clear from the paleoecological record that fire has been present in the Australian Alps during the Holocene (Martin 1986). Fire has been recorded in the post-grazing era as being infrequent, but extensive and sometimes of high intensity (Kirkpatrick & Dickinson 1984; Bridle et al. 2001; Wahren et al. 2001; Kirkpatrick et al. 2002, 2010; Walsh &

McDougall 2004; Williams et al. 2006, 2008). Although some elements of Australian alpine and subalpine communities are thought to be resilient to fire, other elements (e.g., coniferous heaths) are not (Kirkpatrick et al. 2010). In particular, continental *Sphagnum* bogs were thought not to be resilient because their regenerating organs and seed banks would be consumed by the combustion of dry *Sphagnum* and peat down to mineral soil (Good et al. 2010). Our results, however, suggest that *Sphagnum* bogs may be more resilient to fire than expected.

The immediate effects of fire on *Sphagnum* bogs are visually confronting with the consumption of the highly flammable woody component, the removal of emergent sedges and rushes and the collapse of *Sphagnum* hummocks where they were burned to mineral soil (Walsh & McDougall 2004). On most bog surfaces, however, patches of *Sphagnum* escaped the effects of fire because of the high moisture of the bog surface, and all burned bogs had live *Sphagnum* recorded at low frequencies 2 yr after fire. At the whole bog scale, *Sphagnum* frequency recovered to around 85% of pre-fire values within a decade. Where combustion of *Sphagnum* is complete, recovery times could be considerably longer (Whinam & Kirkpatrick 1995; Good et al. 2010) and, indeed, recovery appears slower at one of our sites (Boggy Plain) where fire severity was higher.

The initial colonization of other mosses after fire was very pronounced, but this component decreased to pre-fire frequency a decade after fire, as did some of the forbs (e.g., *Asperula gunnii*), which initially colonized bare ground. As expected, the graminoids resprouted rapidly and attained their pre-fire frequencies within 2 yr of fire. In contrast, shallow-rooted forbs that grow on hummocks, such as *Astelia alpina*, were killed by fire and were very slow to recolonize burned bogs.

The woody component of bog vegetation shows a mixed response to fire, with some species resprouting (*Baeckea gunniana*, *Epacris paludosa*) while others were killed (*Richea continentis*, *Epacris glacialis*, *Oxylobium ellipticum*). Resprouting shrubs rapidly regained their cover within a few years after fire, but none of those species had returned to pre-fire frequencies within 10 yr after the fire. The species killed by fire exhibited contrasting responses: *O. ellipticum* recovered rapidly to, and remained at its, pre-fire frequency; *R. continentis* recovered slowly and was still increasing 10 yr after fire; while *E. glacialis* appeared to have reached a peak frequency and had begun to decline by 10 yr after the fire. These patterns may reflect differences in longevity of standing plants among the three species. Seed germination occurred on mineral soil and on burned *Sphagnum*.

Overall, the bogs exhibited resilience to the fire of 2003, as strongly directional patterns of vegetation change were not detected and two of the less severely burned bogs had

begun to return to floristic composition of their pre-burn state a decade after fire. The floristic composition of the bogs is approaching the pre-burn composition because the community has been assembled from a combination of bud banks from underground rhizomes and rootstocks, together with a persistent fire-cued seed bank. The relative fire resilience of Australian bogs contrasts with most boreal systems, where severe fires are thought to favour *Sphagnum* colonization (Tuittila et al. 2007). Alternatively, in cases where the hydrology has been disrupted by fire, fen vegetation has replaced bogs (Turetsky et al. 2012) and this may have occurred in our region where bogs were more severely burned than those we sampled (Good et al. 2010).

Conclusion

The *Sphagnum* bogs of the subalpine and alpine regions of continental Australia show a degree of stability over the past 50 yr, but also some directional change. This suggests considerable community resilience to both grazing and fire, although the recovery time for grazing appears much longer than that for fire. The progressive increase in the frequency of *Sphagnum*, reduction in the cover of bare ground and changes in shrub frequency all suggest a prolonged recovery from the grazing era, although more subtle effects of changing atmospheric conditions cannot be discounted. These *Sphagnum* communities contain hygrophilous woody species that have fire-responsive attributes linked to regeneration (Walsh & McDougall 2004). These adaptive responses are linked to large-scale periodic fire events driven by the highly variable regional climate. Hence, these systems appear to be resilient to infrequent pulsed disturbances because community structure and composition is re-established. To better understand the potential resilience of these communities, the persistence and regeneration niches of herbaceous species associated with bogs need to be studied.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Comparative analysis of GNMDS in two and three dimensions.

Figure S1. Ordination (DCA) of undisturbed sites with montane bog (Wilsons Valley) included.

Figure S2. Ordination (DCA) of undisturbed subalpine and alpine sites.

Figure S3. Ordination (DCA) of burned sites in 2003 and adjacent unburned sites.

Figure S4. Ordination (GNMDS) of undisturbed subalpine and alpine sites with thin-plate splines representing elevation and time.

Figure S5. Ordination (GNMDS) of burned sites in 2003 and adjacent unburned sites with thin-plate splines representing elevation and time.