Recreational trails as a source of negative impacts on the persistence of keystone species and facilitation

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Abstract

Hiking trails, which are among the most common forms of infrastructure created for nature-based tourism, can alter key ecological processes. Trails can damage plants that facilitate the establishment and growth of other species leading to changes in community and functional composition. This can be a particular concern in harsh alpine ecosystems where plant communities are often dominated by one or two keystone species that provide shelter to a suite of beneficiary species. We analysed how a hiking trail affects interspecific facilitation by a dominant trampling-sensitive nurse shrub in the highest National Park in Australia. First we assessed the effects of the trail on the abundance, size and density of the nurse shrub at different distances from the trail. We then compared species richness and composition between areas in, and out, of the nurse shrub's canopy at different distances from the trail. To better understand why some species may benefit from facilitation and any effects of the trail on the quality of facilitation we compared functional composition between quadrats using community trait weighted means calculated by combining plant composition with species functional traits (canopy height, leaf area, % dry weight of leaves and specific leaf area). The abundance, size and density of nurse shrubs was lower on the trail edges than further away, particularly on the leeward edge, where there was more bare ground and less shrub cover. There were differences in species richness, cover, composition and functional composition in and outside the nurse shrub canopy. The shrubs appeared to facilitate species with more competitive, but less stress tolerant traits (e.g. taller plants with leaves that were larger, had high specific leaf area and low dry matter content). However, despite reductions in nurse shrubs near the trail, where they do exist, they appear to provide the same 'quality' of facilitation as nurse shrubs further away. However, longer-term effects may be occurring as the loss of nurse shrubs alters the wind profile of the ridgeline and therefore succession. The use of a steel mesh walkway along the trail may facilitate the regeneration of nurse shrubs and other plants that require protection from wind. Our results highlight the importance of diversifying recreation ecology research to assess how trails affect important ecological processes.

Keywords: inter-specific interactions, ecological processes, ecosystem functioning, Windswept Feldmark, tourism and recreation.

1. Introduction

Nature-based tourism and recreation are increasingly popular globally, allowing people to experience and engage with the natural environment through activities such as hiking (Kuenzi and McNeely, 2008; Buckley, 2009; Balmford et al., 2009; Newsome et al., 2013; Eagles, 2014). Nature-based tourism, however, can have a range of negative impacts on plant species and communities with impacts from hiking trails among the most well documented (Marion and Leung, 2001; Cole, 2004; Hill and Pickering, 2006; Monz et al., 2010; Marion et al., 2011; Fenu et al., 2013; Ballantyne et al., 2014a). Hiking trails are among the most common types of infrastructure provided for nature-based tourism with over 120,000km of trails in the USA alone (US National Park Service, 2014).

Impacts of hiking trails on vegetation and soils has been a major focus of research (Cole, 2004) and includes direct local effects from trampling, compaction and erosion on the track surface and edges, as well indirect local effects resulting from both direct damage as well as the actual presence of the trail (e.g. changing vegetation and soil composition, nutrient levels and structure) (Godefroid and Koedam, 2004; Hill and Pickering, 2006; Malmivaara-Lämsä et al., 2008; Wimpey and Marion, 2010; Nemec et al., 2011). As a result vegetation and soils adjacent to trails often differs from that further away with more ruderal species and often reduced soil quality close to the trail (Bhuju and Osawa, 1998; Dickens et al., 2005; Malmivaara-Lämsä et al., 2008). Due to the often high spatial proliferation of trails, these effects can replicate across entire landscapes causing cumulative damage (Wimpey and Marion, 2011; Ballantyne et al., 2014b).

Changes in plant composition caused by trails reflect not only the responses of individual species to disturbance but also how trails alter ecological processes. This can include inter-specific interactions among plants such as competition and facilitation. Facilitation occurs when one keystone species (a 'nurse') increases the abundance of another (a 'beneficiary') by modifying biotic and abiotic factors in ways that enhance survival (Holmgren et al., 1997; Nuñez et al., 1999; Stachowicz, 2001; Callaway, 2007). This interaction is more common where conditions are particularly severe such as in very dry, hot or cold environments (Callaway, 2007). On exposed alpine summits and slopes, for instance, facilitation occurs where plants growing in the canopy or lee of larger dominant nurse plants are protected from wind abrasion, desiccation and heat loss (Nuñez et al. 1999; Cavieres et al. 2002; Flores and Jurado 2003; Akhalkatsi et al. 2006; Reid et al. 2010).

Facilitation often results in increased alpha (within habitat) and beta (between habitats) diversity (Whittaker 1972; Krebs, 1994) in plant communities (Butterfield et al. 2013; Cavieres et al., 2014; Ballantyne and Pickering, 2015) when plants that benefit from the nurse canopy include species that

otherwise would be restricted to less extreme environments (Schöb et al., 2012; Schöb et al., 2013). For example, facilitation can allow species with functional traits better adapted for competition (larger, softer leaves and tall growth forms) to grow in these environments in addition to those with traits better adapted to high stress conditions (shorter with tough, small leaves) (Cornelissen et al. 2003; Schöb et al. 2012; Schöb et al., 2013; Ballantyne and Pickering, 2015).

Although there is increasing interest in ecological processes such as facilitation in alpine environments and its effect on diversity, there is limited research assessing how tourism infrastructure, such as trails affects these processes (McDougall and Wright, 2004; Ballantyne et al., 2014a). With hiking trails common in many alpine protected areas globally, there is a strong capacity for trails to be a management issue for the conservation of these communities worldwide. For example, in the highest protected area in Australia, Kosciuszko National Park, there are numerous hiking trails and the alpine zone is visited by over 70,000 people during the snow-free period (Pickering and Buckley, 2003). A popular hiking trail along the highest ridgeline in the park dissects a specialist plant community limited to these exposed conditions: the Windswept Feldmark. The community is of high conservation value providing habitat for rare and endemic plant species (Costin et al., 2000; NSW National Parks and Wildlife Service, 2001; McDougall and Wright, 2004).

The dominant shrub in the community, *Epacris gunnii* (Epacridaceae), appears to facilitate the establishment of other plants on the ridgeline, with numerous dwarf herbs and graminoids growing in its canopy (Edwards, 1977; McDougall and Wright, 2004; Ballantyne and Pickering, 2015). Unfortunately, the sclerophyllous traits, prostrate brittle form and slow growth of *E. gunnii* make it particularly sensitive to damage and slow to recover (Costin et al., 2000; McDougall and Wright, 2004; Ballantyne et al., 2014a). Therefore damage to this nurse shrub from the trail could be interrupting ecological processes within the community by reducing the amount or quality of the facilitative habitat it provides to other plants, resulting in altered community composition and ultimately reduced alpha and beta diversity.

To contribute to our understanding of the ways in which trails affect important ecological processes, this study assesses how the hiking trail affects facilitation in the Windswept Feldmark. To do this we: 1) assessed if there was a reduction in the number, size and density of *E. gunnii* shrubs on the edges of the trail compared to further away, 2) determined if any changes in the abundance and distribution of *E. gunnii* associated with the trail resulted in changes in species richness, cover of important species and both composition and functional composition in the shrub canopy compared to outside, 3) analysed if any such changes were due to changes in the cover of *E. gunnii* shrubs

and/or changes in the quality of the 'facilitative habitat' it provides, and 4) calculated the overall area of Windswept Feldmark directly and indirectly affected by the trail.

2. Methods

2.1 Site and Species Description

Windswept Feldmark is restricted to a tundra-like environment along the Main Range ridgeline of the Snowy Mountains in Kosciuszko National Park; part of the Australian Alps bioregion (Costin et al., 2000) (Figure 1). Due to very strong westerly winds along the ridgeline snow cover is limited, including in winter, with average annual temperatures of just 3°C and regular dips below 0 ^{o}C (Barrow et al., 1968). The strong winds and effect of frost heave also result in thin alpine humus soil and metasediments that are mostly covered by loose sedimentary shales. As a result, vegetative cover and diversity within the community is limited, with *E. gunnii* occupying around 54% of the community and only 19-23 species found here in total (Costin et al., 2000; Ballantyne and Pickering, 2015). Much of the remaining area consists of bare, rocky ground and small scattered herbs, cushions and graminoids (Costin et al., 2000; McDougall and Wright, 2004; Ballantyne et al., 2014a).

Epacris gunnii shrubs initially establish on the leeward, wind-protected side of rocks. As the shrubs grow they in turn alter the wind profile creating their own lee, and at regularly-spaced intervals, a zone of reduced wind action that allows other shrubs to establish (Costin et al., 2000). The winds also rip vegetation off the windward side of *E. gunnii* shrubs and deposit it as litter on the leeward side of the shrub where it breaks down and provides organic matter for the layering of new growth, thus allowing individual shrubs to grow downwind (Barrow et al., 1968). This whole process results in a slow pattern of succession (ca. 1 cm per year) of *E. gunnii* shrubs from west (windward) to east (leeward) across the ridgeline. As a result, there is a distinct wave-form of regularly-spaced ca. 1 m^2 *E. gunnii* shrubs and bare ground in the community (Barrow et al., 1968; McDougall and Wright, 2004). In response to this, community composition appears to be segregated in the community into distinct assemblages associated with either the shrubs or bare ground areas (Ballantyne and Pickering, 2015). In and around the protective canopy of *E. gunnii* there are taller herbs and graminoids with larger leaves, while in exposed areas of bare shale between the shrubs, plants tend to be more stress-tolerant with short canopies and small leaves (Ballantyne and Pickering, 2015).

A 2.5 km section of trail used by around 4,000 hikers a year (Growcock, 2006) intersects several areas of Windswept Feldmark between Mt Kosciuszko (2,228 m) and Mt Townsend (2,209 m). The trail is unhardened and degraded in places with bare ground, eroded gullies and multiple braids

(McDougall and Wright, 2004) and is almost completely devoid of vegetation (Edwards, 1977; Ballantyne et al., 2014a). Essentially it acts as a linear barrier dissecting the community in two (Figure 1).

2.2 Vegetation sampling

We assessed the impact of the trail on facilitation by *E. gunnii* in a 9,300m^2 area of Windswept Feldmark intersected by the trail between Mt Carruthers (36°24'28.63" S, 148°17'29.34" E) and Mt Northcote (36°25'50.44" S, 148°16'50.84" E) at about 2,060 m a.s.l. and ca. 4 km from Mt Kosciuszko, mainland Australia's highest mountain (Figure 1). We concentrated our sampling on one area of the community intersected by the trail to minimise damage as much as possible, and within this one area we tried, whenever possible, to avoid trampling any plants when sampling off trail. Although the sampling, therefore, did not cover all the areas of Feldmark, previous work indicates that the composition and diversity of the community is similar along the ridgeline (McDougall and Wright, 2004; Ballantyne et al., 2014a).

To assess whether the number, size and/or density of *E. gunnii* shrubs was affected by the trail, and if any effect(s) differed between the windward and leeward side of the trail, we measured all shrubs in four 1 m x 50 m belt transects running parallel to the trail. One transect was immediately adjacent to the trail and the other 5 m from the trail with two transects on the windward and two on the leeward side (Figure 2). These four transects were named 'zones': windward 5 m, windward 1 m, leeward 1 m and leeward 5 m. Each zone was then subdivided into five 10 m^2 sections, and the number and average size of all *E. gunnii* shrubs with centroids in each section recorded (Figure 2). The size (area in m^2) of each shrub was measured using the maximum width (distance parallel to the spread of the *E. gunnii*, perpendicular to the wind direction) and maximum length (distance from the central to the leading edge, parallel with wind direction) of the shrub with the size then calculated using the formula πab where a = radius of the width and b = radius of the length, thus generating a series of ellipses (Badano et al., 2005). The density of shrubs was also calculated per 10 m^2 section as the total area of nurse shrubs (m^2) divided by the section (10 m^2) multiplied by 5 for the total area surveyed per zone.

To determine if any changes in the abundance and distribution of *E. gunnii* affected other species in the community, we assessed species richness, cover and composition in 20 randomly-selected 30 x 50 cm paired quadrats (10 quadrats in *E. gunnii* canopies and 10 quadrats in adjacent areas outside *E. gunnii* canopies) in each of the four zones giving 80 quadrats in total. The quadrat size was selected based on preliminary field work suggesting it was the optimum compromise between

ensuring a moderate-sized quadrat while minimising edge effects when sampling within the shrub canopy. For extremely small shrubs (i.e. < 1,200 cm^2, e.g. smaller than quadrat) we only recorded richness, cover and composition data for the central portion of the shrub avoiding a roughly 5cm buffer around the perimeter of the shrub. The cover of all vascular plants, lichens and mosses, bare ground, litter and rock were visually estimated as percentages in each quadrat. Vascular plant taxonomy was according to PlantNET (2013), while lichens and mosses were identified using McVean (1969).

We also assessed the effect of the trail on functional composition across the four zones as well as between the two 'habitats' (in and outside of *E. gunnii* nurse shrub canopies). To do this we measured four functional traits that relate to important ecological processes: canopy height, percentage leaf dry matter content, leaf area and specific leaf area (Cornelissen et al. 2003). Canopy height influences a species' competitive ability, with taller species potentially outcompeting smaller ones (Westoby et al., 2002). Percentage leaf dry matter content is a good determinant of the stress tolerance of plant species with high leaf dry matter content associated with more stressed environments (Cornelissen et al., 2003; Schöb et al., 2012). Leaf area is often positively correlated with productivity such that a species with small leaves is more characteristic of a harsher environment where energy expenditure is focused on stress tolerance. Finally, Specific Leaf Area (SLA), which is correlated with percentage leaf dry matter content, is related to a species' potential growth. Low SLA values represent slow growth rates, high expenditure in stress resistance and increased leaf longevity (Corenlissen et al., 2003; Schöb et al., 2012).

To measure these traits, ten randomly-selected fully mature individual plants for each species were selected from the Feldmark using the protocols of Cornelissen et al. (2003). The species *Hypogymnia lugubris*, *Polytrichum juniperum* and *Lycopodium fastigiatum* were not collected, however, as the protocols do not account for non-vascular plants while *Kelleria dieffenbachii* was not sampled due to its rarity. Canopy height (mm) was measured as the distance between the topmost photosynthetic leaves and the ground, averaging values per species. Following this, ten fully expanded leaves were taken from 10 individuals per species and kept cool and moist in a sealed bag and transported to a laboratory. Here, leaf fresh weights (mg) were calculated and averaged for each species. We then dried the leaves of each species for 3 hours in an 80°C oven and re-weighed them to record dry weights. Leaf dry matter content was then calculated as the ratio of oven-dry mass to its fresh weight (%) (Pickering and Venn, 2013). Leaf areas (mm^2) were measured prior to drying using the Leaf Area Measurement program (available from the University of Sheffield) and then converted to SLA values as the ratio of area to oven dry mass (mm^2 mg^{-1}).
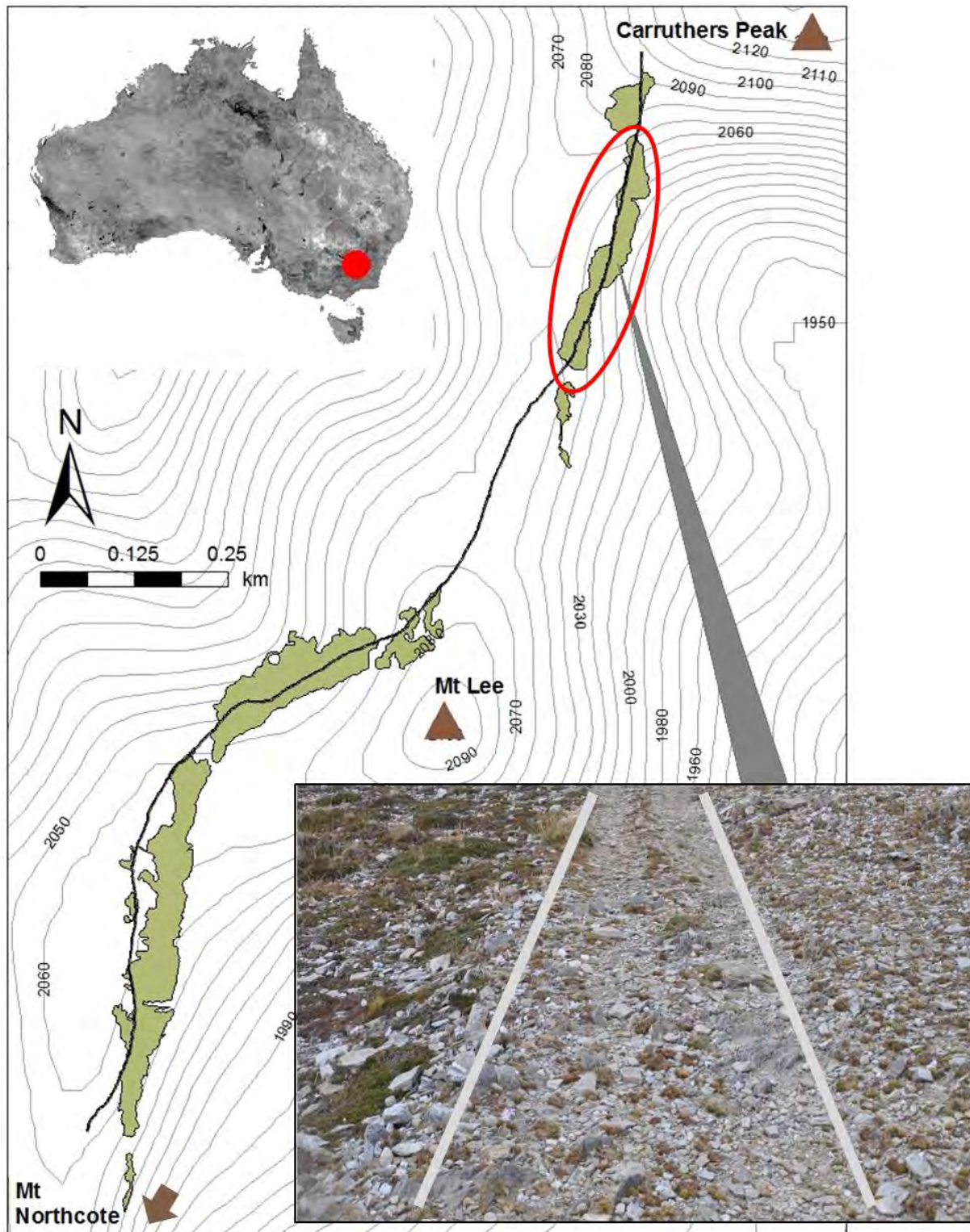
Figure 1: Location of Windswept Feldmark in Kosciuszko National Park, Australia. The map shows the total 5.4 ha of Windswept Feldmark intersected by 2.5 km of hiking trail with a red circle indicating the study area (9,300m^2). The enlarged photograph shows the effect of the trail (between lines) on *Epacris gunnii* with a greater abundance and density of shrubs on the windward (left) side of the trail (Photo: Mark Ballantyne). Contour lines and inset satellite map of Australia from Geoscience Australia: Topo 250K Series 3 package and 1 second SRTM derived 3-second smoothed digital elevation model (DEM-5) 1.0 2010. Map created in ArcMap Version 10.1.
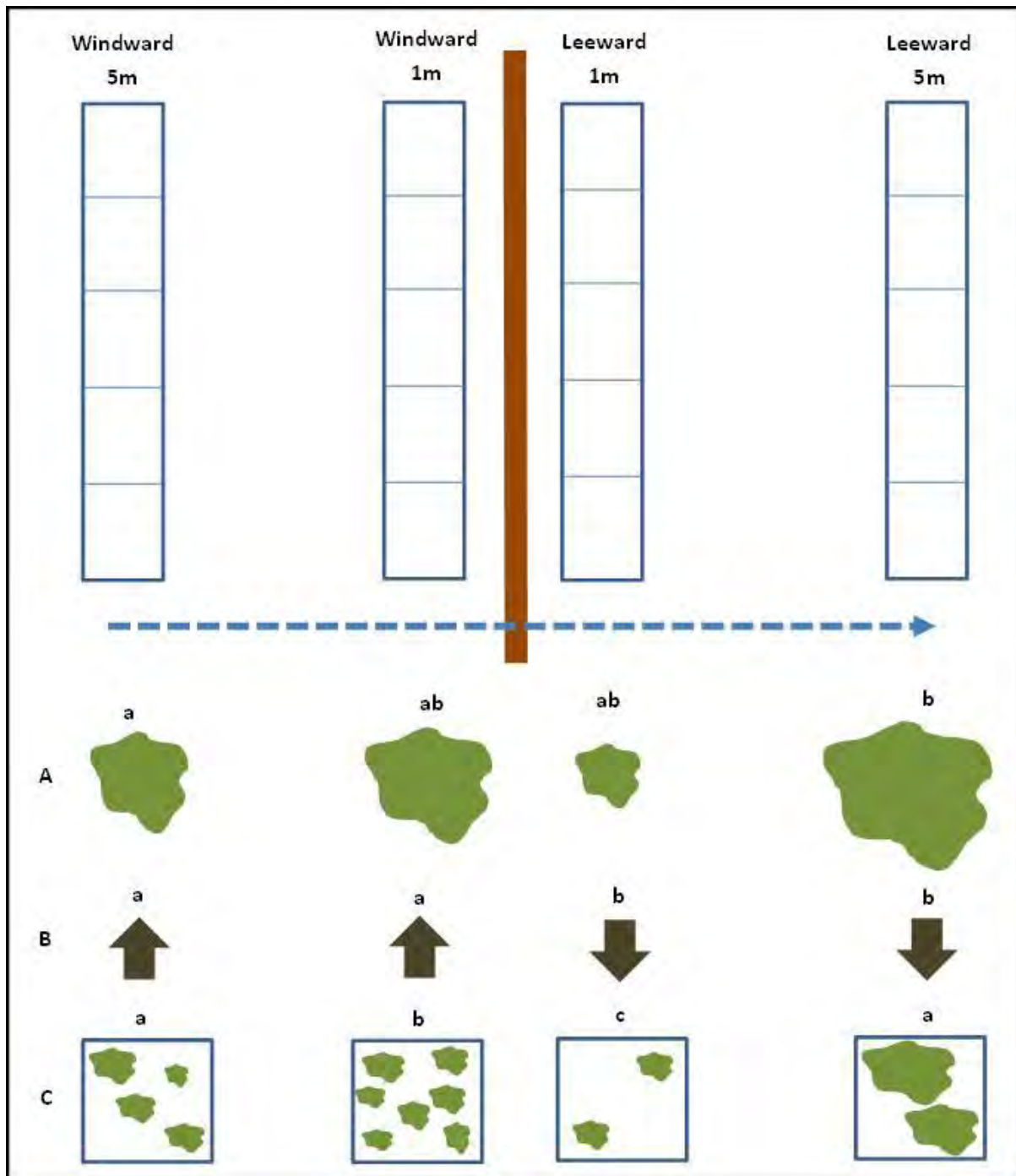
Figure 2: Figure showing the layout of the sampling quadrats and how the size of *E. gunnii* plants (A), the number of plants/10 m^2 (B) and the density of plants (m^2)/10 m^2 (C) change in relation to the wind direction (W to E – signified by blue hashed arrow) and trail (thick brown line). Individual *E. gunnii* plants on the windward side 5 m from the trail were smaller, but there was moderate density of shrubs, while 1m from the windward side of the trail shrub density was higher, but individual shrubs were smaller. On the leeward side at 1 m, shrub density was lowest with small shrubs, whilst 5 m on the leeward side, shrub density was similar to windward 5 m, but individual shrubs were larger but less numerous. There are generally more individual shrubs on the windward side than leeward. Post-hoc significant differences given in lower case letters above graphics. The drawing is not to scale.

2.3 Mapping

To calculate how much Windswept Feldmark has been affected by the trail, we mapped the total 5.4 ha of Windswept Feldmark that occurs along a 2.5 km section of the ridgeline that is traversed by the trail (Figure 1). Mapping was done using a Trimble Juno ST handheld GPS with an average accuracy of between 1-10 m and a sampling interval of 1 m. Polygons of each area were mapped using the geographic co-ordinate system WGS_1984. The hiking trail was mapped as a polyline and trail widths were measured as individual points at systematic intervals of 25 m following a randomised start (Marion and Leung, 2001; Manning *et al.*, 2006; Olive and Marion, 2009). Both Windswept Feldmark areas and the trail were saved as shapefile layers in ArcMap Version 10.1. Trail widths were averaged and a buffer of the average width was applied to the patch layer. The area of this buffer was then erased from the patch layer to show how much Windswept Feldmark had been lost to the trail. All layers were saved and converted to a projected co-ordinate system (GDA_1994_Geoscience_Australia_Lambert) and then to an accurate datum within this projection (GDA_1994_MGA_Zone_56) with both area (ha) and length (m) calculated for the fragmented areas.

To calculate the effect of the trail on the total area of the two habitats, the average densities of *E. gunnii* shrubs recorded at different distances from the trail were extrapolated to the total area of Windswept Feldmark dissected by the trail. Specifically the average density of shrubs along the trail edges was extrapolated for the length of the trail edge, while average shrub densities from the 5 m zones were used to calculate the area of shrub and non-shrub habitat for the rest of the Windswept Feldmark.

2.4 Data Analyses

To analyse the effect of the trail on the abundance and distribution of *E. gunnii*, differences in the number, size (log10 transformed due to non-normality of data) and density of shrubs between the four zones were compared using One-way Analysis of Variance (ANOVA) and Tukey HSD Post-hoc tests in the statistics package SPSS Version 21 with sections nested within zones.

Using the quadrat data, we then assessed the effect of the trail on species richness, cover and composition of other species among the four zones and between habitats (in or outside *E. gunnii* canopy). A linear mixed model was used to analyse the effect of zone, habitat and zone*habitat with habitat pairs nested within zone, for both species richness (excluding *E. gunnii*) and the combined cover of all non-*E. gunnii* species (arcsine square-root transformed data). This was done using zone, habitat and zone*habitat as fixed factors and nested 'habitat' pairs within zones as a random factor.

This model was created to account for possible covariance between habitat pairs within zones. We also used simple Chi-square goodness of fit tests for other species with an abundance > 10 in the two habitats and a minimum expected frequency > 5 to determine associations with each of the habitats.

For plant composition, a nested zone within 'habitat' Two-way Analysis of Similarity (ANOSIM) was run in PRIMER Version 6 (PRIMER, 2015) using a Bray-Curtis dissimilarity matrix on square-root transformed data with the cover of rock, bare ground, litter and *E. gunnii* removed, similarly to that of Bishop *et al*. (2010). Multi-dimensional scaling (MDS) plots portrayed the clustering of samples in 2-dimensional space while the ANOSIM revealed significance in distributions. This method is widely recommended as it (i) graphically portrays patterns in communities by clustering and ordinating samples allowing for the identification of influential processes, and (ii) the non-parametric permutation-based ANOSIM, similar to that of an ANOVA, but not requiring a normalised data distribution, provides statistics on differences between groups of samples (Clarke, 1993).

For those species with sufficient data, a series of One-way ANCOVAs with shrub area as covariate were computed for species known or found to be either strongly associated with *E. gunnii* (*Hypogymnia lugubris*, *Poa fawcettiae*, *Ranunculus acrophilus*, *Senecio pectinatus* var. *major* and *Scleranthus singuliflorus*) or with areas outside its canopy (*Ewartia nubigena*, *Colobanthus pulvinatus*, *Agrostis muelleriana* and *Veronica densifolia*) (Ballantyne and Pickering, 2015). Cover data for all species was arcsine square-root transformed.

To measure differences in functional composition across the four zones and between the two habitats, we used similar analyses. The functional traits data were converted into community trait-weighted means for each of the 80 quadrats (Lepš et al., 2006) by taking the value for each trait per species and adjusting it by each species' relative cover (e.g. proportion of total vegetation cover other than *E. gunnii* in that quadrat). A Two-way ANOSIM using normalised data (to standardise the trait data which is in different units) and a Euclidean distance dissimilarity matrix was calculated. An MDS plot was then used to graphically portray differences among quadrats and an ANOSIM used to calculate significant differences in community trait-weighted means with all data log-transformed.

3. Results

There were 21 taxa recorded in the community including seven herbs, four shrubs, two cushions, five graminoids and one species each of a clubmoss, moss and lichen (Table 1). Twenty taxa were recorded in the *E. gunnii* nurse shrub canopy, while 17 were recorded outside its canopy. Sixteen taxa were recorded at least once in both habitats.

3.1 Is there a reduction in the number, size and density of *E. gunnii* shrubs adjacent to the trail?

Distance to the trail affected the number, size and density of *E. gunnii* nurse shrubs adjacent to it (Table 2, Figure 2). Feldmark adjacent to the trail had on average 3.8 fewer nurse shrubs per 10 m^2, 22% smaller shrubs and 10% fewer shrubs compared to 5 m away (Table 2, Figure 2). The effect of the trail was greater on the leeward edge of the trail with fewer nurse shrubs (7 ± 2.5 plants) than on the windward edge (27.4 ± 5.9) (Table 3). The density of *E. gunnii* was also lower on the leeward edge (0.7 ± 0.3 m^2 per 10 m^2) than on the windward edge (4.7 ± 0.5 m^2 per 10 m^2) of the trail despite the plants being similar in size (Table 3, Figure 2).

The effect of the wind on *E. gunnii* was also apparent further away from the edge of the trail. At 5m from the trail on the windward side, nurse shrubs were smaller and more numerous (1.1 ± 1.4 m^2; 30.4 ± 8.4 plants) than 5 m away from the leeward side of the trail, where nurse shrubs were less common but larger/older (2.4 ± 2.7 m^2; 11.6 ± 5.0 plants) (Table 3, Figure 2).

3.2 Did changes in the abundance and distribution of *E. gunnii* affect species richness, cover and both species and functional composition?

Vegetation within *E. gunnii* canopies differed to that outside their canopies, but these differences did not vary with how far the quadrat was from the trail (Table 2) despite the clear differences in *E. gunnii* number, size and density between the four zones (Table 3). For example there was higher species richness (6.9 ± 2.0 vs. 6.6 ± 1.8) and cover of other species (22.2 ± 10.9% vs. 15.3 ± 9.2%) in *E. gunnii* canopies compared to quadrats out of *E. gunnii* (Table 2), but no trail effect. Species more frequently found in *E. gunnii* canopies than outside included the small herb *Scleranthus singuliflorus* (9 quadrats in, 0 out), the graminoid *Poa fawcettiae* (p < 0.001) and the lichen *Hypogymnia lugubris* (p < 0.001). Species more common outside *E. gunnii* canopies included the cushion plants *Ewartia nubigena* (0 quadrats in, 8 out) and *Colobanthus parviflorus* (p = 0.008), the graminoid *Agrostis muelleriana* (p = 0.004) and the sub-shrub *Veronica densifolia* (p = 0.036) (Table 1).

Table 1: Differences in the frequency (number of quadrats) and average cover (%) of species between quadrats in and out of *E. gunnii* canopy across four zones in relation to the trail and dominant wind direction (W5 = windward 5 m, W1 = windward 1 m, L1 = leeward 1 m and L5 = leeward 5 m). Growth forms according to Costin et al., 2000, species names according to PlantNET and family names according to Angiosperm Phylogeny Group III System. Abbreviations for Growth Form (GF): H – herb, C – cushion, S – shrub, G – graminoid, Cl – clubmoss, L – lichen, M – moss. # indicates a species endemic to the community. Species in bold represent a significant difference in observed frequency between quadrats in and out of *E. gunnii* (based on Chi-square test, $p < 0.05$).

| | | | Frequency among quadrats | | | | | | | | Average % cover per quadrat | | | | | | | |
| | | | In | | | | Out | | | | In | | | | Out | | | |
GF	Species Name	Family	W5	W1	L1	L5	W5	W1	L1	L5	W5	W1	L1	L5	W5	W1	L1	L5
H	*Oreomyrrhis eriopoda*	Apiaceae	1								0.05							
C	*Ewartia nubigena*	Asteraceae					3	2		3					1.05	0.35		2.13
H	*Leptorhynchos squamatus*	Asteraceae	8	4	5	2	5	1	4	2	3.75	1.6	0.88	2.35	1.09	0.01	0.85	0.38
H	*Leucochrysum alpinum*	Asteraceae	4	7	5	4	2	5	3	2	0.6	5.22	0.93	1.75	0.6	2.17	1.51	1.85
H	*Senecio pectinatus* var. *major*	Asteraceae	6	5	6	4		4	5	2	1.85	1.2	0.72	0.73		1.38	0.9	0.3
C	**Colobanthus pulvinatus**	**Caryophyllaceae**	**5**	**3**	**6**	**4**	**10**	**9**	**10**	**9**	0.23	0.2	0.67	0.31	2.25	2.35	1.7	2.26
H	*Scleranthus singuliflorus*	Caryophyllaceae	3	1	1	4					0.39	0.7	0.01	2.4				
S	*Epacris gunnii*	Epacridaceae	10	10	10	10	1	3	2	1	75.5	70.2	77.1	80.7	0.05	0.6	0.31	0.1
S	*Epacris petrophila*	Epacridaceae	2	1	1	1	1				2.15	0.2	1.7	1.3	0.1			
G	*Luzula australasica* ssp. *dura* #	Juncaceae	3	2	4	3	3	1	4	6	0.4	0.55	0.9	0.78	0.56	0.2	0.95	1.75
Cl	*Lycopodium fastigiatum*	Lycopodiaceae					1	1							0.3	0.02		
G	**Agrostis muelleriana**	**Poaceae**	**1**	**2**	**2**	**1**	**7**	**4**	**5**	**5**	0.02	0.1	0.03	1	0.63	0.4	0.72	0.5
G	**Poa fawcettiae**	**Poaceae**	**5**	**7**	**6**	**6**	**2**	**1**	**1**		0.57	1.7	1.78	1.35	0.02	0.04	0.1	
G	*Rytidosperma nudiflorum*	Poaceae	1			1					0.35			0.1				
G	*Trisetum spicatum* ssp. *australiense*	Poaceae	9	8	8	6	6	7	9	7	2.02	1.38	0.89	1.35	0.67	1.9	1.21	1.02
H	*Ranunculus acrophilus* #	Ranunculaceae	9	9	9	8	8	7	5	9	3.07	4.33	1.76	2.15	1.24	1.01	0.49	1.49
H	*Euphrasia collina* ssp. *lapidosa* #	Orobanchaceae	8	5	6	5	10	7	8	10	1.12	0.82	0.73	0.61	2.75	1.23	1.25	1.89
S	**Veronica densifolia**	**Plantaginaceae**	**4**	**3**	**5**	**6**	**8**	**6**	**9**	**10**	0.86	0.31	1.31	0.93	2.92	2.42	4.62	5.41
S	*Kelleria dieffenbachii*	Thymelaeaceae	1								0.02							
L	**Hypogymnia lugubris**	**Parmeliaceae**	**9**	**5**	**6**	**8**		**2**			9.55	4.95	2.9	6.8		0.12		
M	*Polytrichum juniperum*	Polytrichaceae				1	2	1	3	2				0.1	0.12	0.01	0.13	0.22

Table 2: Results of statistical tests comparing differences in *E. gunnii*, species richness, cover and abundance of selected species across the four zones in relation to the trail. Zone signifies the distance from, and side of, the trail (windward 5m, windward edge, leeward edge, leeward 5m) and habitat signifies whether found within the canopy of the nurse shrub *E. gunnii*, or outside of it in areas of exposed ground.

Dependent variable	Test	Independent variable(s)	F Statistic	p value
Is there a reduction in the number, size and density of *E. gunnii* shrubs adjacent to the trail?				
Number of *E. gunnii* per 10m^2 section	Nested One-way ANOVA	Zone	F = 19.585	**<0.001**
Density of *E. gunnii* per 10m^2 section	Nested One-way ANOVA	Zone	F = 51.636	**<0.001**
Average area of *E. gunnii*	One-way ANOVA	Zone	F = 5.260	**0.001**
Did changes to the abundance and distribution of *E. gunnii* affect species richness and cover?				
Species richness	Linear Mixed Model	Zone	F = 2.000	0.131
		Habitat	F = 9.949	**0.003**
		Zone * Habitat	F = 0.481	0.698
Total cover all non-*E. gunnii* species	Linear Mixed Model	Zone	F = 1.708	0.183
		Habitat	F = 11.705	**0.002**
		Zone* Habitat	F = 1.544	0.220
% cover of *Hypogymnia lugubris*	One-way ANCOVA	Zone	F = 2.256	0.099
		E. gunnii area (covariate)	F = 2.348	0.134
% cover of *Poa fawcettiae*	One-way ANCOVA	Zone	F = 0.796	0.504
		E. gunnii area (covariate)	F = 1.010	0.322
% cover of *Ranunculus acrophilus*	One-way ANCOVA	Zone	F = 2.527	0.073
		E. gunnii area (covariate)	F = 0.150	0.701
% cover of *Senecio pectinatus* var. *major*	One-way ANCOVA	Zone	F = 1.000	0.404
		E. gunnii area (covariate)	F = 0.002	0.961
% cover of *Scleranthus singuliflorus*	One-way ANCOVA	Zone	F = 0.429	0.734
		E. gunnii area (covariate)	F = 2.139	0.153
% cover of *Ewartia nubigena*	One-way ANCOVA	Zone	F = 1.064	0.309
% cover of *Colobanthus pulvinatus*	One-way ANCOVA	Zone	F = 0.451	0.718
% cover of *Agrostis muelleriana*	One-way ANCOVA	Zone	F = 0.268	0.848
% cover of *Veronica densifolia*	One-way ANCOVA	Zone	F = 1.056	0.380

Table 3: Average (± SD) abundance, size and density of *E. gunnii* shrubs across the four trail zones. Post-hoc values (Tukey HSD) in lettering (a, b, c) with significant differences indicated by different letters.

Epacris gunnii	Windward 5 m	Windward 1 m	Leeward 1 m	Leeward 5 m	F	P
Number/10 m^2	30.4 ± 8.4[a]	27.4 ± 5.9[a]	7 ± 2.5[b]	11.6 ± 5.0[b]	**19.585**	**<0.001**
Size (cm^2)/50 m^2	1091 ± 1392[a]	1720 ± 2253[ab]	969 ± 892[ab]	2347 ± 2690[b]	**5.260**	**0.001**
Density (m^2)/10 m^2	3.3 ± 0.6[a]	4.7 ± 0.5[b]	0.7 ± 0.3[c]	2.7 ± 0.6[a]	**51.636**	**<0.001**
Total plants/50 m^2	152	137	35	58		

Plant species composition differed between quadrats in and outside *E. gunnii* canopies (Figure 3, Two-Way ANOSIM, Habitat Global Rho = 0.51, p < 0.001, Stress = 0.23), but not by zone (Figure 3, Two-Way ANOSIM, Zone Global Rho = -0.396, p > 0.05). The same results occurred for functional composition, with a significant habitat effect (Figure 4, Two-Way ANOSIM, Habitat Global Rho = 0.18, p < 0.001, Stress = 0.1) but no effect of zone (Figure 4, Two-Way ANOSIM, Zone Global Rho = 0.02, p > 0.05). Functional composition within *E. gunnii* canopies consisted of plants with taller canopies (27.7 ± 4.2 mm vs. 24.5 ± 3.6 mm; F = 9.512, p < 0.001), larger leaves (54.5 ± 23.2 mm^2 vs. 28.6 ± 15.5 mm^2; F = 31.174, p < 0.001), lower dry matter content (29.1 ± 9.4 % vs. 36.8 ± 4.2 %; F = 26.758, p < 0.001) and higher specific leaf area (15.2 ± 6.4 vs. 9.5 ± 4.1; F = 19.075, p < 0.001) than plants outside the canopy (see Supplementary Table 1 for average trait values).

3.3 How much Windswept Feldmark has been affected by the trail?

There was 5.4 ha of Windswept Feldmark consisting of 10 separate areas along the ridgeline, eight of which (5.2 ha; 96%) were dissected by the trail. As there was nearly no vegetation on the trail itself and the trail has an average width of 1.6 m, the trail resulted in the direct loss of 3,000m^2 (5.7%) of Windswept Feldmark. In addition, due to the reduced number and density of *E. gunnii* shrubs on the trail edge, particularly on the leeward edge (e.g. a 33.5% increase in the amount of bare ground habitat), the trail is likely to have damaged at least 6,000 m^2 (11.5%) of Windswept Feldmark.
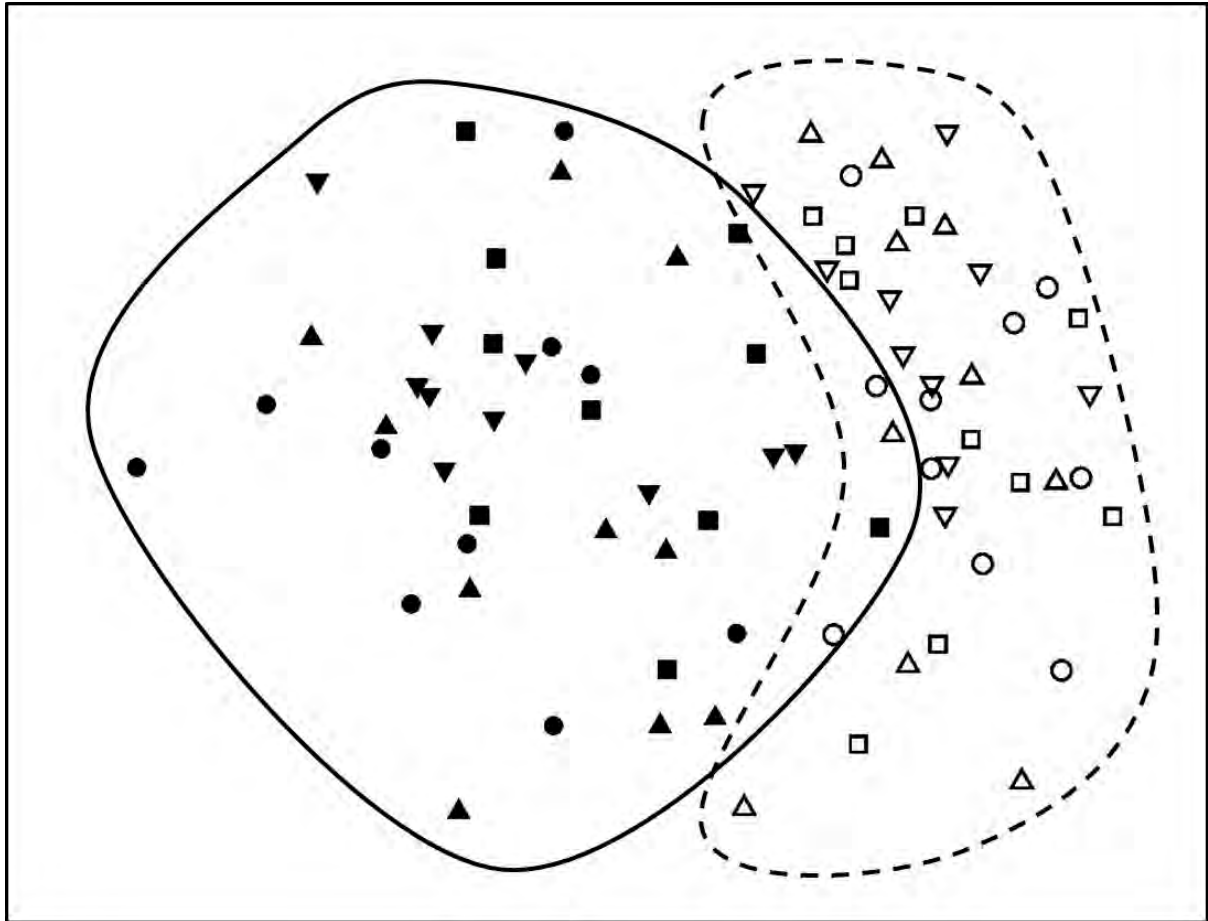
Figure 3: MDS plot showing a significant difference in percentage cover composition between quadrats in *E. gunnii* (black) canopy compared to outside *E. gunnii* (open). There was no significant effect of zone [windward 5 m (▲, △), windward 1 m (▼, ▽), leeward 1 m (■, □), leeward 5 m (●, ○)]. Clustering based on Bray-Curtis similarity. Stress = 0.23.
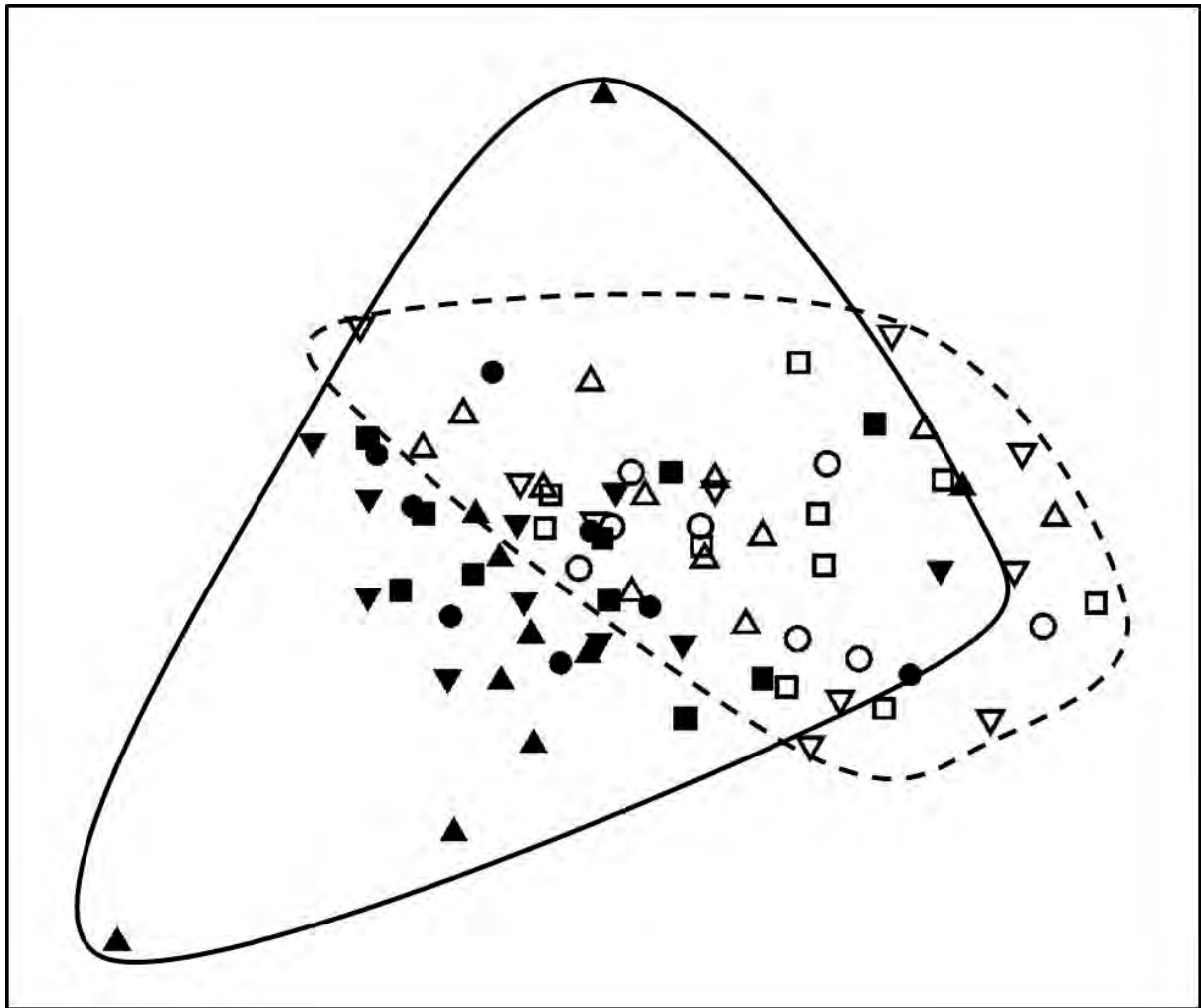
Figure 4: MDS plot showing a significant difference in functional composition between quadrats in *E. gunnii* canopy (black) compared to outside of *E. gunnii* (open). There was no significant effect of zone [windward 5 m (▲, △), windward 1 m (▼, ▽), leeward 1 m (■, □), leeward 5 m (●, ○)]. Clustering based on Bray-Curtis similarity. Stress = 0.1.

4. Discussion

This study shows how a hiking trail has reduced the abundance and density of a dominant alpine nurse shrub that is known to be an important keystone species. As a result, the amount of facilitative habitat it provides for other species in the Windswept Feldmark has been reduced, most prominently along the trail's leeward edge. The reduction in these nurse shrubs may be due, at least in part, to the sensitivity of these brittle plants to direct local impacts (e.g. trampling) along the trail. Sclerophyllous shrubs are often very sensitive to damage from trail use such as hiking and are slow to recover once trampled (Hill and Pickering, 2009; Bernhardt-Römermann et al., 2011; Pescott and Stewart, 2014). This poor tolerance can be due to a combination of their high investment in above-ground structures, the location of the meristems on external branches, slow-growth rates and low productivity (Bayfield, 1979; Liddle, 1997; Bernhardt-Römermann et al., 2011).

The larger reduction in the number of nurse shrubs on the leeward edge of the trail compared to the windward edge may be an indirect local effect. The loss of nurse shrubs on the trail surface would essentially remove any sheltering effect they may have provided for additional plants including *E. gunnii* on the leeward edge of the trail and so cause a gradual cumulative loss of nurse shrubs over time across the leeward side of the community. This theory has been corroborated in a parallel study assessing changes in the cover of shrubs and other key species over ten years in the Windswept Feldmark (Ballantyne et al., 2014a). Such results signify a potentially long-term impact of the trail on the successional regime that makes *E. gunnii* the keystone species in the Windswept Feldmark.

Changes in the abundance and density of this important nurse shrub due to direct and indirect impacts of the trail are important as the shrub is known to increase both alpha and beta diversity in the community (Ballantyne and Pickering, 2015). It does this by expanding the range of species that appear less tolerant of the high winds and cold conditions along the ridgeline, driving strong partitioning in community composition. Species that were more common, or in some cases, only found in *E. gunnii* canopies included comparatively taller herbs with larger, softer leaves and low dry matter content such as *S. pectinatus* var. *major* (endemic to the Australian Alps), *R. acrophilus* (endemic to Windswept Feldmark) and *S. singuliflorus* and the foliose lichen *H. lugubris* (Ballantyne and Pickering, 2015). These functional traits are typical of plants found in more productive, less stressed environments which have rapid growth, higher biomass and fecundity (Cornelissen et al. 2003).

Despite the strong facilitative interaction *E. gunnii* has with these species, and the impact the trail has on the shrub's abundance, there does not appear to have been a significant effect on the quality of facilitation provided by the shrub where it still exists. There was no difference in species richness, cover and composition among *E. gunnii* quadrats in relation to how far away the nurse shrub was from the trail. Instead, the management concern lies with a changing ratio of habitats; *E. gunnii* shrubs to bare ground area. As the amount of nurse shrub habitat decreases, bare ground increases (estimated at 33.5% increase), so favouring species with traits that appear to be better adapted to more stressful growing conditions, such as cushion plants *E. nubigena* and *C. pulvinatus* with characteristically smaller canopies and smaller, tougher leaves (Costin et al., 2000; McDougall and Wright, 2004). It is also important to note that competition within a community can rise if facilitative interactions become less dominant (Dormann and Brooker, 2002). Some species characteristic of bare ground, such as the grass *A. muelleriana*, have moderately competitive traits such as dense caespitose growth and deep roots (Costin et al., 2000) often forming relatively dense mats of vegetation with limited space for the establishment of other species. Unfortunately many of the plants which will likely decline as a result of such change in the facilitation-competition balance include species endemic to the community. In the future, there is likely to be marked compositional changes in this plant community due to the ongoing presence of the trail.

Declines in the abundance of dominant nurse plants and hence the amount of habitat they provide for other species have been documented in other plant communities due to a range of anthropogenic threats (Hastings and Turner, 1965; Turner et al., 1966; Ebenman and Jonsson, 2005; Rutherford and Powrie, 2010). For example, in the Succulent Karroo, South Africa, overgrazing from agriculture has reduced the density of the small succulent *Ruschia cradockensis* and hence the suite of perennial beneficiary species that depended on it for drought protection (Ebenman and Jonsson, 2005; Rutherford and Powrie, 2010). To our knowledge, ours is the first study to specifically analyse how recreational trails can contribute to the disruption of important ecological processes such as facilitation. Although beyond the scope of this study, additional research could tease apart the microclimatic differences that occur between nurse plant and exposed habitats and look at how trails physically alter these abiotic conditions, and hence resultant composition. Recreation ecology research needs to move towards assessing such functional impacts of trail infrastructure and trail-based activities, as the disruption of ecological processes will ultimately lead to changes in other facets of biodiversity such as composition and structure, and may become irreversible over time.

5. Management Implications

Given the popularity of nature-based tourism in alpine regions globally (Hall and Boyd, 2005; Newsome et al., 2013), and the prevalence of facilitation and facilitative growth forms in high altitude regions on almost every continent (Callaway, 2007; Aubert et al., 2014), trails are likely an important threat to the functioning of these communities. In popular mountain destinations such as the seven summits regions (which includes Mt. Kosciuszko and surrounds), nature-based tourism is an important source of income and so closure of trails is not feasible. Instead the use of alternative forms of trail infrastructure is encouraged such as raised walkways (Figure 5) (McDougall and Wright 2004). These types of walkways, constructed from resistant ungalvanised 'cut corrugated grip' steel mesh or, to a lesser extent, wooden slats, have already been used successfully in the Australian Alps (Hill and Pickering, 2006). These structures elevate trail use and therefore damage away from the substrate and vegetation. Where these walkways have been tested on a short section of the Windswept Feldmark, either constructed directly on the ground, or slightly raised (e.g. around 10 cm high), it appears to allow regeneration of plants in the gaps between the mesh therefore acting as nurse environment itself for some species normally restricted to nurse shrubs. The raised walkways have already had a direct conservation benefit causing increases in the abundance of some endemic species (author pers. obs.). Raised walkways should be further trialled and studied in other alpine regions to determine their use in providing alternative and more sustainable trail routes. As an immediate management recommendation however, it seems raised walkways made of steel mesh are a promising, durable way of minimising the impacts trails have on facilitation in alpine plant communities.

6. Conclusion

There is limited recreation ecology research assessing the effects of trails on ecological processes. In this study we found that a recreational trail appears to have reduced the amount of facilitative habitat provided by a dominant sclerophyllous nurse shrub resulting in changes to community and functional composition as nurse shrubs decline and bare ground increases. This effect could continue into the future and even worsen due to the added effect of the trail interrupting shrub succession from windward to leeward sides of the community. Further research assessing the indirect local impacts of trails on important ecological process such as facilitation should be conducted in other plant communities and ecosystems (including non-alpine) in addition to more commonly-measured direct local impacts such as trampling and erosion.

Acknowledgements

Figure 5: Example of a steel metal walkway constructed in 1998 as a trial to observe the effects of elevating recreational trampling. The walkway is constructed from ungalvanised 'cut corrugated grip' steel mesh and seems to facilitate the establishment of many Feldmark plants. (Photo: Mark Ballantyne).

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