

Research article

Using functional traits to assess the resistance of subalpine grassland to trampling by mountain biking and hiking



Catherine Marina Pickering*, Agustina Barros

Environmental Futures Research Institute, School of Environment, Griffith University, Gold Coast, Queensland, 4222, Australia

ARTICLE INFO

Article history:

Received 21 November 2014

Received in revised form

26 May 2015

Accepted 1 July 2015

Available online 9 September 2015

Keywords:

Functional composition

Impacts

Mountain biking

Recreation ecology

Australia

Walking

ABSTRACT

Functional traits reflect plant responses to disturbance, including from visitor impacts. The impacts of mountain biking and hiking on functional composition were compared using a common experimental protocol in a subalpine grassland in the Australian Alps. The overlapping cover of all species was recorded two weeks after different intensities of hiking (200 and 500 passes) and mountain biking (none, 25, 75, 200 and 500 passes). Species' functional trait data were combined with their relative cover to calculate community trait weighted means for plant height, leaf area, percentage leaf dry matter content and Specific Leaf Area (SLA). Species such as *Poa fawcettiae* with larger leaves and SLA but lower dry weight content of leaves were more resistant to use, with differences between bikers and hikers only apparent at the highest levels of use tested. This differs from some vegetation communities in Europe where plants with smaller leaves were more resistant to hiking. More research using functional traits may account for differences in species responses to trampling. Managers of conservation areas used for hiking and biking need to minimise off trail use by both user groups.

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1. Introduction

There is increasing interest in using functional traits to predict how plants respond to anthropogenic and natural disturbances (Suding et al., 2008; Laliberte et al., 2010; Pakeman, 2011). Plant functional traits refer to measurable phenotypic characteristics of individual species that influence plant performance and fitness through their effects on growth, reproduction and survival (Casanoves et al., 2011). The use of functional traits to calculate measures of functional composition, such as Community Trait Weighted Means, that quantify the dominant trait values of a community provides insights into the underlying ecological mechanisms driving changes in community assemblages (Diaz et al., 2004; Laliberte et al., 2010; Casanoves et al., 2011). They can also be used to compare the responses of taxonomically distinct floras across different regions (Díaz et al., 1999; Gaucherand and Lavorel, 2007).

Despite the increased use of functional traits to assess disturbance from agriculture and grazing (Díaz et al., 1999; Kahmen et al., 2002; Diaz et al., 2007), roads and logging (Tecco et al., 2010; Meers

et al., 2012) and other types of land use (Garnier et al., 2007; Laliberte et al., 2010; Mayfield et al., 2010), there appears to be only one study that has used functional traits to assess responses to human trampling (Bernhardt-Römermann et al., 2011). This study of 35 plant communities in Europe examined the resistance and resilience of vegetation to different intensities of trampling. It used a modification of the methodology developed by Cole and Bayfield (1993) in the United States where different intensities of trampling were applied to vegetation in a manipulative experimental randomized block design to assess the relative resistance (initial damage) and resilience (recovery time) of plant communities to trampling. The European study found that resistance depended on functional traits related to a history of intensive land use with trampling favouring plants with small leaves and a rosette growth form (Bernhardt-Römermann et al., 2011).

There are many others studies assessing the impacts of hiking using similar methods (Hill and Pickering, 2009; Pickering et al., 2010a). They often find that low and moderate levels of trampling result in reductions in vegetation height, vegetation cover, as well as changes in plant composition and species richness (Cole, 1995; Liddle, 1997; Yorks et al., 1997; Talora et al., 2007; Hill and Pickering, 2009; Törn et al., 2009; Pescott and Stewart, 2014). The resistance of vegetation varies among plant communities and species with the resistance of communities mainly determined by

* Corresponding author.

E-mail address: c.pickering@griffith.edu.au (C.M. Pickering).

the traits of the dominant species (Kuss, 1986; Liddle, 1997; Hill and Pickering, 2009). Communities dominated by grasses are often more resistant to trampling than those dominated by shrubs (Kuss, 1986; Liddle, 1997; Hill and Pickering, 2009). In some cases, the presence of horizontal and flexible stems in many grasses, for example, may make them better able to deal with trampling than the ridged stems of more upright shrubs (Kuss, 1986; Liddle, 1997).

The Cole and Bayfield (1993) methodology is useful when determining the potential for the creation of informal trails. These trails can be created by hikers when accessing sites that are not on formal trail networks (Olive and Marion, 2009; Barros et al., 2013; Ballantyne et al., 2014a). They can also be created by mountain bikers when seeking new challenges or “free riding opportunities” beyond official trails (Goefit and Alder, 2001; Newsome and Davies, 2009; Hardiman and Burgin, 2013). Informal trails are a problem in popular protected areas when they damage plant communities of high conservation value (Newsome et al., 2002; Leung et al., 2011; Barros et al., 2013; Ballantyne et al., 2014a).

Despite the potential for mountain biking to contribute to informal trail networks (Ballantyne et al., 2014a), there appears to be only two studies comparing mountain biking and hiking impacts using modifications of the Cole and Bayfield (1993) methodology (Pickering et al., 2010a). One was in a forb dominated understory in Canada (Thurston and Reader, 2001) and the other in subalpine grassland in the Australia Alps (Pickering et al., 2011). Both found that mountain biking caused similar impacts to hiking at low levels of use, but at higher levels of use mountain biking did more damage (Thurston and Reader, 2001; Pickering et al., 2011). In the forb dominated community, 500 passes by mountain bikers resulted in more exposed soil but no differences in vegetation cover (Thurston and Reader, 2001), while in a grassland it resulted in reduced cover of vegetation including herbs and more litter compared to 500 passes by hikers (Pickering et al., 2011).

To better understand the ecological processes driving the response of plant communities to these two types of disturbance, we reanalyse existing plant cover data from the subalpine grassland experiment in the Australian Alps (Pickering et al., 2011). These data were combined with new data on functional traits for species in the community to calculate functional composition using Community Trait Weighted Means (CTWM). We then assessed differences in CTWM among different levels of use and between mountain biking and hiking. Specifically we compared the impacts of the two activities on (1) vegetation cover and the cover of the dominant grass and most common herb and (2) CTWM for four functional traits (plant height, leaf area, Specific Leaf Area [SLA], and percentage leaf dry matter content) that are important in terms of competitive ability and responses to disturbance (Cornelissen et al., 2003; Diaz et al., 2007; Bernhardt-Römermann et al., 2011).

2. Methods

2.1. Study area

The study was conducted in the largest (6900 km²) and most popular (~3 million visits per year) National Park in the Australian Alps: Kosciuszko National Park (Fig. 1). Both hiking and mountain biking are popular in the subalpine areas of the Park in summer on a range of formal trails. Hikers are allowed to walk off formal trails but mountain bikers are not, although not all riders comply with these rules (Pickering et al., 2011). Many formal trails traverse areas of native grassland which is the most common plant community in the subalpine zone (1500–1850 m a.s.l.) in the Park where it occurs interspersed with snow gum woodlands (*Eucalyptus niphophila*) on alpine humus soils (Costin et al., 2000). Along these formal trails through the grassland, informal trails are found where hikers and

riders have moved off the formal hardened tracks damaging vegetation. The subalpine grassland is dominated by the large tussock grass *Poa fawcettiae* and contains a range of low growing small leaved shrubs including *Hovea montanus* and soft leaved sprawling herbs mainly *Asperula gunnii* (Costin et al., 2000; Pickering et al., 2011). This grassland appears to be relatively resistant to human trampling (Pickering and Growcock, 2009; Hill and Pickering, 2009), but takes a long time to recover once damaged (Pickering and Growcock, 2009).

2.2. Experimental design and sampling

The experiment was conducted close to a major ski resort in January (mid-summer) 2010 in dry conditions. This is when there is peak plant growth and peak use of the region for hiking and mountain biking (Pickering et al., 2011) (Fig. 1). The site selected (613,484 m E, 5,956,530 m N, 1604 m a.s.l.) was close to an existing track used for hiking and mountain bike riding, and was representative of unburnt subalpine grasslands. The climate for this area is cool temperate with mean maximum temperature of 13.5 °C, ranging from 5.4 °C in the middle of winter in July to 21.4 °C in January in the middle of summer. Mean minimum temperature is 1.8 °C and ranges from –3.7 °C in mid-winter to 7.3 °C in the middle of summer. Rainfall averages 1744 mm annually, with snow covering the site from 1 to 3 months per year.

A modification of the Cole and Bayfield methodology (1993) was used to compare the impacts of different intensities of mountain biking (none, 25, 75, 200 and 500 passes) and hiking (200 and 500 passes). A stratified block (transect) random design was used. First six parallel replicate transects 40 m long and 0.25 m wide were laid out across the site, with a 3.5 m gap between transects. Each transect was then subdivided into seven quadrats (0.25 m wide, 4 m long) separated by 2 m gaps, with the seven treatments randomly allocated to quadrats. Two weeks after riding/hiking, the overlapping cover of all plants in each quadrat was measured using point quadrats (120 points per quadrat), with each species touching a point recorded as a ‘hit’. The hit data was converted to an overlapping cover value by dividing the number of hits per species by 120, and then multiplying it by 100 to generate absolute cover values. The top cover of vegetation in untrampled quadrats was 98% (Pickering et al., 2011), and when absolute cover values for individual plants were combined they often summed to more than 100% because species cover overlapped resulting in multiple ‘hits’ per point (e.g. multiple species hit per point). Therefore, absolute cover values per species were converted to relative cover by calculating the proportion of all vegetation cover in each quadrat that each species accounted for.

2.3. Selection and measurement of functional traits

Data on the four functional traits: plant height, leaf area, SLA and percentage leaf dry matter content, were collected as part of a larger project assessing above ground functional trait data for alpine and subalpine plants in the Park (Pickering and Venn, 2013) using protocols from Cornelissen et al. (2003). Details of the sampling methods used to obtain the trait data is available in this report (Pickering and Venn, 2013) and in other papers arising from the project (Pickering et al., 2014; Venn et al., 2014; Ballantyne and Pickering, 2015).

The four traits provide important information about how the species may respond to trampling in terms of their competitive ability, capacity to deal with stress and resistance to damage, and some have previously been found to vary with trampling (Bernhardt-Römermann et al., 2011). Plant height reflects the competitive ability of plants, with taller plants often able to

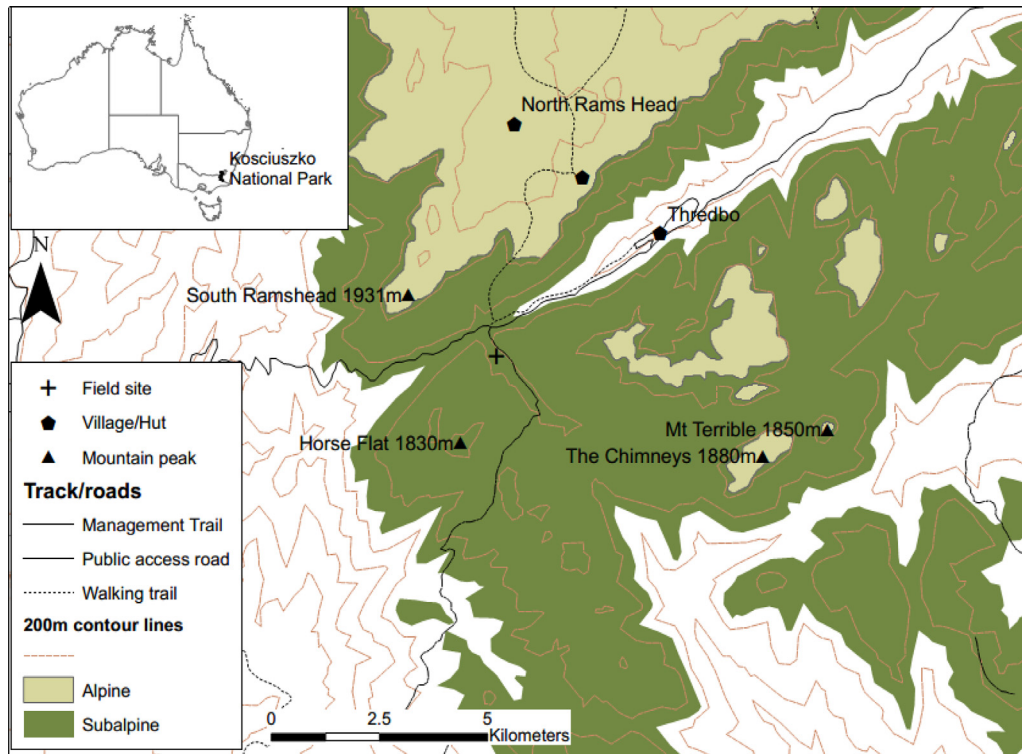


Fig. 1. Location of the site in subalpine grassland in Kosciuszko National Park, New South Wales, Australia.

outcompete shorter plants (Cornelissen et al., 2003) but also potentially more sensitive to trampling damage. Leaf area is also associated with the competitive ability of the plants with bigger leaves often associated with faster growth, while smaller leaves are beneficial in high stress conditions (Cornelissen et al., 2003). Leaf area is also associated with tolerance to disturbance with smaller leaves often more resistant to trampling by hikers (Bernhardt-Römermann et al., 2011). Specific Leaf Area, reflects the plants investment in growth, and hence reflects competitive ability as well as plant defence and leaf longevity. Plants with high SLA values tend to have faster growth rates, while low values are associated with leaf longevity and defence (Cornelissen et al., 2003). Plants with higher SLA are slightly more resilient to trampling by hikers (Bernhardt-Römermann et al., 2011). The fourth functional trait, percentage leaf dry matter content, represents the mean density of leaf tissue, with low values often associated with fast growth rates, while those with high values tend to have long-lived tough leaves (Cornelissen et al., 2003). Plants with lower leaf dry matter content have lower resilience to trampling by hikers (Bernhardt-Römermann et al., 2011).

2.4. Data analysis

Of the 33 taxa recorded across the 42 quadrats (Pickering et al., 2011), data on the four functional traits were available for 27 species, with the combined relative cover of the remaining six species less than 1.3%. The composition data for the 27 species were converted into relative cover values prior to calculating functional composition. The trait values per species were then combined with the relative cover values of each species to calculate CTWM for each trait per quadrat (Mason et al., 2003) using the software from Lepš and de Bello (2008).

The effects of mountain biking and hiking on functional composition as estimated by CTWM for plant height, leaf area, SLA and percentage leaf dry matter content, were analysed using a

series of One-Way Randomized Complete Block (RCB) ANOVAs in SPSS (version 22). The same type of analysis was conducted on the relative cover of the dominant tussock grass *P. fawcettiae* and the most common herb, the small leaved sprawling herb *A. gunnii*. Treatment was included as a fixed factor whilst replicate blocks (transects in this case) were analysed as a random variable with Tukey's post hoc tests used to compare treatments. The relative cover values were arcsine square root transformed prior to analysis to satisfy the assumptions of the ANOVA.

2.5. Ordinations

To assess variation in (1) species and (2) functional composition (CTWMs for the four traits), ordinations were performed in the multivariate statistical package Primer (Version 6). To assess variation in relative cover of species, dissimilarity matrices were calculated using Bray–Curtis dissimilarity measures on untransformed relative cover data. To assess variation in functional composition using the CTWM's, ordinations were performed on Euclidean dissimilarity matrices of normalised values.

Non-metric multidimensional scaling (n-MDS, Axes 1 and 2) was then used to graphically describe in two dimensions variation in species and functional composition among the seven treatments. To determine if there were significant differences in species and functional composition among treatments, One-way Analyses of Similarities (ANOSIM) were performed. This is a non-parametric permutation procedure applied to the rank dissimilarity matrix that is analogous to ANOVAs; except that it is distribution free (Clarke, 1993).

3. Results

Trampling by hikers and mountain bikers resulted in reductions in the total vegetation cover ($F = 12.992$, $p < 0.001$), in the absolute cover of the dominant grass *P. fawcettiae* ($F = 2.847$, $p = 0.027$) and

Table 1
Mean (± 1 SE) absolute and relative cover and average values for the functional traits of the three most common species in control quadrats and quadrats receiving 500 passes by mountain bikers (500b) or hikers (500h) in a subalpine grassland. GF = growth form, LF = life form, SLA = Specific Leaf Area, %LDMC = percentage leaf dry matter content, G = grass, H = herb, S = shrub, Hm = hemicryptophyte, Ch = chamaephyte.

| Species | GF | LF | Absolute cover | | | Relative cover | | | Height (mm) | Leaf area (mm ²) | SLA (mm ² mg ⁻¹) | %LDMC |
|------------------------|----|-----|----------------|------------|-------------|----------------|------------|------------|-------------|------------------------------|---|-------|
| | | | Control | 500h | 500b | Control | 500h | 500b | | | | |
| <i>Poa fawcettiae</i> | G | Hm. | 95 \pm 2 | 80 \pm 4 | 77 \pm 7 | 55 \pm 0.2 | 73 \pm 1 | 83 \pm 4 | 159 | 366 | 61 | 11 |
| <i>Asperula gunnii</i> | H | Ch. | 34 \pm 6 | 9 \pm 2 | 5 \pm 1 | 19 \pm 3 | 8 \pm 2 | 5 \pm 1 | 43 | 4 | 22 | 59 |
| <i>Hovea montanus</i> | S | Ch. | 18 \pm 2 | 7 \pm 2 | 1 \pm 0.5 | 10 \pm 1 | 7 \pm 2 | 3 \pm 1 | 293 | 52 | 5 | 54 |

the absolute cover of the most common herb, *A. gunnii* ($F = 6.498$, $p < 0.001$).

The impact of trampling was greater for the herb *A. gunnii* than the grass *P. fawcettiae*. The absolute cover of *A. gunnii* was $34 \pm 6\%$ in control quadrats, but only $9 \pm 2\%$ in quadrats after 500 passes by hikers and only $5 \pm 1\%$ in quadrats after 500 passes by bikers. Although absolute cover values for *P. fawcettiae* also declined, the differences were not as great with absolute cover values of $95 \pm 2\%$ in control lanes, $80 \pm 4\%$ after 500 passes by hikers, and $77 \pm 7\%$ after 500 passes by bikers (Table 1). As a result, the relative cover of the grass actually increased after trampling as it accounted for more of the remaining vegetation (Tables 1 and 2, Fig. 2a). For instance, the relative cover of *P. fawcettiae* accounted for only 54% of all vegetation in the control quadrats but 83% of all vegetation after 500 passes by a mountain biker (Tables 2 and 3, Fig. 2a). In contrast, the relative cover of the herb *A. gunnii* was 19% in control quadrats but only 5% of the remaining vegetation after 500 passes by mountain bikers (Tables 2 and 3, Fig. 2b).

In part as a result of changes in the relative cover of these two common species, there were significant changes in functional composition as measured by CTWM between control quadrats and those trampled by mountain bikers or hikers (Tables 2 and 3). Of the four traits measured, the CTWM for SLA and percentage leaf dry matter content differed the most as a result of mountain biking and hiking (Table 3, Fig. 3c, d). The CTWM for leaf area was affected by mountain biking, but not hiking (Table 3, Fig. 3b), while the CTWM for plant height was not affected by either activity (Table 2, Fig. 3a).

With mountain biking, differences in the CTWM for percentage leaf dry matter content were apparent after 200 passes, while differences in CTWM for SLA and leaf area were only evident after 500 passes by a biker (Table 3, Fig. 3b, c, d). After trampling by hikers, differences in the CTWM for percentage leaf dry matter content were only apparent after 500 passes (Table 3, Fig. 3d). Differences in the CTWM for SLA were only evident after 200 passes by hikers (Table 3, Fig. 3c).

When the four CTWM were combined, significant differences were found between the controls and the quadrats trampled by

mountain bikers or hikers (Global Rho = 0.308, $p = 0.001$, Fig. 4a). The remaining vegetation in quadrats trampled by mountain bikers or hikers was dominated by plants with higher leaf areas and SLA, but lower percentage leaf dry matter content compared to the controls (Fig. 4a). Differences were apparent after 75 passes by mountain bikers and after 200 passes by hikers (Table 4).

Again, these differences in functional composition were driven by changes in species composition, reflecting the increase in the relative cover of *P. fawcettiae*, but decreases in the cover of the less

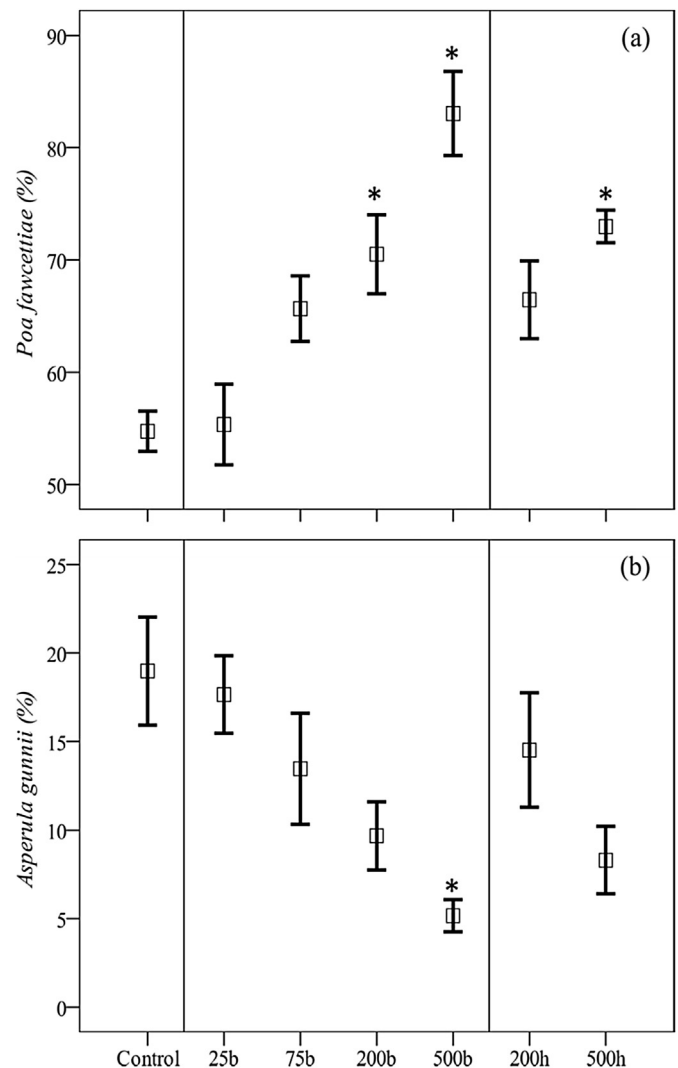


Fig. 2. Mean (\pm Standard Error) relative cover values for *Poa fawcettiae* (a) and *Asperula gunnii* (b) in control quadrats and quadrats subject to different intensities of trampling by mountain bikers (b) or hikers (h) in a subalpine grassland. * Significant differences between control quadrats and quadrats subject to different intensities of trampling are indicated with an asterisk.

Table 2
Results from One-Way ANOVAs comparing transects and treatments (different intensities of trampling by mountain bikers or hikers) for the relative cover of the dominant grass *Poa fawcettiae* and the most common herb, *Asperula gunnii* and functional composition (Community Trait Weighted Means) in a subalpine grassland. %LDMC = percentage leaf dry matter content. Values in bold are significant at $\alpha = 0.05$.

| | Treatment | | Transect | |
|--------------------------------|-----------|--------------|----------|-------|
| | F | P | F | P |
| Relative cover | | | | |
| <i>Poa fawcettiae</i> | 10.700 | <0.001 | 1.071 | 0.397 |
| <i>Asperula gunnii</i> | 3.903 | 0.006 | 0.634 | 0.675 |
| Community Trait Weighted Means | | | | |
| Plant height (mm) | 2.290 | 0.062 | 0.503 | 0.772 |
| Leaf area in mm ² | 4.896 | 0.001 | 0.752 | 0.591 |
| Specific Leaf Area | 7.136 | <0.001 | 1.220 | 0.325 |
| % LDMC | 7.574 | <0.001 | 0.484 | 0.786 |

Table 3

Significance (p) values from Tukey's post hoc tests from One-Way Randomized Blocks for the two dominant species and for community trait weighted means for leaf area, Specific Leaf Area (SLA) and percentage leaf dry matter content in a sub-alpine grassland for control quadrats, and quadrats subject to different intensities of trampling by mountain bikers (b) or hikers (h). Values in bold are significant at $\alpha = 0.05$.

| | Control | 25b | 75b | 200b | 500b | 200h | 500h |
|---|------------------|------------------|--------------|--------------|------------------|-------|--------------|
| <i>Asperula gunnii</i> (top diagonal) <i>Poa fawcettiae</i> (bottom diagonal) | | | | | | | |
| Control | | 1.000 | 0.811 | 0.206 | 0.010 | 0.905 | 0.110 |
| 25b | 1.000 | | 0.920 | 0.348 | 0.025 | 0.969 | 0.208 |
| 75b | 0.126 | 0.198 | | 0.923 | 0.208 | 1.000 | 0.783 |
| 200b | 0.009 | 0.019 | 0.912 | | 0.833 | 0.859 | 1.000 |
| 500b | <0.001 | <0.001 | 0.008 | 0.109 | | 0.138 | 0.939 |
| 200h | 0.087 | 0.144 | 1.000 | 0.996 | 0.012 | | 0.671 |
| 500h | 0.002 | 0.004 | 0.591 | 0.996 | 0.330 | 0.144 | |
| Leaf area (top diagonal), SLA (bottom diagonal) | | | | | | | |
| Control | | 0.999 | 0.408 | 0.198 | 0.001 | 0.195 | 0.129 |
| 25b | 1.000 | | 0.742 | 0.479 | 0.004 | 0.474 | 0.357 |
| 75b | 0.348 | 0.483 | | 0.999 | 0.107 | 0.999 | 0.993 |
| 200b | 0.075 | 0.132 | 0.980 | | 0.249 | 1.000 | 1.000 |
| 500b | <0.001 | <0.001 | 0.042 | 0.227 | | 0.413 | 0.533 |
| 200h | 0.005 | 0.012 | 0.489 | 0.927 | 0.832 | | 1.000 |
| 500h | 0.054 | 0.099 | 0.956 | 1.000 | 0.293 | 0.832 | |
| Percentage leaf dry matter content | | | | | | | |
| Control | | 0.991 | 0.107 | 0.019 | <0.001 | 0.078 | 0.020 |
| 25b | | | 0.452 | 0.135 | <0.001 | 0.369 | 0.141 |
| 75b | | | | 0.987 | 0.048 | 1.000 | 0.989 |
| 200b | | | | | 0.226 | 0.996 | 1.000 |
| 500b | | | | | | 0.068 | 0.216 |
| 200h | | | | | | | 0.997 |
| 500h | | | | | | | |

resistance species such as *A. gunnii* and the shrub *H. montanus* ($Rho = 0.286$, $p = 0.001$, Fig. 4b). The grass *P. fawcettiae* had large leaves, with low percentage leaf dry matter content, while the herb *A. gunnii* had small light-weight leaves and high percentage leaf dry matter content. The shrub *H. montanus* was taller with larger leaves

but it had high percentage leaf dry matter content and low SLA (Table 1).

When assessing the relative impacts of mountain biking and hiking for the same intensity of use (200 and 500 passes), significant differences were only found in functional composition when the four CTWM were combined and only after 500 passes. Vegetation after mountain bike riding was characterized by higher SLA and leaf areas compared to vegetation after hiking (Table 4, Fig. 4a). No significant differences between quadrats used by mountain bikers or hikers were found for the other parameters, including for the two dominant species, and the four CTWM separately (Tables 3 and 4, Fig. 4b).

4. Discussion

This study supports previous research that found that changes in functional composition are often driven by the response of dominant species in plant communities (Diaz and Cabido, 2001; Venn et al., 2011; Barros and Pickering, 2015). Following recreational use of the subalpine grassland, there was an increase in the relative cover of the dominant grass *P. fawcettiae* and a decrease in the relative cover of the common herb *A. gunnii*. These species have distinct functional traits, with *P. fawcettiae* characterized by much larger leaves (366 mm^2 vs 4 mm^2) and SLA (61 vs 22) and much lower percentage leaf dry matter content (11% vs 59%) than *A. gunnii*. As a result, changes in functional composition, including the increase in the dominance of plants with larger leaves and lower percentage leaf dry matter content after trampling, reflect the resistance of *P. fawcettiae* to disturbance by hikers and mountain bikers.

These results differ in part from those predicted based on previous research. As expected, the grassland was relatively resistant to trampling as are many other grasslands (Hill and Pickering, 2009), including in Europe (Bernhardt-Römmerman et al., 2011).

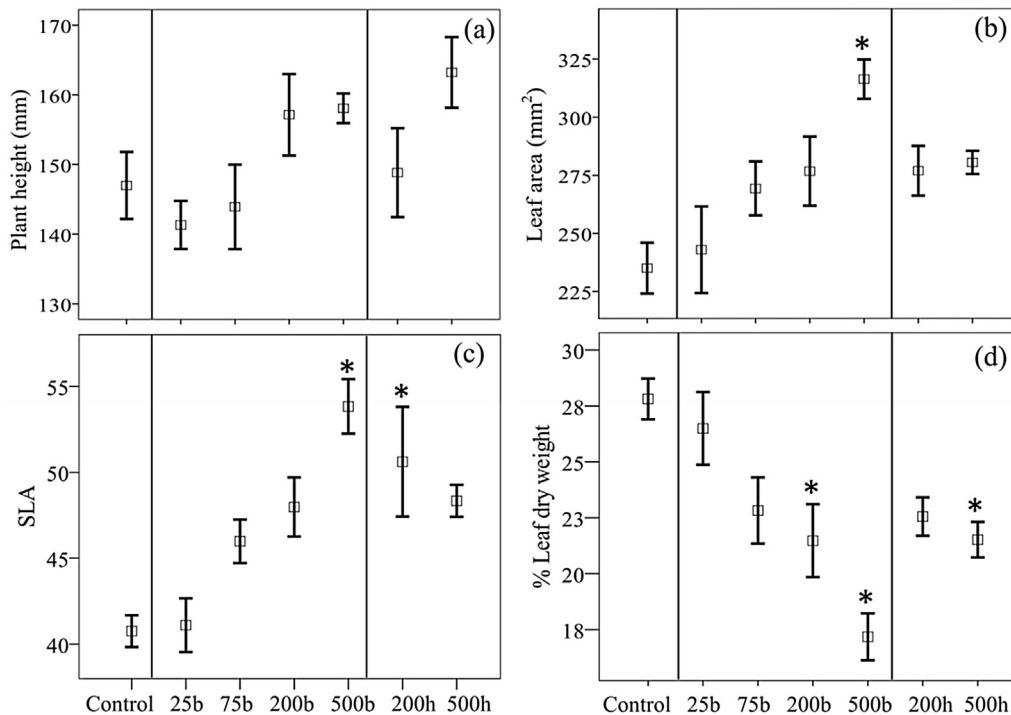


Fig. 3. Mean (\pm Standard Error) of the community trait weighted means (CTWMs) for plant height (a), leaf area, (b) Specific Leaf Area (c), and percentage leaf dry weight (d) for control quadrats, and quadrats subject to different intensities of trampling by mountain bikers (b) or hikers (h). *Significant differences between control quadrats and quadrats subject to different intensities of trampling are indicated with an asterisk.

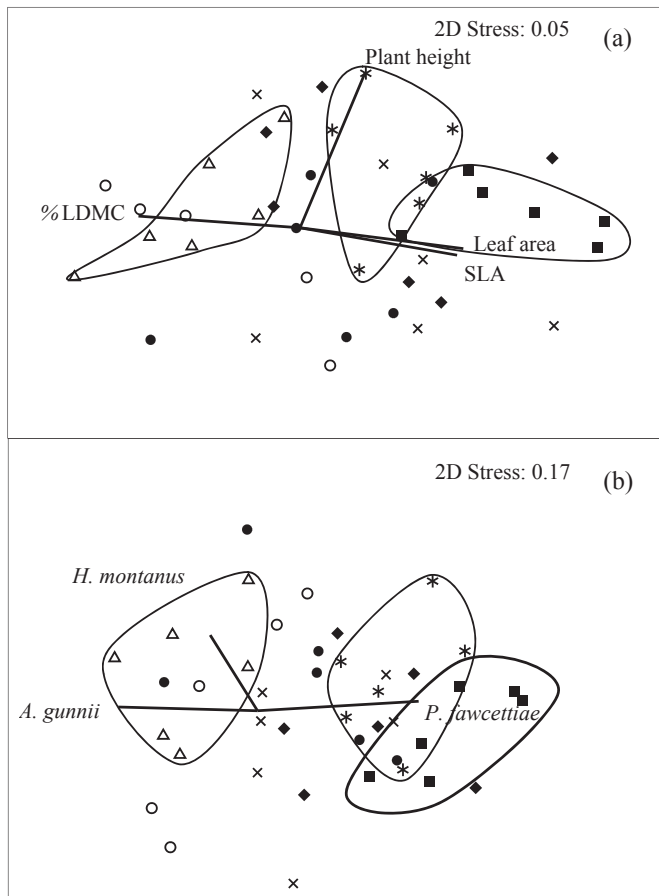


Fig. 4. Two dimensional n-MDS of (a) functional composition as measured by the CTWMs of four functional traits (plant height, Specific Leaf Area, leaf area and percentage leaf dry matter content (%LDMC) (normalised and Euclidean distances) and (b) the relative cover of species in control quadrats and quadrats subject to different intensities of trampling by mountain bikers and hikers in a subalpine grassland. Clear triangles = control, clear circles = 25 mountain bike passes, dark circle = 75 mountain bike passes, dark diamond = 200 mountain bike passes, dark square = 500 mountain bike passes, cross = 200 hiker passes, star = 500 hiker passes. * Control quadrats and quadrats with 500 passes by hikers or mountain bikers are highlighted.

As an Australian alpine plant community, however, it would have been expected to be less rather than more resistant to trampling. Several studies have found that alpine and subalpine plant communities are less resistant and resilient to trampling compared to lower altitude plant communities (Hill and Pickering, 2009; Ballantyne et al., 2014b). Also, low hemeroby (past human use)

Table 4

Significance (p) values from pairwise tests comparing different treatments for community trait weighted means (CTWM) (normalised and Euclidean distances) and for species composition (dissimilarity matrices) in control quadrats and quadrats subject to different intensities of trampling by mountain bikers (b) and hikers (h). For functional composition CTWM for plant height, Specific Leaf Area, leaf area and percentage leaf dry matter content were used.

| | CTWM (top diagonal) Species composition (bottom diagonal) | | | | | | |
|---------|---|--------------|--------------|--------------|--------------|--------------|--------------|
| | Control | 25b | 75b | 200b | 500b | 200h | 500h |
| Control | | 0.522 | 0.030 | 0.011 | 0.002 | 0.011 | 0.002 |
| 25b | 0.329 | | 0.188 | 0.071 | 0.002 | 0.063 | 0.002 |
| 75b | 0.024 | 0.358 | | 0.721 | 0.040 | 0.695 | 0.167 |
| 200b | 0.002 | 0.032 | 0.695 | | 0.069 | 0.727 | 0.385 |
| 500b | 0.002 | 0.002 | 0.004 | 0.171 | | 0.009 | 0.011 |
| 200h | 0.004 | 0.275 | 0.968 | 0.593 | 0.011 | | |
| 500h | 0.007 | 0.002 | 0.292 | 0.582 | 0.052 | 0.130 | |

was associated with lower levels of resistance to trampling in Europe (Bernhardt-Römmerman et al., 2011) and there has been very low hemeroby in the subalpine and alpine regions in Australia (Costin et al., 2000), particularly when compared with Europe. Finally, Australian plant communities evolved in the absence of trampling by hard hooved animals, and hence were not subject to a long period of selection for trampling resistant species compared to those in many parts of Europe, Africa and North America with native hard hooved grazing animals (Costin et al., 2000; Pickering and Hill, 2007).

When the responses of the two main species are assessed, they also only partly match predictions based on previous research. As predicted based on its growth form (Liddle, 1997; Bernhardt-Römmerman et al., 2011; Hill and Pickering, 2009), the dominant tussock grass *P. fawcettiae*, was more resistant to trampling than the herb *A. gunnii*. However, *P. fawcettiae* had moderate sized leaves, with larger leaves associated with lower levels of resistance to trampling in Europe (Bernhardt-Römmerman et al., 2011). It also had very high SLA, which was associated with higher levels of resilience in Europe (Bernhardt-Römmerman et al., 2011). The less resistant sprawling herb *A. gunnii* had regular leaf distributions along the stem matching the pattern in Europe where this type of leaf arrangement was associated with lower resistance to trampling than species with rosette leaf arrangements (Bernhardt-Römmerman et al., 2011). *A. Gunnii*, however, had very small leaves which were associated with higher resistance in Europe and moderate SLA values which were associated with lower resilience in Europe (Bernhardt-Römmerman et al., 2011). Clearly, studies for different plant communities comparing functional traits with resistance and resilience to trampling are required to tease out trends that apply more broadly, from those that are specific to particular locations.

This study and others have found that the response of vegetation to disturbance can differ depending on the vegetation parameter assessed as some parameters are more sensitive and respond to lower levels of use than others (Growcock, 2005; Pickering et al., 2011; Barros and Pickering, 2015). In the current study, for example, changes were found in functional (four CTWM in combination) and species composition after as few as 75 passes by mountain bikers and 200 passes by hikers. These results have important ecological implications because changes in functional composition and species composition may alter important ecosystem functions such as productivity, nutrient retention and resistance to plant invasions (Chapin et al., 2000; Smith and Knapp, 2003; Grman et al., 2010). These results highlight the importance of careful consideration when selecting vegetation parameters to assess disturbance because they influence the capacity of the study to detect important ecological changes.

When the relative impacts between mountain bikers and hikers were assessed for functional and species relative composition, mountain biking caused more damage than hiking at the highest level of use tested. Also, when compared to the controls, more vegetation parameters were affected by mountain bikers than hikers, including the CTWM for leaf area and the relative cover of the herb *A. gunnii*. This indicates that under controlled conditions, mountain biking and hiking at lower levels of use are likely to have similar impacts, but with increased use mountain biking may have greater impacts on vegetation, highlighting the importance of regulating this increasingly popular activity in protected areas.

This is particularly important as mountain biking contributes to the creation of informal trails, increasing disturbance (Newsome and Davies, 2009; Pickering et al., 2010a, b; Ballantyne et al., 2014a). In an endangered urban forest in Australia, for example, 6% of the forest was directly lost to informal trails, which were mainly created and used by mountain bikers (Ballantyne et al.,

2014a). Management recommendations for minimizing these types of impacts include information on mountain biker preferences to allow for the design of suitable trails with good signage and borders to avoid riders going off-trail. Other strategies include providing information and education to mountain bike users about the potential impacts of mountain biking, including posting information signs on trails, promoting trail etiquette guidelines such as minimum impact codes, and teaching trail ethics (Goft and Alder, 2001; IMBA, 2007).

5. Conclusions

This study contributes to our understanding of the impacts of popular recreational activities. We found that some of the patterns found by Bernhardt-Römermann et al., 2011 in Europe applied here, but not others. This suggests that trait responses to disturbance, including those from recreational use, may not always be generalizable. It is therefore important to increase the number of studies incorporating functional traits to better predict the response of vegetation to different types of recreational disturbance. Also, although it was not possible to assess vegetation recovery (resilience) in the present study (Pickering et al., 2011), it is important to incorporate resilience in further research as traits related to resistance may differ from those related to resilience (Bernhardt-Römermann et al., 2011).

Our reanalysis of the data from Pickering et al. (2011) emphasises that although mountain biking and hiking can have similar impacts at lower levels of use, mountain biking caused more damage than hiking at high use levels in this community. This again highlights the importance of regulating activities including mountain bike use in protected areas and other wilderness sites given its increased popularity worldwide and the potential to adversely affect plant communities including creating informal trails (Pickering et al., 2010a, b).

Acknowledgements

The research was supported by the New South Wales National Parks and Wildlife Service, the Australian Government and the partners in the National Climate Change Adaptation Research Facility (NCCARF) consortium. The views expressed herein are not necessarily the views of the Commonwealth of Australia, and the Commonwealth does not accept responsibility for any information or advice contained herein. We thank Sebastian Rossi, Rochelle Steven and Mark Ballantyne for their assistance in the field. We thank Dr Clare Morrison and three anonymous reviewers for their comments on the paper.

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