

CONTRIBUTED PAPER

Exotic herbivores dominate Australian high-elevation grasslands

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Funding information

This research was supported by an Australian Government Research Training Program (RTP) Scholarship, the NSW Government Saving our Species program, a Royal Zoological Society of NSW Paddy Pallin Science Grant, and the National Environmental Science Program; none of which were involved in the study design, data collection, analysis or interpretation, writing, or decision to publish.

Abstract

Invasive species are major drivers of ecosystem degradation globally. How invasive herbivore impacts differ from native herbivore impacts remains understudied. We examined the relationships between herbivore sign and vegetation height, foliage density, cover of forbs, weeds, bare ground, and soil compaction across environmental and herbivore activity gradients in the mainland Australian Alps. We detected native and exotic herbivore sign at 32.8% and 94.0% of sites, respectively. Total herbivore activity was primarily attributed to exotic herbivores and was associated with elevation and grassland type. Greater horse (exotic) activity was associated with lower vegetation height, lower foliage density, higher forb cover, and higher soil compaction. Greater rabbit and hare (exotic) activity was associated with lower vegetation height, lower foliage density, and a higher cover of bare ground. Greater total herbivore activity was associated with greater weed cover. Neither deer (exotic) nor kangaroo and wallaby (native) activity was related to response variables. We demonstrate that exotic herbivores dominate mammalian herbivory in these grasslands, which evolved without analogous hooved species. Given the restricted distribution and high endemism of these ecosystems, and associations between exotic herbivores and characteristics of degraded grasslands, we recommend landscape-scale exotic herbivore management, focusing on maintaining ground cover and vegetation structure.

KEYWORDS

grazing, herbaceous, invasive species, landscape elements, mountain, nonindigenous, non-native, plant–herbivore interactions, subalpine, vegetation structure

1 | INTRODUCTION

Invasive species are a major contributor to ecosystem degradation and their impacts are accelerating (Pyšek et al., 2020). Exotic herbivore numbers are increasing

globally, with livestock now 14 times more abundant than wildlife per unit mass (Gordon & Prins, 2019). While native herbivores may play key roles in maintaining biodiversity and ecosystem functions (Gordon & Prins, 2019), there is strong evidence that

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exotic herbivores have primarily detrimental effects when introduced to new areas (Barbar & Lambertucci, 2018; Nuñez et al., 2010). However, the differing and combined effects of exotic and native herbivores on ecosystems requires further research to better inform biodiversity conservation and effective herbivore management (Davis et al., 2016; Foster et al., 2014; Nuñez et al., 2010).

The impacts of herbivores on ecosystem characteristics, such as habitat structure, species assemblages, and soils, are numerous and nuanced, often influenced by climate and grazing history (Eldridge, Ding, & Travers, 2020; Sitters et al., 2020; Spake et al., 2020). For example, livestock grazing is used to maintain high-elevation grasslands for conservation and agriculture in some regions with a long history of herbivory (e.g., Komac et al., 2014; Pakeman et al., 2019). However, in ecosystems that evolved in the absence of grazing, native species can lack defensive traits, and ecosystems may be vulnerable to the impacts of exotic herbivores (Antonelli et al., 2011; Bailey & Schweitzer, 2010).

Native grasslands are among the most extensive and threatened ecosystems worldwide (Sala et al., 2013). The high-elevation grasslands of the Australian Alps Bioregion (hereafter the Alps) evolved with limited mammalian herbivory and are highly vulnerable to exotic herbivore impacts (Pickering et al., 2010). In this region, large native herbivores are mostly absent from elevations higher than 1650 meters above sea level (a.s.l.) (Green, 2016). In recent years, there have been marked increases in exotic herbivore populations in the Alps, and there is growing evidence of their negative impacts on native grassland ecosystems (Cairns, 2019; Claridge, 2016a; Eldridge, Travers, et al., 2020; Leigh et al., 1987; Matthews & Spooner, 2014; Schulz et al., 2019). However, investigations to date have typically considered a single target herbivore taxon, e.g. horse (Driscoll et al., 2019), deer (Davis et al., 2016), pig (Hone, 2002), hare (Green & Pickering, 2013), or rabbit (Leigh et al., 1987). Multispecies research is therefore required to determine the differing effects of co-occurring native and exotic herbivores in grasslands of the Alps.

Williams et al. (2014) identified exotic species as the most pressing threat to ecosystems in the Alps and recommended control of invasive species populations. Management of exotic herbivore populations can be guided by understanding herbivore habitat use and spatial variation in the effects of herbivory (Foster et al., 2014, 2021). However, the associations between herbivore activity and landscape elements have not been investigated in the Alps.

To address these key research gaps, we examined the following questions:

1. Are landscape elements associated with: (a) herbivore presence and (b) total herbivore activity?

Herbivore habitat use can be influenced by proximity to natural and constructed landscape elements, such as roads, ecotones, and waterbodies (Davies et al., 2020; Forsyth et al., 2009; Girard et al., 2013; Green et al., 2014; Matthews & Spooner, 2014). We therefore predict herbivore presence and total herbivore activity will be positively associated with proximity to woodland as a form of shelter, roads and tracks that may facilitate movement, water sources and low positions in the landscape, and negatively associated with higher elevations due to snow cover. We predict that each herbivore family will have a different probability of presence associated with each grassland type.

2. Is activity of exotic and native herbivores associated with a more simple vegetation structure, differences in vegetation composition, and higher soil compaction?

Both exotic (Eldridge, Ding, & Travers, 2020; Mutze et al., 2016) and native (Donaldson et al., 2018; Vandegehuchte et al., 2017) herbivores can modify vegetation structure by reducing biomass, lowering vegetation height, altering plant composition, and increasing soil compaction. The associations between horses, rabbits, and hares and reduced vegetation biomass in grasslands of the Alps are well documented (e.g., Eldridge et al., 2019; Leigh et al., 1987), whereas such associations have not been investigated for the majority of herbivores. As ecosystem responses to herbivory can depend on whether a herbivore is novel to an ecosystem (Antonelli et al., 2011; Bailey & Schweitzer, 2010; Spear & Chown, 2009), we hypothesize that exotic herbivore activity will be associated with lower vegetation height, lower foliage density, greater weed and forb cover, and greater soil compaction, while native herbivores will have neutral associations with these characteristics.

This research provides critical information on the effects of co-occurring native and exotic herbivore species in high-elevation grasslands that can be used to guide conservation and management in these areas of social and conservation importance.

2 | METHODS

2.1 | Study area

We conducted this study in the high-elevation grasslands of Kosciuszko National Park (Figure 1), a 690,660 ha United Nations Educational Scientific and Cultural Organization (UNESCO) Biosphere Reserve on Dätjilmamitang, Ngarigo, and Walgalu Country in south-eastern Australia (Doherty, Wright, & McDougall, 2015; UNESCO, 2019). Treeless vegetation communities total almost 90,000 ha of

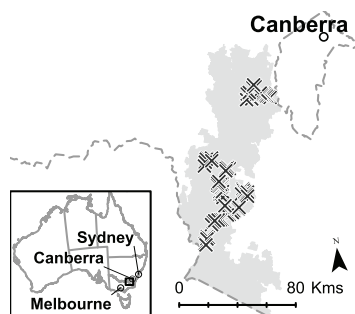


FIGURE 1 Study area, showing site locations (x) within Kosciuszko National Park (shaded gray). Dashed lines show jurisdiction boundaries. Inset shows location of study area within Australia

Kosciuszko National Park, supporting several endemic and threatened flora species (McDougall & Walsh, 2007). The landscape includes broad, flat valleys, and steep slopes with diverse climates (Doherty, Wright, & McDougall, 2015; McDougall & Walsh, 2007). Annual precipitation ranges from 770 mm in subalpine areas to 3100 mm in alpine areas (Green & Osborne, 2012). Areas above 1200 m a.s.l. receive regular winter snow, and above 1400 m a.s.l., the snow often persists for several months (McDougall et al., 2015).

Only two native mammalian herbivores regularly graze in grasslands above 1500 m a.s.l.; *Mastacomys fuscus* (Thomas 1882 broad-toothed rat) and *Vombatus ursinus* (Shaw 1800 common wombat) (Green & Osborne, 2012). However, the reduction in snow depth and duration in recent decades due to climate change has facilitated macropod and wombat range expansions (Green, 2016; Matthews & Spooner, 2014). Domestic livestock grazing by sheep and cattle occurred in Kosciuszko National Park from the early 1800s until 1967 (Good & Johnston, 2019). Horse, rabbit, and hare populations had established by the late 1800s (Dyring, 1990; Leigh et al., 1987). However, by the late 1900s, rabbits were resident throughout the year and associated with significant changes in vegetation in subalpine grasslands, while horses and hares remained infrequent occupants (Green & Osborne, 2012; Leigh et al., 1987). Deer were first observed in Kosciuszko National Park in the 1990s but not recorded in high-elevation grasslands until 2008 (T. Stubbs personal communication, January 2021). The New South Wales government has legislative responsibilities to manage invasive species in Kosciuszko National Park (Biosecurity Act, 2015; Kosciuszko Wild Horse Heritage Bill, 2018) and in 2020, undertook 23 Asset Protection and Containment programs to manage exotic herbivores (NSW National Parks and Wildlife Service unpublished data).

2.2 | Experimental design

We established 67 sites, each composed of one 50 m transect, to quantify herbivore presence and activity. We used a stratified random sampling design to select sites by overlaying a 15 km² grid onto a map of Kosciuszko National Park. We excluded grid cells containing less than 10% grassland (identified from satellite imagery) or less than 10% area above 1200 m a.s.l. We excluded areas beyond 300 m from a vehicle track, burnt in the preceding year, or subject to access restrictions or disturbance from infrastructure development. We randomly selected locations using a random number generator to provide distance measures from the northwest corner of each grid cell. If randomly located sites were not in grasslands, on a northern or minor slope, or separated by a minimum of 800 m, we moved the site to the nearest suitable location.

All sites, except two, were dominated by grass (>60% overlapping cover; predominantly *Poa* spp.). We categorized the grassland type at each site according to whether (i) a midstorey was present (“shrub grassland”), (ii) a midstorey was absent and there was greater than 15% nongrass graminoid cover (“graminoid grassland”), or (iii) a midstorey was absent and there was less than 15% nongrass graminoid cover (“tussock grassland”). Our sites were between 1220 and 1951 m elevation, and spanned gradients of landscape attributes (landscape position, distance from the nearest waterbody, distance from the nearest road or track, distance from the nearest woodland, latitude, and longitude) and herbivore activities (see Supporting Information S1, Figure S1.1–2).

2.3 | Data collection methods

We derived landscape elements from publicly available spatial datasets. These included elevation (m a.s.l.), landscape position (Topographic Wetness Index), distance from the nearest waterbody (m), distance from the nearest road or track (m), and distance from the nearest woodland (m) (see Supporting Information S2 for source information). We manually corrected a small number of distance measures where elements were present on-ground but not captured by the spatial classification.

Along each 50 m transect, we recorded the overlapping percent cover of nongrass graminoids, shrubs, forbs (native and exotic combined), grasses, weeds (exotic flora, all forms) and bare ground within circular plots of 2 m radius at 10 m intervals. We calculated the mean groundstorey vegetation height (cm) and foliage density (number of foliage intercepts in 10 cm bands of a structure pole up to 50 cm), excluding flowering parts, for each site. We measured soil compaction in kilopascals

(kPa) at 20 points along the transect using a handheld penetrometer according to manufacturer specifications (ST 315, Prospectors, Australia). As soil moisture can affect soil compaction, we classified the soil as wet or dry at the time of measurement according to whether soil stuck to our fingers upon touch.

We considered a “herbivore” to be any mammal with a diet consisting primarily of plant material. We used a relative index of evidence of herbivory, quantified by the frequency of herbivore sign at each site. We calculated herbivore activity by recording the presence or absence of herbivore sign, such as scats and diggings, within each half of a 2 m radius plot at 5 m intervals along the transect to give a frequency measure (out of 20) per sign type (Forsyth et al., 2007; Hone, 2002). We moved elevated vegetation but did not disturb the litter layer or dense ground cover to uncover sign. We classified sign types to family according to Triggs (1996) and Claridge (2016b), as species-level differences between sign cannot always be reliably distinguished. We classified worn paths, consumed vegetation, and pulled vegetation as “generic”. We did not include pellets with evidence of decay, nor did we convert indices to animal densities (Forsyth et al., 2007). We conducted all surveys within a 4-week period, in February and March 2020, to minimize seasonal and weather variability between sites. At this time, snow cover was absent and mammal populations were likely to be occupying their maximal elevational ranges within the bounds of their current distribution (Foster et al., 2021).

2.4 | Statistical analyses

When included as predictor variables in models, we log-transformed distance and sign frequency to minimize the effect of extreme values. Prior to log transformation, we added a small value to the zero values to avoid taking the logarithm of zero. We excluded two sites from soil compaction analyses and one site from height analyses due to missing data. We standardized data for continuous predictor variables (mean = 0, SD = 1).

We modeled the probability of presence of each herbivore family using a Bayesian Generalized Linear Model (BGLM) (Gelman et al., 2013) with a Bernoulli distribution and a logistic link function. We included the following predictor variables: elevation, log-distance to woodland, log-distance to a waterbody, log-distance to a road or track, landscape position, and grassland type. We selected the best-fitting model (see below for details) from all possible models (64 candidate models; Table S3.6a–d).

Using the same predictor variables, we examined associations between landscape elements and total herbivore activity (all herbivore families and generic sign

combined). We used a BGLM with a negative binomial distribution and a log link function. We selected the best-fitting model from all possible models (64 candidate models; Table S3.6e).

We quantified associations between vegetation and soil variables and observed herbivore sign at each site. We modeled each response variable (mean groundstorey vegetation height, foliage density, forb cover, weed cover, proportion of bare ground, and soil compaction) with total herbivore activity on the log scale as the predictor variable. We then modeled horse (Equidae), deer (Cervidae), rabbit and hare (Leporidae), and kangaroo and wallaby (Macropodidae) activities on the log scale as additive predictor variables. We selected the best-fitting model from all possible models (17 candidate models; Table S4.7). For each analysis, we fit BGLM using a Gamma distribution for continuous response variables (vegetation height, foliage density, soil compaction) and a Beta distribution for proportion response variables (forbs, weeds, bare ground).

Vegetation and soil variables may be associated with landscape elements; for example, plant height and weed species richness generally decline with increasing elevation (Green, 2016; McDougall & Walsh, 2007). We checked for Pearson and Spearman correlations between vegetation and soil variables and landscape elements using a two-sided *t*-test with the “cor.test” function in the R package “stats” (R Core Team, 2020). While herbivory has the potential to mask underlying associations, we found that weed cover and soil compaction were significantly (negatively) correlated with elevation (Figure S1.2 and Table S1.1).

We conducted all BGLM in R (R Core Team, 2020), using the package “brms” (Bürkner, 2017) and an uninformative prior distribution using a student-*t* distribution ($df = 7$, mean = 0, SD = 2.5). We used Markov chain Monte Carlo (MCMC) methods and the Gelman–Rubin convergence diagnostic (\hat{R}) based on four MCMC chains (Gelman & Rubin, 1992). For all models, \hat{R} was equal to 1.00. We used four Markov chains and ran them for 2000 iterations discarding the first 1000 as a burn-in with a thinning factor of 1. Where we performed model selection, we used the Widely Applicable Information Criterion (WAIC) (Vehtari et al., 2017a, 2017b) to select the best-fitting model from the candidate models. Where the difference in the WAIC of the best-fitting models was <1, we selected the most parsimonious model. We checked for multicollinearity in all models with multiple predictor variables using the “car” package to calculate the Variance Inflation Factor (Fox & Weisberg, 2019). No values for the Generalized Variance Inflation Factor were ≥ 2 . We used the “DHARMa” package to check the residuals for model fit and evidence of nonlinearity (Hartig &

Lohse, 2020). We found no clear indications of non-linearity and therefore did not investigate alternative functions. We conducted post hoc calculations of estimated marginal means and pairwise comparisons using the R package “emmeans” (Lenth et al., 2018).

3 | RESULTS

3.1 | Distribution of herbivore families

We detected herbivore sign (exotic and native) at 98.5% of sites; with exotic species at 94.0% of sites, and native species at 32.8% of sites. Exotic and native herbivores co-occurred at 28.4% of sites. Exotic herbivores were represented by more families than native herbivores and contributed the majority of the herbivore activity (Figure 2). For native herbivores, we detected Macropodidae (*Macropus giganteus* Shaw 1790 eastern gray kangaroo, *Macropus rufogriseus* Desmarest 1817 red-necked wallaby), Vombatidae (common wombat), and Muridae (broad-toothed rat) sign. For exotic herbivores,

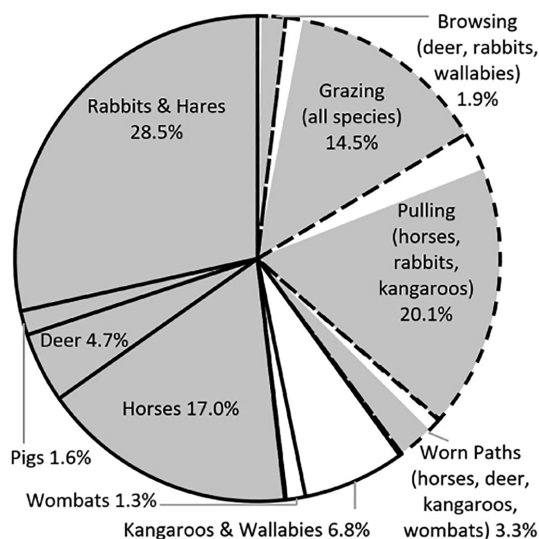


FIGURE 2 Relative contribution of each herbivore family (continuous segment borders) and generic (dashed segment borders) sign to total herbivore activity across all sites. The shading shows the proportion of native (white) and exotic (gray) herbivore activity contributing to each sign type. Herbivores with the potential to contribute to each generic sign are listed in parentheses (Claridge, 2016a; Leigh et al., 1987; Triggs, 1996; Green & Osborne, 2012; Green et al., 2013, 2014; Eldridge et al., 2019; Schulz et al., 2019). The proportion of native and exotic herbivores within generic sign segments is inferred from the proportion of each herbivores' contribution to nongeneric sign. Roll pits and pugging (horses, deer, pigs; 0.08%), unidentified sign (0.17%), and broad-toothed rat sign (0.08%) are included but not visible in the chart due to their small contributions

we detected the sign of Equidae (*Equus caballus* Linnaeus 1758 domesticated horse), Cervidae (*Cervus unicolor* Kerr 1792 sambar deer and *Dama dama* Linnaeus 1758 fallow deer), Suidae (*Sus scrofa* Linnaeus 1758 pig), and Leporidae (*Lepus europaeus* Pallas 1778 European hare and *Oryctolagus cuniculus* Linnaeus 1758 European rabbit). We detected rabbit and hare sign at the highest number of sites (85%), followed by horse (42%), deer (30%) and kangaroo and wallaby (28%) sign. The elevation range was greatest for the rabbits and hares (1221–1951 m a.s.l.), followed by deer (1221–1750 m), horses (1253–1721 m), and kangaroos and wallabies (1256–1537 m). Pigs, wombats, and broad-toothed rats were present at less than 10% of sites and we therefore excluded them from family-level statistical analyses. We detected horses, deer, rabbits and hares, and kangaroos and wallabies with each of the other families at three or more sites (Table S1.1).

3.2 | Landscape elements associated with each herbivore family

We present the associations between landscape elements and each herbivore family derived from the best-fitting models in Figure 3a–h (see Tables S1.3a and S1.4a for details). The probability of horse presence increased as elevation decreased and as distance to water increased. The probability of deer presence was lower in graminoid grasslands than in shrub or tussock grasslands. The probability of deer presence also increased as elevation increased, and as distance from a waterbody decreased. The probability of rabbit and hare presence increased as distance from a waterbody increased. The probability of kangaroo and wallaby presence increased as elevation decreased, and was lower in shrub and tussock grasslands. The probability of presence of any family was not significantly related to the log-distance to roads and tracks, log-distance to woodland or landscape position. However, we note that the range of distances to roads and tracks sampled in our study was limited to achieve rigorous sampling across a large spatial scale, and therefore associations between roads and herbivore presence warrant further investigation across a greater range of distances.

3.3 | Landscape elements associated with total herbivore activity

We present the associations between landscape elements and total herbivore activity derived from the best-fitting model in Figure 3i,j) (see Tables S1.3b and S1.4b for details). Total herbivore activity increased as elevation

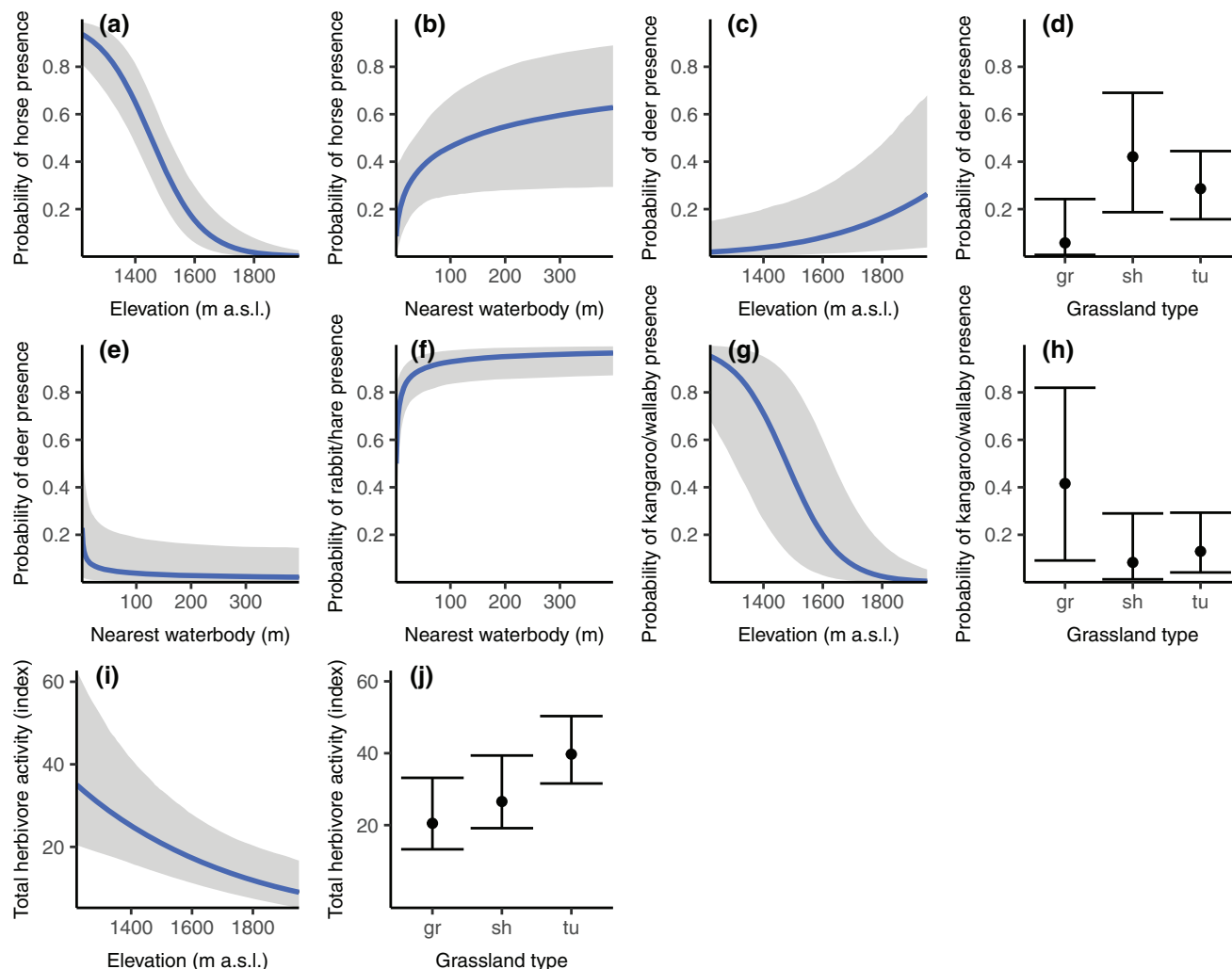


FIGURE 3 Associations between the probability of presence of each herbivore family (y-axes, a–h) and total herbivore activity (y-axes, i–j), and landscape elements (x-axes) derived from the best-fitting models. Grassland types are graminoid (gr), shrub (sh), and tussock (tu). Gray shading and error bars represent the upper and lower 95% credible intervals

decreased. Total herbivore activity was greater in tussock grasslands than in graminoid grasslands. Total herbivore activity in shrub grasslands did not differ significantly from tussock or graminoid grasslands.

3.4 | Vegetation and soil characteristics in relation to herbivore activity

We present the associations between vegetation and soil variables and log-herbivore activity derived from the best-fitting models in Figure 4 (see Table S1.5 for details). Vegetation height and foliage density both decreased with increasing horse and rabbit and hare activity. Forb cover increased as horse activity increased. Weed cover increased as total herbivore activity increased. There was little bare ground recorded across the sites, with a mean proportion of <0.01 cover (min = 0, max = 0.18). However, the proportion of bare ground increased as rabbit

and hare activity increased. Soil compaction increased as horse activity increased. Soil compaction was not associated with soil moisture at the time of sampling.

None of the response variables was significantly related to deer or kangaroo and wallaby activity.

4 | DISCUSSION

Using a landscape-scale, multispecies study, we show that exotic taxa are the dominant mammalian herbivores in Australian high-elevation grasslands. Native herbivore sign was detected at approximately one-third of sites, primarily below 1540 m a.s.l. In contrast, exotic herbivores were almost ubiquitous across the study grasslands, which have evolved largely in the absence of grazing (Green & Osborne, 2012). A lack of shared coevolutionary history indicates that such grasslands are likely to be highly vulnerable to grazing impacts (Antonelli et al., 2011; Bailey &

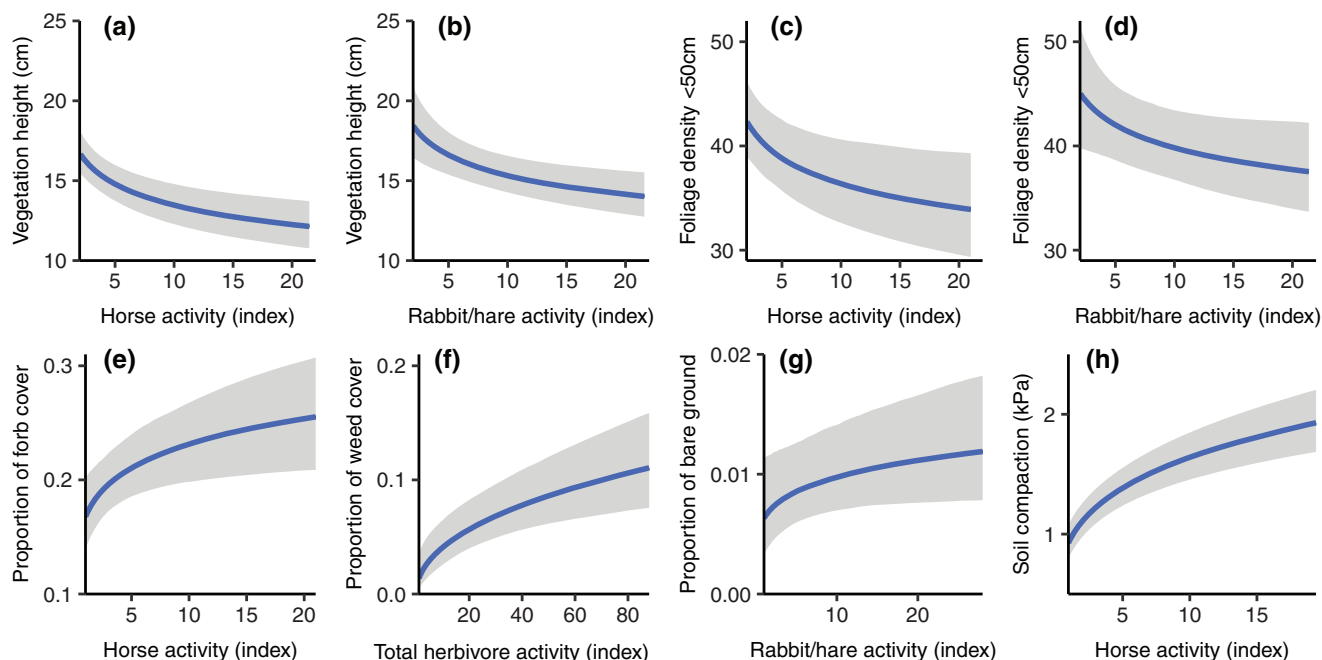


FIGURE 4 Associations between the vegetation and soil response variables (y-axes) and the relative indices of herbivore activity (x-axes) derived from the best-fitting models. Gray shading represents the upper and lower 95% credible intervals

Schweitzer, 2010; Milchunas & Lauenroth, 1993; Spear & Chown, 2009). Consistent with studies in high-elevation grasslands around the world (Davies & Boyd, 2019; Lu et al., 2017; Schütz et al., 2003), our results demonstrate an association between exotic herbivore taxa and lower grassland height, lower foliage density, greater forb and weed covers, and greater soil compaction; characteristics that may result in substantial negative impacts on biodiversity and grassland ecosystems.

4.1 | Are landscape elements associated with herbivore presence?

Each herbivore family had an association with one or more landscape element. As elevation increased, the probability of deer presence increased, while the probability of horse and kangaroo and wallaby presence decreased. Kangaroos and wallabies are restricted to elevations with little or no snow cover due to their diet and locomotion (Green, 2016). The presence of exotic herbivores at higher elevations than kangaroos and wallabies (1540 m a.s.l.) suggests exotic herbivores have a greater ability to either migrate to higher elevations during snow-free periods, or move through snow and consume exposed woody browse (Green et al., 2014). The continuing reduction of snow cover (Green & Pickering, 2013) and increase in temperatures with climate change may facilitate grassland grazing in winter (Giroux et al., 2016) and enable horse, deer, kangaroo, and

wallaby establishment on sites at higher elevations in the future (Boone, 2019; but see Green, 2016).

Deer were more likely to occur in shrub and tussock grasslands and closer to waterbodies. Previous investigations of the impacts of deer (e.g., Brown et al., 2016; Claridge, 2016a) and horses (e.g., Foster & Scheele, 2019; Robertson et al., 2019) in our study region have often focused on waterbodies. However, our study showed there was a greater probability of horse presence away from, rather than close to, waterbodies. These findings do not detract from evidence of damage to waterbodies associated with horses, rather they highlight the potential for less visible impacts away from the soft soils adjacent to waterbodies and the need to assess impact across the landscape. The probability of rabbit and hare presence also increased further from waterbodies. The establishment of rabbits and hares throughout the study area is consistent with observations that these species have been successful invaders of ecosystems worldwide, largely due to their rapid dispersal and reproduction, diverse diet and ability to adapt to harsh conditions (Barbar & Lambertucci, 2018; Courchamp et al., 2003; Foster et al., 2021).

4.2 | Are landscape elements associated with total herbivore activity?

Total herbivore activity was associated with elevation and grassland type, and the contribution of exotic herbivore sign to the measure of total herbivore activity was

considerably greater than of native herbivore sign. The higher total herbivore activity at lower elevations is unsurprising, as snow cover is ephemeral and herbivore populations can persist throughout the winter (Green et al., 2014). The greater total herbivore activity associated with tussock grasslands is of significance to land managers as tussock grasslands are habitat for threatened species, such as Max Mueller's burr-daisy (*Calotis pubescens* Muell. Ex Benth., Walsh & McDougall 2002) (McDougall & Walsh, 2007) and the broad-toothed rat, which depends on large, dense native grasses (Eldridge et al., 2019) for shelter.

4.2.1 | Is activity of exotic and native herbivores associated with a more simple vegetation structure, differences in vegetation composition and higher soil compaction?

Our study is consistent with research from other regions showing exotic horse activity is associated with lower vegetation height and density, and higher forb cover and soil compaction in grasslands (Beever et al., 2018; de Villalobos & Schwerdt, 2020). Soil compaction can alter plant composition and hinder plant growth by reducing gas exchange and water infiltration (Czortek et al., 2018; Pineiro et al., 2010). Grazing by horses in the Alps differs most notably from domestic livestock grazing because there is no rest period to allow plants to complete their lifecycle, resulting in the potential extirpation of native species (Davies & Boyd, 2019). The resulting changes in grassland structure and composition can have cascading community-level impacts and negatively impact on threatened species (Daskin & Pringle, 2016; Eldridge et al., 2019; Vandegehuchte et al., 2017). Similarly, vegetation height and density decreased and bare ground increased with greater rabbit and hare activity. Rabbits and hares can reduce biodiversity by removing palatable native flora before such impacts on plant structure are detected (Mutze et al., 2016). Further, exposed soils can lead to a shift from grasslands to shrublands (McDougall & Walsh, 2007). Therefore, uncontrolled rabbit and hare populations could result in long-term loss of biodiversity and grassland ecosystems.

We found weed cover was best explained by total herbivore activity. While mountain plant communities tend to be resistant to weed invasion largely due to climatic filtering and fewer disturbances, this result suggests the cumulative impacts of multiple herbivore taxa provides the necessary disturbance to facilitate weed establishment (Alexander et al., 2016). Under a warming climate, this facilitation may extend to higher elevations. High weed cover can reduce native plant species richness, alter

vegetation composition (Pyšek et al., 2020) simplify structure, and reduce habitat suitability for native fauna (Sato et al., 2014), in high-elevation grasslands.

4.3 | Recommendations for management and policy

The wide distribution of exotic herbivores in the Alps highlights the need for landscape-scale management, accounting for emigration and dispersal. Priority should be given to removal of horses and deer from elevations above 1500 m a.s.l. where ecosystems evolved with limited mammalian grazing (Costin et al., 1982). Their impacts also should be greatly reduced in all other areas. Although we found no significant associations between deer and grassland characteristics, this may be a result of their relatively recent invasion of the region. There is evidence that even small populations of exotic horses (Driscoll et al., 2019) and deer (Tanentzap et al., 2009) can heavily impact ecosystems, and eradication is therefore likely to be the most appropriate management goal (Prior et al., 2018). As leporids are almost ubiquitous, population suppression should be prioritized in areas of high conservation significance, such as where competition with threatened species occurs, and above the treeline where ecosystems are most threatened by climate change and species endemism is high (Doherty, Wright, & McDougall, 2015). Leporids can support exotic predator persistence in habitats that are otherwise marginal for the predators, or increase exotic predator abundance (Courchamp et al., 2003; Foster et al., 2021). Exotic predator suppression may need to accompany leporid control to limit "prey-switching" in habitats with conservation-significant fauna (Doherty, Dickman, et al., 2015). As the major contributors to total herbivore activity, we recommend leporid and horse population control be prioritized in areas where weed cover or weed invasion are of management concern.

We recommend strategic, long-term, and landscape-scale exotic herbivore management, integrated with weed and exotic predator management and accounting for climate change. Specific aims should be to: (i) suppress or eradicate exotic herbivores from ecosystems that did not evolve with analogous herbivory (Norris, 2018), (ii) prevent expansion and establishment of new exotic herbivore populations, (iii) reduce total herbivore activity in all areas by focusing efforts on major exotic contributors, and (iv) protect areas of high conservation value to avoid loss of native species. Long-term monitoring of herbivore management activities is needed to assess whether management goals for ecosystems are being met (Prior et al., 2018).

ACKNOWLEDGMENTS

The authors acknowledge the Djilamatang, Ngambri, Ngarigo, Ngunnawal, Ngunawal, Walgalu, and Wiradjuri people as the Traditional Custodians of the lands on which this study was conducted. The authors thanks Rob Gibbs, Nick Clemann, Geoffrey Robertson, and Dr Gillian Fuller for invaluable advice, local knowledge, and field assistance.

CONFLICT OF INTEREST

The authors do not have conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data will be published on Dryad upon acceptance for publication; <https://datadryad.org/stash>.

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How to cite this article: Hartley, R., Blanchard, W., Schroder, M., Lindenmayer, D. B., Sato, C., & Scheele, B. C. (2022). Exotic herbivores dominate Australian high-elevation grasslands. *Conservation Science and Practice*, 4(2), e601. <https://doi.org/10.1111/csp2.601>