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RESEARCH PAPER

Rear-edge populations of an endemic alpine daisy are most impacted by invasive sambar deer, even with targeted feral animal control

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ABSTRACT

Management of endangered species requires that threats to their persistence are identified and then mitigated. We document how an invasive ungulate that has recently and rapidly colonised Australian high mountain vegetation, sambar deer (*Rusa unicolor*), impacts a highly palatable endemic alpine daisy (*Celmisia sericophylla*, silky snow daisy). Further, we assess the effectiveness that lethal control conducted across the landscape, as part of a program for reducing deer numbers, has had on minimising impacts to the threatened daisy. We quantified the impact of deer at 57 *Celmisia* populations in relation to landscape context and herbivore control intensity by the land manager. Despite sustained lethal control being conducted across the landscape, we detected spatial differences in ongoing sambar deer impacts on the threatened species. Evidence of sambar deer were detected at 46 % of *Celmisia* populations sampled, and we found that rear-edge populations - nearest the treeline - were at highest risk of being occupied relative to populations further from the treeline. Activity of sambar deer at occupied *Celmisia* populations ranged from low level browsing of foliage and/or flowers (at 25 % of sites) to severe trampling and browsing; 5 % of sites). The probability of deer occupancy was higher with an increasing number of deer controlled with 1 km of *Celmisia* populations. This points to an ongoing and potentially predictable dispersal of deer into the alpine zone from subalpine forests, with such movements negatively affecting *Celmisia* populations nearest the invasion pathways, despite ongoing lethal control. Given the limited capacity of the broader deer control program to eliminate activity nearest the rear-edge populations, we recommend that landscape-scale sambar deer management needs to ramp-up in frequency and/or intensity, targeting alpine treelines, where most occupancy of *Celmisia* populations are currently being observed.

Introduction

Invasive non-indigenous ungulates have expanded their ranges and increased their abundances worldwide, causing profound changes in structure, diversity and functioning of many different ecosystems via their grazing and trampling effects (Côté et al., 2004; Driscoll et al., 2019; Husheer & Tanentzap, 2024; Nuñez et al., 2010; Spear & Chown, 2009; Tanentzap et al., 2009). High densities of invasive ungulates can impact soil properties (Bressette et al., 2012; Wardle et al., 2001), water quality (McDowell, 2007; Nolan et al., 2013), and hamper the persistence and regeneration of native vegetation (Davis et al., 2016; Eldridge et al., 2019; Husheer & Tanentzap, 2024; Husheer et al., 2003). In some cases, overabundant invasive herbivores are endangering rare and restricted species that are highly palatable (Bennett & Coulson, 2010; Bilney, 2013; Peel et al., 2005). Consequently, the management of invasive ungulates has become a major priority for conservation managers (Brown et al., 2016; Côté et al., 2004; Tanentzap et al., 2009), with the aim to reduce their negative impacts to allow ecosystems to recover before permanent change occurs (Hobbs & Norton, 1996).

In the mountainous areas of south-eastern Australia, densities of invasive ungulates have increased in recent decades and many are substantially changing their geographical distribution (Driscoll et al., 2019; Forsyth et al., 2015; Hartley et al., 2022; Moriarty, 2004; Watter et al., 2020). Sambar deer (*Rusa unicolor*) have expanded their historic low elevation distribution upslope into the alpine and subalpine regions; this seemingly has corresponded with recent landscape-scale bushfires (Forsyth et al., 2012; Fig S1), into landscapes where top order native carnivores (i.e. dingoes) have largely been eliminated by lethal control

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(Fleming et al., 2006, 2014). Defaunation of carnivores can facilitate increased abundance and altered behaviour of large herbivores, which can lead to a substantial change in ecosystem dynamics (Estes et al., 2011; Gómez & Hódar, 2008; Ripple et al., 2001; but see Brice et al. (2022) for an example of where non-random sample design can over-estimate impacts). Sambar deer are thought to disperse into alpine areas from lower elevations through forest communities (Quin et al., 2023), with dispersal occurring on a seasonal basis in response to habitat suitability change due to the extent of snow cover; upslope migrations occur in spring as snow cover recedes, with the reverse pattern in autumn (Hartley et al., 2022). Sambar deer movement patterns also occur on a daily basis at high elevations, with deer sheltering in subalpine woodland and forest during the day before foraging above the treeline at night (Comte et al., 2022; Quin et al., 2023). This is likely a consequence of behavioural choices made about predation risk above the treeline (e.g. the landscape of fear; Laundre et al., 2010). It is therefore likely that sambar deer occupancy and impacts on plants will be greater at populations nearer to the treeline, because such animals spend more of their seasonal and daily activity nearest tree cover. Hence, for plant species that occur across an elevational gradient in this region, lower elevation 'rear-edge' plant populations (*sensu* Hampe & Petit, 2005*;* populations residing at the current low elevation margins of a species distribution range) may be more at risk from invasive sambar deer than core or upper-edge populations.

Invasive ungulates such as deer have reached such high densities in some natural ecosystems that culling is frequently used to reduce their impacts on threatened species and plant communities (Bengsen et al., 2020; Davis et al., 2016; Tanentzap et al., 2009). Where management (such as lethal control) is practised, success of the action can be quantified by simple metrics such as how many animals have been removed from a target area, or as a function of the management input intensity (e.g. time invested in control). It is harder, however, to quantify whether such management actions have improved outcomes for the conservation assets that are threatened by the invasive species (Tanentzap et al., 2011); monitoring of vegetation recovery is necessary, often over many years (Tanentzap et al., 2009). In our study area, management of sambar deer in high mountains is undertaken by seasonal ground and aerial shooting. The number of deer removed varies across the landscape and across years in response to management accessibility and public safety and happens in the context of imprecise estimates of the number of deer in the landscape (Watter et al., 2020).

Our study aims to identify the factors that affect the occupancy of sambar deer on populations of an endemic alpine plant species, *Celmisia sericophylla,* a species highly palatable to deer (Quin et al., 2023) and restricted to discrete populations in a small geographic area of the Australian Alps (Blackburn-Smith & Morgan, 2022). We ask this question in relation to the landscape position of *Celmisia* populations (rear-edge populations nearest treelines versus core and upper edge populations in alpine areas), and how management intensity by lethal control affects deer occupancy of *Celmisia* populations. We hypothesised that rear-edge populations (lower elevation, closer to treeline) would have higher probability of sambar deer occupancy. We also hypothesised that we would see no activity in *Celmisia* populations if deer numbers have been reduced sufficiently by lethal control to eliminate visitation to *Celmisia sericophylla* patches that are discrete, spatially-dispersed landscape features. Our study was conceived to understand how current land management (lethal control of deer) is impacting on assets (species of conservation concern), and to better understand where best to intervene in future, thereby using limited resources most effectively and efficiently.

Materials and methods

Study area

The study was conducted on the Bogong High Plains within the Alpine National Park, on the traditional lands of the Jaithmathang and Dhudhuroa people, approximately 240 km northeast of Melbourne, Victoria, Australia (36° 50′ S, 147° 20′ E). The Bogong High Plains occupy an area of approximately 120 km^2 and comprise plant communities ranging from woodlands, open and closed-heathlands, tussock grasslands, wetlands and snowpatch herbfields (McDougall, 1982). The region is characterised by low mean monthly daily maximum temperatures (2.5–18.9 °C), frequent frosts (>100 per annum, that can occur at any time of the year) and high precipitation (>2000 mm per annum), much of which falls as snow (Bureau of Meteorology, 2024).

The study area has no native ungulates and few large native herbivores above the treeline (Green & Osborne, 2012), but has had a long history of free-ranging livestock grazing, with the first cattle being introduced to the area in the 1850s (Lawrence, 1995). Livestock grazing levels have been variable across time (Wahren et al., 1999), with grazing gradually being banned across the landscape between 1972 and 2005 (Lawrence, 1995; Williams et al., 2014). Invasive herbivores on the Bogong High Plains include hares and rabbits, both of which are resident in the area, with numbers fluctuating through time. Feral horses and pigs are common elsewhere in the Australian Alps (Driscoll et al., 2019; Hone, 2002; Saunders, 1993), but are exceedingly rare in our study area. Sambar deer (*Rusa unicolor*) are the only species of deer observed on the Bogong High Plains, inhabiting the area following snowmelt in late spring and remaining until the beginning of winter, when they descend to lower elevations (Comte et al., 2022; Watter et al., 2020).

In the past decade, sambar deer have become common across the Australian Alps (Claridge, 2016; Forsyth et al., 2015; Hartley et al., 2022). In the study area, there were few sightings two decades ago but deer are now frequently encountered at elevations above 1300 m asl (Fig S1). The presence and impacts of deer on the Bogong High Plains has become widespread (authors, *pers. obser.*). The impacts of deer have been documented in many plant communities in this region, but of particular concern are impacts in rare groundwater-dependent ecosystems such as alpine bogs, gravelly pavement herbfields, and *Celmisia sericophylla* herbfields (Blackburn-Smith & Morgan, 2022). Concerns about deer impacts have led the local land management agency, Parks Victoria, to implement a landscape-wide, on-going deer control program (Brown et al., 2016); aerial- and ground-based shooting is used to cull deer in the snow-free summer period (October to April). All deer shot as part of this program have their spatial coordinates and several measures (sex, age class) recorded. We utilise this data to quantify deer spatial patterns across the Bogong High Plains and relate these patterns to impacts on *Celmisia* populations.

Focal plant species

Celmisia sericophylla (silky snow daisy, Asteraceae) is an endemic species largely restricted to Bogong High Plains where it occurs across the alpine zone (~1600 to ~1900 m asl). It is listed as Vulnerable under Victorian state legislation (DEECA, 2024). It is a rhizomatous perennial that grows near, and in, flowing water, forming a conspicuous closed canopy in gravelly pavement herbfields (Blackburn-Smith et al., 2024), as well as on the edges of small streams below groundwater outflows. Populations are discrete and distributed across the wider alpine landscape (Blackburn-Smith & Morgan, 2022). The species flowers annually in early summer, and local dispersal by vegetative fragments (ramets) has been observed after heavy rainfall (authors, *pers. obser.*). It was vulnerable to grazing by cattle (van Rees, 1984) and sambar deer are known to graze the species (Quin et al., 2023; Fig S2).

Study design

We sampled 57 discrete populations of *Celmisia sericophylla* across the species' altitudinal range on the Bogong High Plains (between Mt Bogong and Mt Hotham) to quantify sambar deer presence and activity at each population. We visited all populations that were known to us, or

found during the survey, provided the local population was larger than 1 m^2 in area. We excluded several populations that were close to major roads or disturbance from infrastructure such as ski lifts; we assumed deer behaviour and activity would be negatively affected in these locations. Survey sites captured the full elevation range of the species (1630 to 1915 m), and spanned gradients of landscape attributes (slope, distance from the nearest treeline) and land management intervention intensity (deer control by shooting).

Culling regime

Ground-based shooting was performed by contract shooters during the snow-free period, typically between October to April each year, at monthly intervals. The control program was established and implemented for part of the Bogong High Plains between 2015 and 2019, before expanding the program to encompass the entire Bogong High Plains between 2019 and 2022. Shooting is clustered spatially at the landscape-scale (Fig 1), driven by variation in deer distribution across the landscape, as well as accessibility constraints for shooters (e.g. tracks) and public safety concerns. A total of 608 Sambar deer were culled between October 2018 and January 2022 (Fig 1).

Data collection methods

All study *Celmisia* populations on the Bogong High Plains were visited once. We conducted surveys in austral summer, between January and March 2022, to minimise seasonal variability between sites. At this time, snow cover was absent and sambar deer were likely to be occupying their maximal elevational ranges within the bounds of their current distribution (Foster et al., 2021; Hartley et al., 2022). During a site visit, we recorded the environmental setting of each *Celmisia* population (slope [flat, moderate, or steep], aspect, elevation and areal extent). We recorded further environmental attributes of populations (distance to nearest road/ management track and distance from alpine treeline) in QGIS 3.22.6 using landscape elements derived from satellite imagery and publicly available spatial datasets (www.data.vic.gov.au).

To determine deer occupancy of each *Celmisia* population, we identified recent (i.e. the current growing season) deer activity by observing signs such as fresh scats, hoof pugging, active tracks, wallows (where bare ground was evident) and browsing of vegetation. To understand the severity of deer impacts on each population, we scored the activity of deer at each population using a qualitative measure of the degree of trampling, browsing and/or bare ground present at each population: 0 = no sign, 1 = minor impacts (pugging and browsing present but uncommon, < 5 % population affected), 2 = moderate impacts (pugging and/or browsing common throughout *Celmisia* patch, >5 % population affected), and 3 = severe impacts (pugging and browsing very common, >30 % population affected, with high proportion of vegetation removed due to trampling and browsing; see Fig S3).

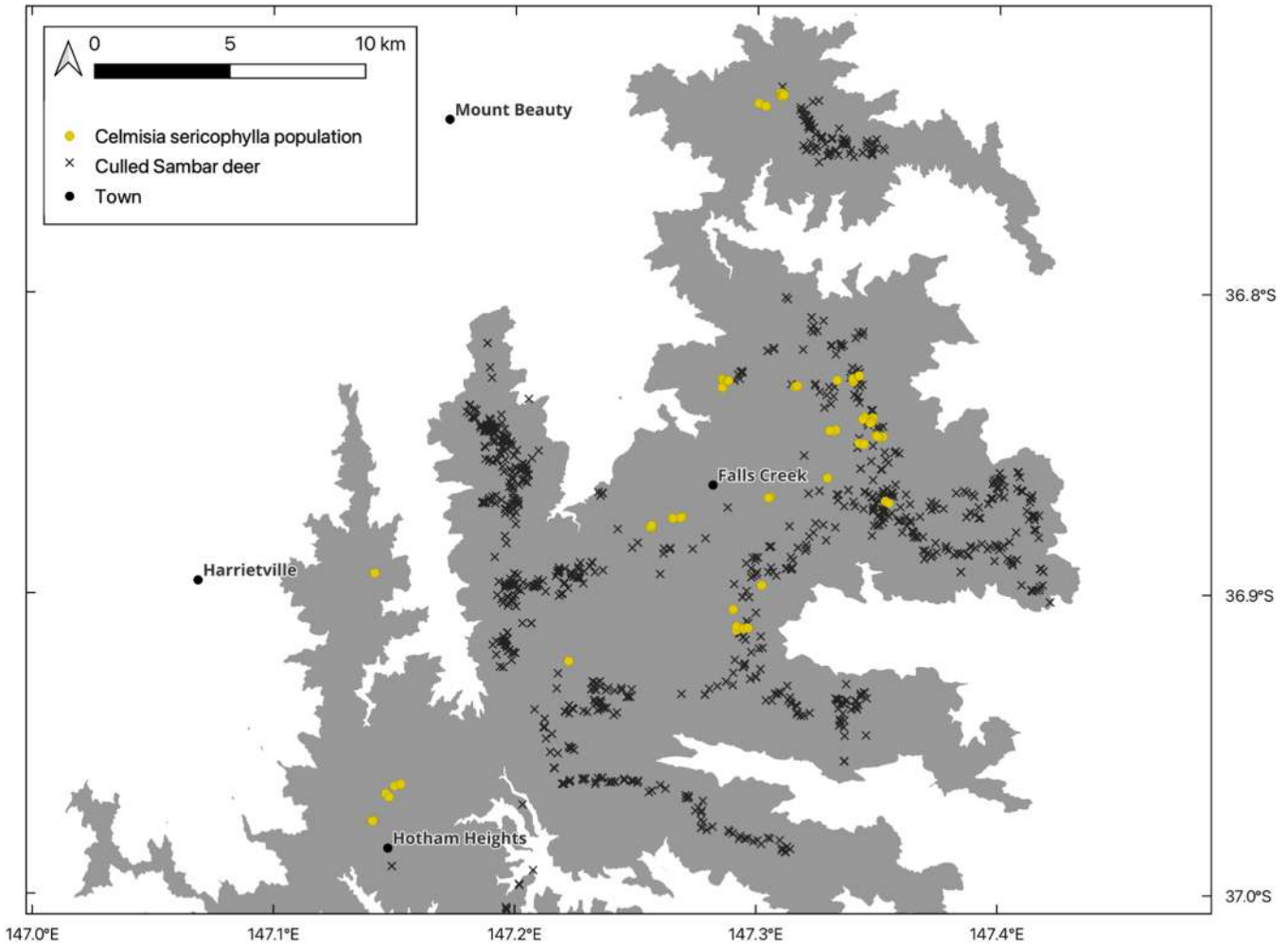

Fig. 1. The location of *Celmisia sericophylla* populations across the Bogong High Plains, Australia (shown in yellow) and the location of 608 Sambar deer that were culled between October 2018 and January 2022 (shown in black). The grey polygon indicates areas above 1300 m elevation.

Statistical analyses

We modelled deer occupancy (indicated by presence of any deer impact at a site) in relation to the degree of 'alpine-ism' of each population to assess our core hypothesis – that lower elevation, rear-edge populations are more likely to be impacted by deer than populations at higher elevations and/or further away from the treeline. Additional factors that may affect the desirability of populations to sambar deer activity were also included (e.g. distance from treeline, distance from walking or management tracks). We modelled the probability of presence of deer impact using a generalised linear model (GLM) with a binomial distribution and a logistic link function. The GLM was fit using the 'glm' function in R (Crawley, 2013; R Core Team, 2023). We included the following predictor variables as main effects in a global model: elevation, distance to alpine treeline, slope, patch area, track density (within 1 km^2) and culling density (number of deer shot between October 2018 and January 2022 within 1000 m of a *Celmisia* population). Collinearity between variables was assessed with Pearson correlation coefficients. All pairwise correlations were $r < 0.65$, indicating low concern for collinearity (Dormann et al. 2013). Each variable was scaled prior to fitting the models to account for differences in the scale of units between variables. We selected the best-fitting model from all possible models using the 'dredge' function in the {MuMIn} package (Bartoń, 2022). Models were ranked using Akaike's Information Criterion corrected for small samples (AICc) with models within 2 AICc values from the lowest considered to be equally parsimonious (Burnham & Anderson, 2010). The top performing models were averaged using the 'model.avg' function in the {MuMIn} package. For each variable, predicted values from the full model averaged coefficients were back-transformed to their original scale and plotted. Model assumptions were validated using {DHARMa} package to assess residual diagnostics (Hartig, 2024). All analyses were conducted in R version 4.2.0.

Results

We detected sambar deer at 46 % of the 57 *Celmisia* populations sampled across their entire elevation gradient on the Bogong High Plains (Fig 2). Impacts of sambar deer varied between sites and ranged from minor browsing of foliage and flower heads at 25 % of sites, to severe trampling, pugging and browsing at 5 % of sites (Fig 2; Fig S3).

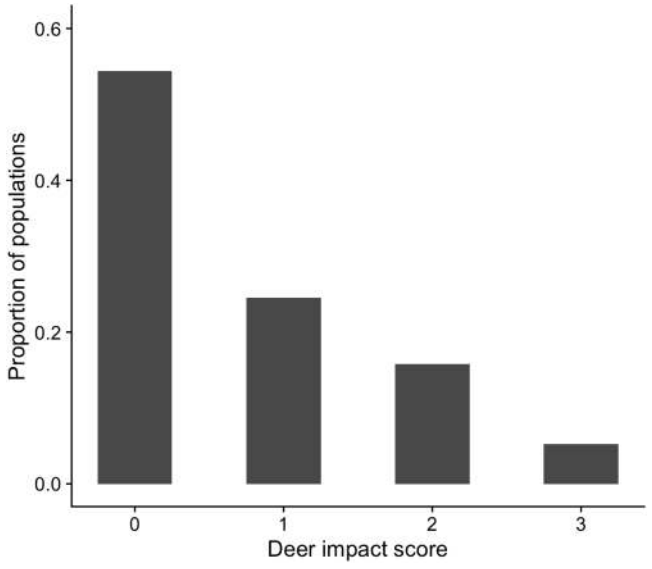

Fig. 2. Proportion of *Celmisia sericophylla* populations in 2022 for each deer impact score (0 - no impacts, 1 - minor impacts, 2 - moderate impacts, 3 - severe impacts; see methods for more detailed explanation, and Fig S3 for examples) across 57 sites distributed across the Bogong High Plains, Australia.

The probability of sambar deer presence in *Celmisia* patches substantially decreased with increasing distance from the alpine treeline (Fig 3; Table S1; Fig S4). *Celmisia* populations nearest the treeline had a high probability of being occupied (~70 %), dropping to only 10 % probability of occupancy for populations ~400 m from trees. The probability of occupancy was found to be positively influenced by *Celmisia* patch size, with smaller patches much less likely to be occupied (Fig 3; Table S1). There was a positive relationship between the number of sambar deer shot at the landscape scale (i.e. within 1 km of a *Celmisia* patch) and the probability of deer occupying a *Celmisia* population in 2022 (Fig 3, Table S1). Track density had a negative effect on deer occupancy (Fig 3, Table S1). Elevation had a positive effect on deer occupancy (Fig 3, Table S1). Slope was not included in any of the top performing models (Table S2).

Discussion

We demonstrate that invasive sambar deer occupancy and impacts are common in populations of a range-restricted alpine herb, *Celmisia sericophylla*, and that these impacts differ across the landscape. Sambar deer are a previously absent functional group in the Australian alps, so there has been a substantial effort to reduce their potentially negative impacts on native ecosystems (Brown et al., 2016). By far the most important landscape factor affecting sambar deer occupancy at *Celmisia* patches was distance from the alpine treeline, with populations of *Celmisia* nearer to trees having substantially higher occupancy by deer than those populations much further away from the treeline. This supports our hypothesis that 'rear-edge' populations (*sensu* Hampe & Petit, 2005) should be most frequently impacted by sambar deer because they spend more of their seasonal and daily activity nearest the treeline and hence, encounter rear-edge plant populations more often than they do upper-edge populations. This is likely a consequence of behavioural choices made about predation risk above the treeline (e.g. the landscape of fear; Laundre et al., 2010), whereby deer exhibit anti-predatory behaviour in response to the perceived predatory threat (Price et al., 2014). Larger populations of *Celmisia* (with respect to their areal extent) were also more likely to be occupied by deer than smaller patches. Imbalanced networks of herbivores are therefore a potentially important driver of reduced demographic resilience in rear-edge populations of alpine species (Cairns & Moen, 2004; Munier et al., 2010), and more broadly (Miller & McGill, 2019; Miller et al., 2023; Nuttle et al., 2014). Our results are consistent with other studies on spatial patterns of sambar deer presence and impacts in the Australian Alps (Comte et al., 2022; Hartley et al., 2022) which show deer activity and frequency of impacts are higher near the shelter of trees. On-ground impacts were detected despite several years of sustained summer ground and aerial shooting by the land manager that had specifically targeted a reduction in sambar deer numbers in this landscape.

Sambar deer impacts were variable across *Celmisia* populations and ranged from absent to minor grazing of leaves and flower heads, to severe trampling and pugging of vegetation and soils. Where grazing was moderate to severe, often all flowering heads were removed, eliminating the opportunity for these populations to produce seed and recruit sexually. The importance of seed for within-patch and between-patch dispersal, as well as the generation of new genets, is unknown and hence, whether deer browsing leads to a 'regeneration debt' (*sensu* Miller & McGill, 2019) in *Celmisia* is unclear. Seed may not be important for persistence of plant populations in the short-term owing to the rhizomatous nature of *Celmisia*, although ramet longevity in this species also remains unknown. Where trampling disturbances are high, however, the number of *Celmisia* ramets can be greatly reduced and bare ground is created (Fig S3). High ramet mortality appears to be associated with lower site occupation in this species, as is expected by theory (Benedek & Englert, 2019). Bare ground is susceptible to erosion in high mountain areas, removing the highly organic soil upon which large *Celmisia* populations grow (Blackburn-Smith & Morgan, 2022). This may

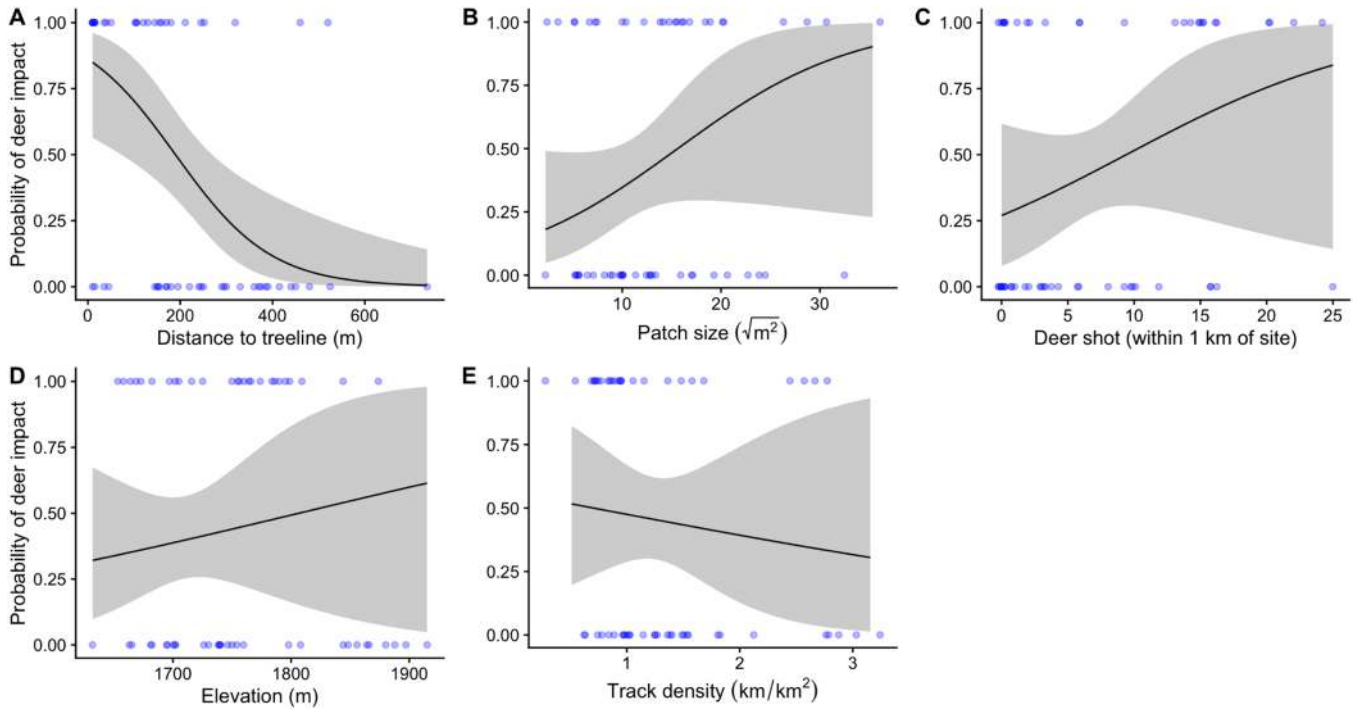

Fig. 3. Probability of deer impacting a *Celmisia sericophylla* population in 2022 on the Bogong High Plains, Australia as a function of A) distance to the alpine treeline, B) square-root transformed areal extent of the population, C) the number of deer that had been shot in the landscape between October 2018 and January 2022, D) the elevation of the population, and E) the density of tracks within 1 km^2 of the population.

reduce the likelihood of recolonisation by both genets and ramets if the substrate is reduced to the rocky bedrock, i.e. suitable habitats for the threatened plant are compromised because of the activities of invasive ungulates.

Given that *Celmisia* is palatable to sambar deer (Quin et al., 2023), management by lethal control should benefit this species (Miller et al., 2023; Rose & Platt, 1987). On-going targeted feral animal control by the land management agency, however, has not eliminated deer from *Celmisia* populations nearest the treeline. Sambar deer densities were not reduced below a threshold necessary to protect this palatable species from continuing occupancy. It also suggests that there was an ongoing and regular pathway of sambar deer re-colonisation into the alpine zone from downslope subalpine forests. Intriguingly, there was a trend for sambar deer occupancy of *Celmisia* populations to be highest where more deer were shot at the landscape scale. Our findings - that impact was still occurring in *Celmisia* populations that had the highest number of sambar deer culled in their near vicinity - underscores the technical difficulty of managing invasive species populations that range over large spatial scales, with temporal variation in their use of the landscape.

It is apparent that even more sambar deer will need to be culled by land managers if threatened *Celmisia* populations nearest treelines are to be protected from their negative impacts. The rear-edge populations of *Celmisia* that are most impacted by sambar deer (i.e. the warm-edge) are likely to be the populations under the most immediate (and marked increasing) stress from a warmer, drier climate, reducing snowcover and late spring snowmelt that feeds many of the habitats that *Celmisia* occupies (Blackburn-Smith & Morgan, 2022; Williams et al., 2015). Sambar deer will likely exacerbate climate stress in plant populations (Carnicer et al., 2021; Stevens et al., 2015), with the potential to affect population growth rates and, ultimately, population persistence.

The promotion of native apex predator populations, such as dingoes (*Canis dingo*), may be an important mechanism to directly reduce the number of sambar deer in the long-term, as well as change their behaviour at, and above, the treeline (Thompson et al., 2022). Increased herbivore pressure on plants in areas lacking efficient apex predators has been observed many times (e.g. Carnicer et al., 2021), suggesting that local persistence of plant populations is strongly modulated by local-scale biotic interactions (Miller et al., 2023). The loss of predators is a key driver of changed interactions, but their return to ecosystems is likely a key lever for change (Ripple et al., 2001). Sambar deer are a key prey item for dingoes in areas where the deer are now common (Davis et al., 2016; Forsyth et al., 2018; Thompson et al., 2022) but it remains unclear just how much predation these carnivores could exert on deer across the high mountains of south-eastern Australia; they currently occur at low densities (Fleming et al., 2014; Vendersteen et al., 2023). In the short-term, it is imperative that ground and aerial shooting of sambar deer continues, re-emphasising that the reduction of negative impacts of exotic ungulates on populations of threatened species will be an ongoing management objective. The metric used by managers (number of deer culled, or area treated) has not necessarily correlated with protection of the target species and hence, monitoring that assesses conservation goals should be embedded into all programs designed to deliver environmental benefits.

Conclusions

The wide distribution of sambar deer across our study area highlights the need for landscape-scale management, accounting for immigration and dispersal of animals both within and across seasons. Priority by decision-makers should be given to removal of deer from above the treeline in areas of high conservation significance, where ecosystems are most threatened by climate change (Williams et al., 2015) and species endemism is high (Endo et al., 2015; McDougall & Walsh, 2007). Specific management actions should be (i) to prevent expansion and establishment of new deer populations, (ii) to reduce total deer activity and (iii) to identify and protect areas of high conservation value. Our study shows that monitoring of deer culling outcomes, not just activities (such as the number of animals controlled), is needed to assess whether management goals - that reduced abundance of deer translate to protection of a rare alpine daisy - are being met. Given the limited success of current deer control programs to eliminate activity at rear-edge populations, despite sustained effort, we recommend that landscape-scale

sambar deer management needs to ramp-up in frequency and/or intensity near alpine treelines where most negative impacts on *Celmisia* populations are being recorded. Knowing when, where, and how best to intervene is critical for land managers to use limited resources most effectively. Given the Australian alpine flora is poorly adapted to the impacts of ungulates (van Rees, 1984; Wahren et al., 1994; Wimbush & Costin, 1979), deer densities should continue to be lowered as much as technically feasible. Our recommendations echo those of Hartley et al. (2022) who focused on exotic herbivore management in the Australian Alps more broadly, and mirror concerns elsewhere about the need to control over-abundant deer (e.g. Miller & McGill, 2019; Miller et al., 2023).

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Data availability

All data and code used in this study are available at: https://github.com/zacwalkr/celser/

CRediT authorship contribution statement

John W. Morgan: Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Conceptualization. **Zac C. Walker:** Writing – review & editing, Visualization, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

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