


Long-term impacts of an introduced ungulate in native grasslands: Himalayan tahr (*Hemitragus jemlahicus*) in New Zealand's Southern Alps

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Abstract Ungulates have been widely introduced to new locations, often increasing to high densities that impact on native plant communities. Himalayan tahr (*Hemitragus jemlahicus*) were introduced to New Zealand in 1904 and now occupy about 9600 km² of the Southern Alps. Managers aim to control tahr to reduce impacts to native montane grasslands. We used a network of 111 permanent plots in eight catchments to estimate the long-term impacts of tahr on total vegetation cover and snow tussock (*Chionochloa* spp.) height. The proportion of sub-plots containing faecal

pellets was used as a measure of tahr activity. Total vegetation cover increased during the study period but declined non-linearly with increasing tahr activity, with the most rapid decline occurring as tahr activity increased from low levels (i.e. a highly-vulnerable relationship). Tussock height declined weakly as a function of time during the study period, but declined strongly with increasing tahr activity (a proportionate relationship). A proportional effect of tahr activity on adult tussock height and a non-linear logarithmic effect of tahr activity on vegetation cover indicate that species other than tussocks were highly sensitive to tahr activity, even at very low levels. We conclude that tahr had significantly impacted total vegetation cover and tussock height during 1990–2013. Although vegetation cover appears to still be recovering from the high tahr densities that occurred prior to the 1970s, managers need to control tahr to lower levels, to further reduce their impacts on montane grasslands.

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Introduction

Ungulate species (Order: Artiodactyla) can become overabundant in their native (Côté et al. 2004) and non-native ranges (Forsyth and Caley 2006)

generating concerns about their impacts on the receiving ecosystems (Mysterud 2006; Ohashi et al. 2014). The long-term impacts of overabundant ungulates in native forest ecosystems are well documented and include altered soil processes (Stritar et al. 2010); reduced forest regeneration (Husheer et al. 2006), abundance and biomass of preferred species (Nugent et al. 2001), understory biomass and species diversity (Wardle et al. 2001; Côté et al. 2004); and increased abundance and biomass of unpalatable species (Husheer et al. 2006; Beguin et al. 2011). In contrast, the long-term impacts of ungulates in native grassland ecosystems are less well documented but include changes in species composition (Mayer et al. 2009), reduced abundance (Pardo et al. 2015), regeneration and recruitment; and increased senescence of palatable species (Rose and Platt 1992; Tanentzap et al. 2009).

The responses of native plant communities to increasing pressure from ungulates depend on multiple factors including the plant species' traits, such as their ability to tolerate herbivory (Evju et al. 2009), the presence of refugia, and the overall community composition (Nugent et al. 2001; Forsyth et al. 2010). These factors shape the relationships between ungulates and native plant species, which can be described using 'damage functions' (Hone 2007) that can take three linear (non-threshold) and three non-linear (threshold) forms (Yokomizo et al. 2009; Norbury et al. 2015). The threshold forms describe the points where abrupt changes in the response occur. For example, beyond given thresholds, small changes in the driver (e.g. ungulates) can produce large changes in the response (Groffman et al. 2006). Knowing the form of damage functions between ungulates and useful response measures can guide ungulate management. For example, negative non-threshold relationships suggest that increased reductions in ungulates (through management) will proportionally benefit native species (Norbury et al. 2015). Conversely, threshold forms provide values that managers can set as targets for ungulate control (Yokomizo et al. 2009; Norbury et al. 2015) under an adaptive management approach (Parkes et al. 2006; McCarthy and Possingham 2007).

Here, we report on a long-term study of the impacts of non-native Himalayan tahr (or 'thar'; *Hemitragus jemlahicus*) on native montane grasslands in New

Zealand's Southern Alps. New Zealand's flora evolved in the absence of mammalian herbivores (but did evolve with browsing birds such as moas; review in Forsyth et al. 2010), and hence there is particular concern about the impacts of ungulates on New Zealand's plant communities (Atkinson and Greenwood 1989; Simberloff 1995). Himalayan tahr were introduced to New Zealand's Southern Alps in 1904 to establish a hunting resource (Donne 1924). A population established and rapidly increased in range and abundance, with all restrictions on harvesting removed in 1930 (Forsyth and Tustin 2005). However, tahr continued to increase their range and abundance (up to 30 per km²; Tustin and Challies 1978), resulting in a shift from tall, slow-growing tussock species to shorter tussock species, and an increase in the proportion of bare ground (Caughley 1970a). From 1970, commercial harvesting using helicopters reduced the tahr population from ~50,000 to ~2000 in 1983 within an estimated 6000 km² of the Southern Alps (Parkes 2006). There has been little commercial harvesting of tahr since 1983, and the tahr population has subsequently increased (Forsyth and Hickling 1998; Parkes 2006). A 'Himalayan Thar Control Plan' (HTPC; Department of Conservation 1993) proposed recreational hunting and government-funded helicopter-based culling to prevent tahr from colonising new areas and to limit abundances in areas of lesser conservation value (Forsyth and Tustin 2005). The HTPC stipulated that the long-term impacts of tahr in montane grasslands would be monitored at a sample of locations throughout the range.

In this paper we report the results of that monitoring. Sampling locations were a representative network of permanent plots that was established during the 1990s. Exclosures, which are commonly used to evaluate long-term impacts of ungulates in forests (Wardle et al. 2001), cannot be used in alpine grasslands as they are destroyed by heavy snow. Periodic re-measurements of the permanent plots (most recently in 2013) enabled us to evaluate the damage relationships (threshold or non-threshold) between two indicators of vegetation condition (height of adult snow tussocks (*Chionochloa* spp.) and total vegetation cover of all plant species) and tahr activity, while accounting for additional factors that could influence the vegetation responses (such as elevation and aspect; Rose and Platt 1990).

Methods

Study area and species

The range of Himalayan tahr in the Southern Alps is dominated by grasslands of snow tussocks including *Chionochloa pallens*, *C. flavescens* and *C. rigida*; in association with shorter grasses including *Poa colensoi*, *Festuca* and *Rytidosperma* spp.; a wide range of forbs including *Celmisia*, *Aciphylla* and *Ranunculus* spp.; and small shrubs such as *Coprosma*, *Hebe* and *Gaultheria* spp. (Wardle 1991). The vegetation is intergraded with scree and bluffs (Tustin and Parkes 1988; Forsyth 1999). Diet and movement studies indicated that tahr are likely to have the greatest impact on the tussock communities (Tustin and Parkes 1988; Parkes and Forsyth 2008). Tahr are sometimes sympatric with up to four other non-native mammalian herbivores: alpine chamois (*Rupicapra rupicapra*), red deer (*Cervus elaphus scoticus*), brushtail possum (*Trichosurus vulpecula*), and brown hare (*Lepus europaeus occidentalis*) (Forsyth et al. 2000). However, since the late 1970s red deer have been held at low densities throughout the tahr range by commercial harvesting (Forsyth 1997), and increasing densities of tahr have displaced chamois (Forsyth and Hickling 1998). Snow tussocks constitute roughly 30 % of tahr's diet, while chamois consume snow tussocks only in small amounts (<3 % of their diet; Parkes and Forsyth 2008). The biomass of hares (Flux 1967) and possums (Hickling and Forsyth 2000) in native grasslands are low relative to tahr (Forsyth et al. 2000) and hence the current impacts of these sympatric species on snow tussocks are presumed to be small.

Eight catchments dominated by snow tussock grasslands were selected for monitoring: four in the wetter western Southern Alps and four in the drier eastern Southern Alps (Fig. 1). The history of tahr in each catchment is summarised in Table A1 of the Appendix. Briefly, tahr colonised the catchments in different decades ranging from 1904 (Hooker) to 1960 (Whymper). After colonising a catchment, tahr took about 25 years to attain peak densities before declining (Caughley 1970b). Hence, except for Whymper, all catchments had undergone a population irruption and associated grassland impacts before commercial harvesting resulted in substantial reductions to tahr densities in the 1970s. Following the cessation of



Fig. 1 Location of the eight study catchments within the Himalayan tahr's breeding range in the Southern Alps, South Island, New Zealand

commercial harvesting in 1983, all catchments were subject to unrestricted recreational hunting. All catchments, except Carneys Creek and North Branch, were also subject to different levels of government-funded helicopter-based culling (Table A1 of the Appendix). Tahr densities (and consequently their activity levels) therefore differed among catchments when monitoring began in the 1990s.

Permanent plot establishment and re-measurement

In each study catchment, permanently marked plots (up to $n = 111$) were established between 1990 and 1999 and re-measured up to five times since establishment (further details in Table A2 of the Appendix). Vegetation plots were located on slopes with elevations ranging between 1150 to 1600 m above sea level. Each vegetation plot was of a variable area sufficient to include a minimum of 20 snow tussocks usually of either *Chionochloa pallens*, *C. flavescens* or *C. rigida*

and their hybrids, but with a small proportion (<15 %) of *C. crassiuscula* (when it was mistaken for one of the other species), and *C. macra* (Rose and Platt 1990). At establishment and re-measurement, plots were gridded into 1-m² contiguous quadrats in which all live snow tussocks were mapped, measured, and assigned to a species and age class following Rose and Platt (1990). Individual tussocks were classified as seedlings (≤ 1 -cm live diameter), juveniles (1- to ≤ 5 -cm live diameter), senescent (> 5 -cm diameter and > 50 % crown death), and adults (the remainder). The following were recorded for each individual: basal live diameter (cm), maximum height of the extended live leaves (cm), and the percentage of crown death (± 5 %). The combined percentage cover of all plant species within each plot (± 2.5 %) was also visually estimated.

We searched ‘pellet plots’ to determine whether or not they contained ungulate faecal pellets. Up to 1999, pellet plots were the 1 \times 1 m quadrats on the vegetation plots, but thereafter the pellet plots were 40 or 64 circular plots (each 1 m²) located at 5-m intervals on eight transects radiating from each permanent vegetation plot. We accounted for varying sampling effort by dividing the number of ‘active’ pellet plots (with pellets) by the total number of sampled plots to estimate the proportion of active pellet plots, which we used as an index of tahr activity at the vegetation plot. Catchment-level counts of tahr were also carried out but sampling protocols were inconsistent and hence could not be used in our analyses (Cruz et al. 2014). Additionally, measures of tahr activity about the vegetation plots were expected to better represent the likely damage that the vegetation in those plots was likely to incur from tahr.

Statistical analyses

Chionochloa species were pooled for analysis because they were difficult to distinguish in the field and sometimes hybridised. The abundance and condition of tussock juvenile and seedlings are likely influenced by a variety of extrinsic factors besides tahr including the timing of masting events, abundance of seed predators such as mice (*Mus musculus*) and insects, and the availability of nearby adult tussocks (e.g. Kelly et al. 2000). We therefore did not evaluate population dynamics including recruitment and turnover, but instead focused our analysis on adult

condition (measured as height) as a measure that could detect impacts of herbivory before adult survival was compromised. Survival of adults is likely to have the biggest impact on overall population growth of slow-growing, long-lived species (García et al. 2008). We evaluated the form (threshold or non-threshold) and significance of the relationship between tahr activity and height of adult *Chionochloa* plants while accounting for additional factors that could also impact height. We compared two competing Generalised Linear Mixed Effects Models (GLMMs; Zuur et al. 2009) that included random intercepts at two hierarchical levels to account for variable sampling effort between catchments and unaccounted differences between plots: (1) plot ID within catchments, and (2) catchment ID. Both models also included additional fixed effects including crown death (%), live diameter (cm), aspect ($^{\circ}$), elevation (m) and year of monitoring, which accounted for repeated measures throughout the monitoring period (Rose and Platt 1990). Diameter and aspect were included as quadratic effects (Rose and Platt 1990). Both models included tahr activity as fixed and random effects. Inclusion of tahr as a fixed effect allowed evaluation of average effects across catchments, while inclusion as a random effect allowed evaluation of individual catchment-level differences in the slope of the relationship. The competing models differed in how tahr activity was included, which allowed for different threshold and non-threshold relationships (Norbury et al. 2015). The first model included untransformed tahr activity, while the second model included the log of tahr activity. Model coefficients were estimated using the *lme4* package (Bates et al. 2014) in R version 3.0.2 (R Core Team 2013).

We assessed the form and significance of the relationship between tahr activity and the percentage of total vegetation cover of all plant species while accounting for additional factors likely to affect cover. We compared two competing GLMMs (with a Poisson error structure) that included random intercepts for catchment, and for plots within catchments, as well as the same fixed effects used in the tussock height models. The Poisson error structure accounted for the skewed distribution and positive values of the response. Small estimated random variances indicated that the use of random effects resulted in over-fitted models so we removed the random effects and focused on the average relationship across catchments using

Generalised Linear Models with Poisson error (GLMs, Crawley 2013). Similarly to the analysis of tussock height, the two competing models included the same fixed effects but varied in how tahr activity was included (untransformed or logged) to test for threshold and non-threshold relationships between vegetation cover and tahr activity. Model coefficients were estimated using the *glm* function in R version 3.0.2 (R Core Team 2013).

Relative support for the two competing models of tussock height, and the two competing models of vegetation cover was evaluated using the Akaike Information Criterion (AIC; Burnham and Anderson 2002). The competing model for each indicator (height or cover) with the smallest AIC was strongly supported, and hence used for inference, if its Akaike difference (Δ AIC) against the alternative model was greater than two units (Burnham and Anderson 2002). Parameters in the best models were deemed significant if their 95 % Confidence Intervals (CIs) excluded zero. The predicted partial relationships between significant parameters and response variables for the best models were plotted by keeping all other predictor variables at their mean values.

Results

Tussock height

The number of vegetation plots and adult tussocks measured throughout the study are summarised in the Appendix (Table A2). The GLMM estimating a linear (non-threshold) relationship between tahr and tussock height (by including untransformed tahr activity) had the smallest AIC and was overwhelmingly supported compared to the alternative model (Δ AIC = 131). The inclusion of all random effects (plot ID within catchment, catchment ID and tahr abundance) was supported by their large variance estimates (104, 197 and 380, respectively) and indicated large differences between plots and catchments. All fixed effects (including tahr activity) were significant except for the quadratic relationship with aspect (Table 1). The height of adult tussocks related to tussock diameter through a quadratic relationship, with greater heights associated with intermediate diameters (Fig. 2a). There was a weak positive relationship between tussock height and crown death (Fig. 2b), and a

negative relationship with elevation (Fig. 2c). On average (i.e. across catchments), tussock height declined during the monitoring period (1900–2013; Fig. 2d).

Averaged across catchments, tussock height declined with increasing tahr activity (Fig. 2e). However, the strength of the relationship varied widely among catchments (Fig. 3). Relatively weak negative relationships (i.e. flat slopes) were estimated between tussock height and tahr activity for four of the eight catchments sampled (Carney's Creek, Hooker, Townsend, and Whymper; Fig. 3). These catchments also had relatively low levels of tahr activity over time (Fig. 4). North Branch and Zora had higher tahr activity (Fig. 4), and stronger negative relationships (i.e. steeper slopes) between tussock height and tahr activity levels (Fig. 3). The estimated relationship between tussock height and tahr activity was strong for Fitzgerald, but tussocks were estimated to attain tall heights when tahr were inactive (\sim 70 cm) and to only decline to moderate heights ($>$ 50 cm) for the remaining observed activity levels by tahr (Fig. 3). Carney's Creek and North Branch were estimated to have tall tussocks ($>$ 65 cm) across the range of tahr activity levels recorded at those catchments (Fig. 3). Townsend, Hooker and Whymper catchments were estimated to have tussocks with moderate heights (50–60 cm) across the range of tahr activity levels recorded there (Fig. 3). Tussocks at Zora ranged in height from moderate ($<$ 60 cm) to short ($>$ 30 cm) with increasing tahr activity (Fig. 3). Finally, for Arbor Rift the relationship between tussock height and tahr activity was estimated as weak despite tahr activity being highest (Fig. 4) and tussocks being estimated to be shortest (\sim 25 cm height, Fig. 3) at this catchment.

Vegetation cover

The GLM estimating a non-linear (threshold) relationship between tahr activity and total vegetation cover (by including the log of tahr activity) had the smallest AIC and was overwhelmingly supported (Δ AIC = 33) compared to the alternative model. Total vegetation cover within a plot was significantly associated with plot aspect, year of monitoring, and the log of tahr activity, but was not significantly related to plot elevation (Table 1). Total vegetation cover increased on south-facing slopes (Fig. 5a) as

Table 1 Fixed effect coefficients (means and 95 % CIs) of best models (based on Δ AIC criterion) estimating long-term changes in tussock height and vegetation cover

	Tussock height	Vegetation cover
Intercept	344.501	−8.985
Diameter (cm)	0.747 (0.709–0.785)	
Diameter ²	− 0.003 (− 0.004 to − 0.003)	
Crown death (%)	0.030 (0.010–0.050)	
Year	− 0.167 (− 0.217 to − 0.117)	0.00 (0.005–0.008)
Aspect (°)	0.057 (−0.042 to 0.156)	0.003 (0.002–0.003)
Aspect ²	0.000 (−0.000 to 0.000)	0.000 (0.000–0.000)
Elevation (m)	− 0.056 (− 0.69 to − 0.043)	0.000 (0.000–0.000)
Tahr activity	− 16.684 (− 32.455 to − 0.933)	
Log (tahr activity)		− 0.029 (− 0.037 to − 0.020)

The tussock height model is a GLMM that also includes random effects: catchment and plot as random intercepts, and tahr activity as a random coefficient. The vegetation cover model is a GLM with Poisson error structure. Significant fixed covariates (in bold) have 95 % confidence intervals that do not overlap zero

expressed by the negative coefficient for the quadratic term for aspect (Table 1). Total vegetation cover increased throughout the monitoring period (Fig. 5b). Total vegetation cover decreased non-linearly with increasing tahr activity, and most rapidly so at very low levels of tahr activity (≤ 15 % plots containing pellets; Fig. 5c).

Discussion

We used a representative network of 111 permanent vegetation plots to quantify the long-term impacts of non-native Himalayan tahr on native grassland communities in New Zealand's Southern Alps. Total vegetation cover and snow tussock height exhibited contrasting trends during 1990–2013, with the former increasing and the latter decreasing. Himalayan tahr had significant impacts on total vegetation cover and tussock height. The forms of the relationships differed, being linear (non-threshold) for tussock height and non-linear (threshold) for vegetation cover.

Montane grasslands often respond slowly to release from herbivory (Tanentzap et al. 2009; Pardo et al. 2015). In New Zealand, snow tussock heights increased following long-term release from herbivory

by domestic sheep (*Ovis aries*; Rose and Platt 1992) and red deer (Rose and Platt 1987; Tanentzap et al. 2009), and such a response was expected to occur following release from herbivory by Himalayan tahr. Surprisingly, our results showed that snow tussock height continued to decline across the eight study catchments during 1990–2013. The overall relationship between tussock height and tahr activity showed a negative linear decline in tussock height with increasing tahr activity, which was termed 'proportionate' by Norbury et al. (2015). This result is consistent with observed ongoing impacts of ungulates on palatable plant species in forests without refuge from herbivory (Pekelharing et al. 1998; Horsley et al. 2003). The temporal decline in tussock height, coupled with the negative effect of increasing tahr activity, suggest that adult tussocks were grazed by Himalayan tahr faster than they could recover. However, the impacts of tahr were spatially variable. In general, catchments with higher tahr activity (North Branch and Zora), had 'proportionate' (strong negative) relationships between tahr and tussock height, while those with lower tahr activity (Carney's Creek, Hooker, Townsend and Whymper) had 'insensitive' (flat slope) relationships (sensu Norbury et al. 2015). Some catchments (Arbor Rift, Hooker and Townsend)

Fig. 2 Estimated relationships (means and 95 % CIs) between tussock height and significant fixed effects from the best GLMM (based on Δ AIC). The GLMM included random intercepts for catchment and study plots; random coefficients for tahr activity; and fixed effects including tahr activity (proportion of plots with faecal pellets), tussock crown death (%), tussock live diameter (cm), aspect ($^{\circ}$), elevation (m) and year of monitoring

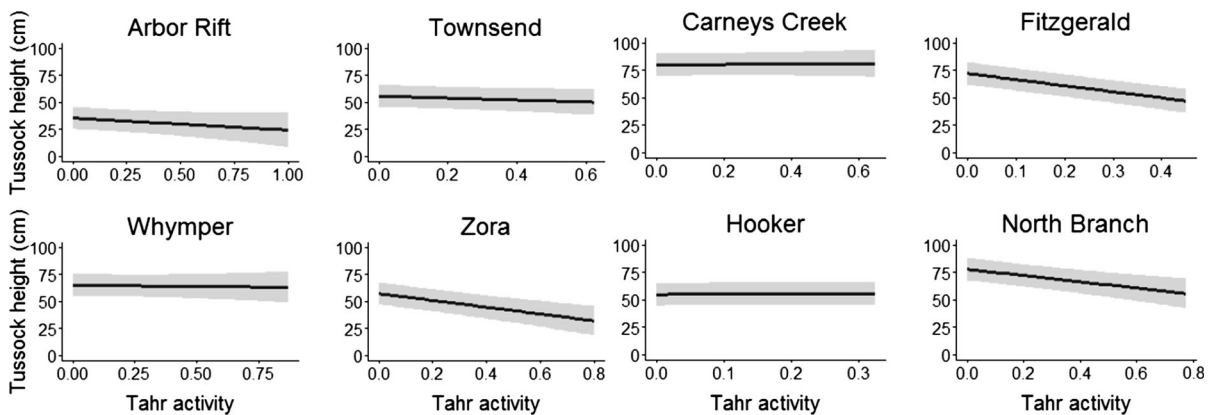
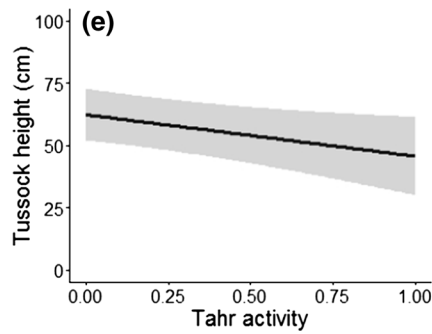
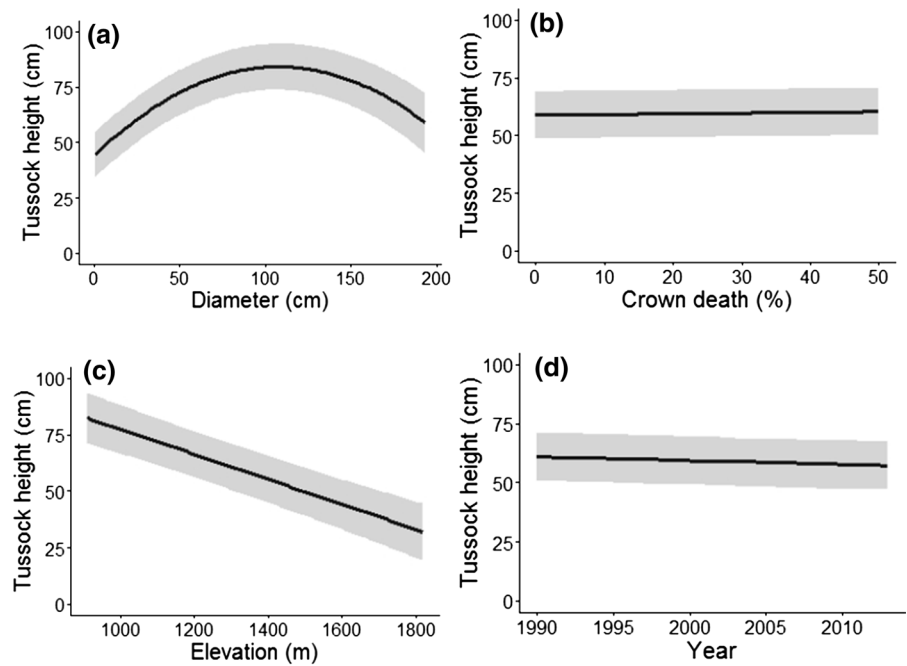


Fig. 3 Estimated relationships (means and 95 % CIs) between tussock height and tahr activity (proportion of plots with faecal pellets) from the best GLMM (based on Δ AIC), over the observed range of tahr activity levels at each study catchment.

The GLMM included random intercepts for catchment and study plots; random coefficients for tahr activity; and fixed effects including tahr activity, crown death (%), live diameter (cm), aspect ($^{\circ}$), elevation (m) and year of monitoring

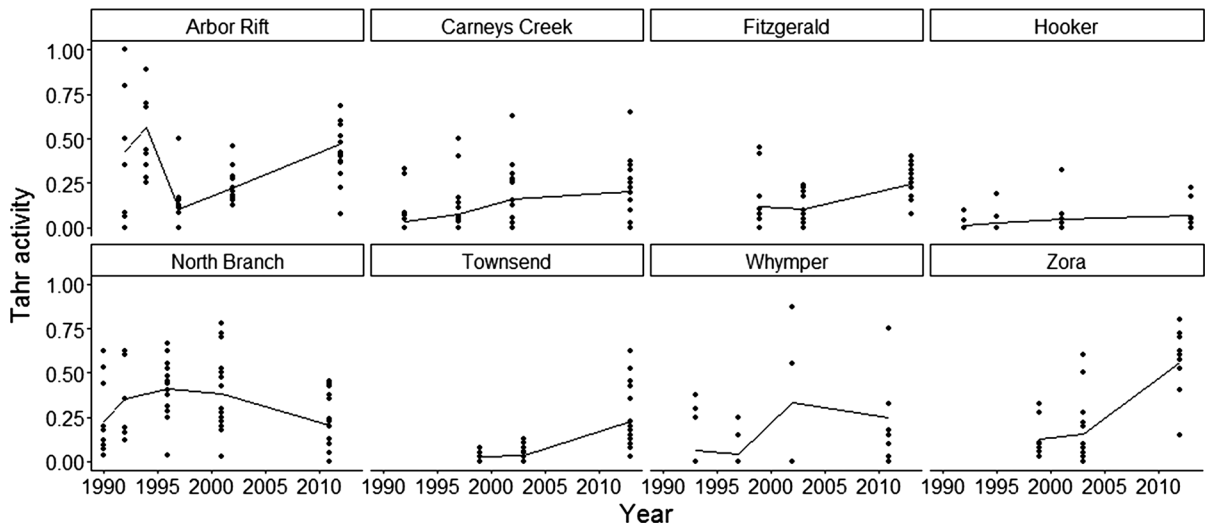


Fig. 4 Observed tahr activity levels (defined as the proportion of ‘active’ plots with faecal pellets) at each study catchment during the monitoring period. The lines indicate the mean values

were predicted to attain shorter adult tussocks, suggesting that they have not recovered from the impacts of very high tahr abundance (>30 km²; Tustin and Challies 1978) in the 1960s and early 1970s (Caughley 1970a). Recovery of *Chionochloa pallens* that were artificially defoliated to mimic severe red deer herbivory took close to three decades, and is predicted to take even longer for other *Chionochloa* species (Lee et al. 2000). Arbor Rift was predicted to have the shortest tussocks overall and had the highest observed activity of tahr, suggesting that tussocks at this catchment had not recovered from historically high tahr activity levels, but that they also continue to be impacted by current high levels of tahr activity.

Total vegetation cover exhibited a non-linear (threshold) relationship with tahr activity, with the largest declines occurring as tahr activity increased from low levels. This threshold relationship was termed ‘highly vulnerable’ by Norbury et al. (2015). The most likely explanation for this relationship is that the forbs, shrubs and sub-adult tussocks growing between the adult snow tussocks are less tolerant to current levels of tahr herbivory than adult snow tussocks (Augustine and McNaughton 1998; Mysterud 2006). Himalayan tahr in the Southern Alps eat many species other than snow tussocks (e.g. grasses such as *Poa*; herbs including *Celmisia* and *Aciphylla*; and shrubs such as *Gaultheria* and *Carmichaelia*; Parkes and Forsyth 2008). Trampling

by Himalayan tahr (sensu Duncan and Holdaway 1989) may also impact these species more than the adult snow tussocks.

Total vegetation cover increased during 1990–2013. One explanation for this seemingly counter-intuitive result is that the montane grasslands of the Southern Alps were still recovering from over-browsing by high densities of tahr, and in places also red deer, that existed prior to the advent of helicopter-based commercial harvesting in the 1970s (Tustin and Challies 1978; Nugent et al. 1987). Red deer also feed on tussocks and herbs in montane grasslands (Bee et al. 2010; Forsyth et al. 2010), feeding on an increasing number of unpalatable species as palatable species are progressively reduced (Nugent et al. 2001; Coomes et al. 2003). Unpalatable species recover faster than palatable species following reductions in ungulate density (Tanentzap et al. 2009). Therefore increases in total vegetation cover during the monitoring period (~20 years after very high ungulate densities had been reduced by helicopter-based commercial harvesting) may be due to the recovery of palatable species. These palatable species are likely to be tolerant to some herbivory as the observed highly-vulnerable relationship between total vegetation cover and tahr activity suggests ongoing impacts at observed levels of tahr activity. Increases in vegetation cover may also be related to warming climatic conditions (Molau 2010).

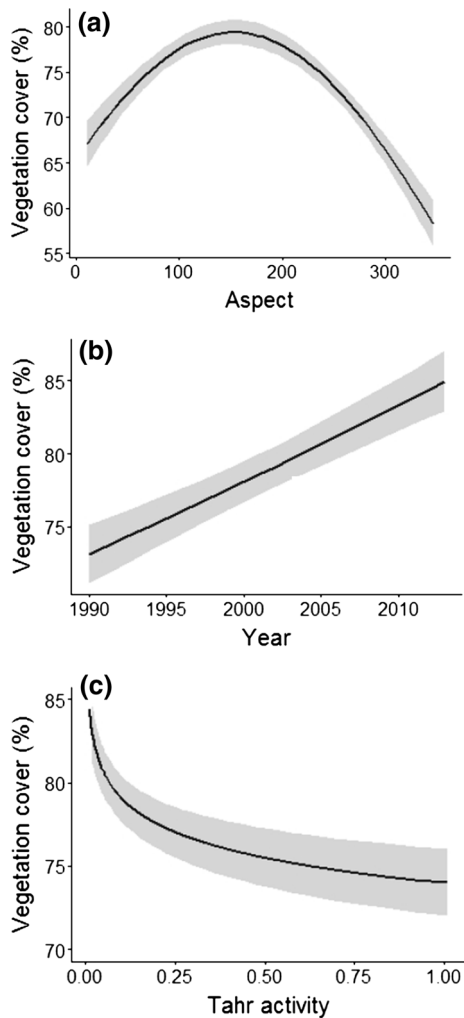


Fig. 5 Estimated relationships (means and 95 % CIs) between total vegetation cover and significant effects from the best GLM (based on Δ AIC). The GLM included a Poisson error structure and fixed effects including log of tahr activity, crown death (%), live diameter (cm), aspect ($^{\circ}$), elevation (m) and year of monitoring

Elevation and aspect are important determinants of the structure and composition of montane grasslands globally (Körner 1999) and in New Zealand (Mark et al. 1989; Wardle 1991). Adult snow tussock height declined with increasing elevation, a likely consequence of a shorter growing season and increasing snow cover (Körner 1999). Vegetation cover varied with aspect, being greatest on south-facing plots and least on north-facing plots. This relationship likely reflects higher soil moisture in the south-facing plots during the spring and summer growing season (Mark et al. 1989).

Norbury et al. (2015) called for increased use of single-factor damage (or density-impact) functions as an evidence-based approach for the management of invasive species (see also Hone 2007) but cautioned that failing to account for alternative factors known to also impact the response, could lead to spurious relationships. Our GLMMs and GLMs enabled multiple factors, additional to tahr activity, to be simultaneously accounted for (Zuur et al. 2009; Crawley 2013). For example, our tussock height model also allowed declines in tussock height with increasing elevation, as well as additional partial relationships with diameter, crown death and time. The partial relationship between the response (tussock height or vegetation cover) and tahr activity can be used to guide tahr management. By including tahr activity as untransformed or log-transformed (i.e. two competing models) we evaluated support for five of the six possible theoretical forms outlined by Norbury et al. (2015), including threshold and non-threshold relationships. Using an information-theoretic approach (Burnham and Anderson 2002) enabled us to formally evaluate the relative support for alternative relationship forms. We recommend this approach (i.e. assessing the significance of relationships with GLMs or GLMMs and comparing possible forms with AIC) as an improved version of damage functions that accounts for the effects of additional factors impacting the response variable, and evaluates support for alternative threshold and non-threshold relationships.

Management implications

Assessing whether the montane grasslands examined are at an 'ecologically acceptable' state, as suggested by the Himalayan Tahr Control Plan (Department of Conservation 1993) is challenging without guidelines of what is meant by ecologically acceptable. Nonetheless, our results indicate that overall tussock height declined proportionally with increasing tahr activity, during 1990–2013. The shape of this relationship provides no threshold value to guide management. However, the impacts of tahr were greatest at Zora and Arbor Rift, where tahr activity levels were high. Managers aiming to protect adult snow tussocks need to control Himalayan tahr so activity remains low in these catchments. More generally, total vegetation cover appears to still be recovering from the high tahr densities that occurred prior to the advent of helicopter-

based commercial harvesting (which targeted Himalayan tahr, red deer and alpine chamois) in the 1970s. The highly vulnerable relationship between vegetation cover and tahr activity suggests that the steepest declines in cover occur when tahr activity is very low (<15 % of pellet plots with pellets). This suggests that to achieve overall recovery of montane grasslands (including highly sensitive, palatable species), managers need to control tahr to very low activity levels (or exclude them completely). The need to maintain non-native ungulates at very low levels to facilitate recovery of palatable species has also been documented in forest ecosystems (Coomes et al. 2003; Wright et al. 2012).

Ungulates have a long history of being moved around the world to establish new populations for hunting (Donne 1924; Lever 1994; Long 2003), and Himalayan tahr were recently exported from New Zealand to South America for this purpose (Flueck 2010). Our study demonstrates deleterious long-term impacts of a non-native ungulate on the receiving native grassland community, even with some level of ungulate control. These impacts need to be explicitly considered when proposing to introduce ungulate species to new locations.

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