Impacts of Himalayan tahr (*Hemitragus jemlahicus*) on snow tussock in the Southern Alps from 1990–2023

Prepared for: Department of Conservation

April 2025

Impacts of Himalayan tahr on snow tussock in the Southern Alps from 1990–2023

Contract Report: LC4553

Amy Whitehead, Laureline Rossignaud, Sarah Richardson

Manaaki Whenua – Landcare Research

Reviewed by:	*Approved for release by:*
Duane Peltzer	Gary Houliston
Principal Scientist – Ecosystem Ecology	Portfolio Leader – Plant Biodiversity & Biosecurity
Manaaki Whenua – Landcare Research	Manaaki Whenua – Landcare Research

Contents

Summary

Project and client

- The impacts of Himalayan tahr (*Hemitragus jemlahicus*) on alpine vegetation have been monitored in eight study catchments in the Southern Alps since 1990. In 2024 the Department of Conservation (DOC) commissioned Manaaki Whenua – Landcare Research (MWLR) to update the most recent analysis published in 2014 to include data collected since 2013.
- The overall aim of this report was to determine whether there have been changes in native snow tussock height and vegetation cover from 1990 to 2023, and whether those changes correspond to changes in the relative activity of tahr and other non-native ungulates or co-occurring hares.

Objectives

The specific objectives of this report were to:

1. evaluate whether the activity index of tahr and other ungulates (i.e. relative abundance) at the plot level can be related to the activity index of hares (i.e. relative abundance) and catchment-level estimates of tahr density (i.e. absolute abundance)
2. determine whether the activity index of tahr and other ungulates at the plot level is related to changes in snow tussock height (particularly *Chionochloa pallens, C. flavescens, C. rigida*), and in overall vegetation cover since the catchments were first measured
3. evaluate whether changes in snow tussock height and vegetation cover can be related to catchment-level estimates of tahr density to inform intervention densities for tahr that will maintain tussock condition and allow vegetation recovery.

Methods

- Individual snow tussocks were measured on 117 variable-area plots across eight study catchments. Each plot initially contained at least 20 individuals across all snow tussock species and was measured up to five times since 1990. The percentage of each plot covered in vegetation was also measured.
- The proportion of pellet plots with faecal pellets from ungulates (assumed to be mostly tahr) and hares was used as an index of ungulate and hare activity, respectively, around each vegetation plot.[1] Estimates of tahr density (animals/km^2) were also made by counting the number of tahr in each study catchment, although the method has changed over time. From 2016 onwards tahr counts were undertaken by helicopter on an 8 km grid that did not align spatially with the eight study catchments. Therefore, for this

[1] From 1994 to 1999 the pellet plots were the same 1 m^2 quadrats used for the vegetation monitoring, but thereafter the pellet plots were 40 or 64 circular plots (each 1 m^2) depending on terrain, set at 5 m intervals on eight transects radiating out from each vegetation plot

period we estimated catchment-level tahr density using environmentally relevant predictors in a random forest model.

- The relationship between plot-level ungulate activity and hare activity was assessed using a binomial generalised linear mixed effects model (GLMM). We then assessed the relationship between catchment-level estimates of tahr density and ungulate activity around the vegetation plots using a GLMM with a binomial distribution.
- The relationship between snow tussock height and ungulate activity over time was assessed using a GLMM with a Gaussian distribution. Alongside ungulate activity and year of monitoring as predictors, supplementary covariables were included in the models to account for tussock growth (i.e. crown death, live diameter) and site characteristics (i.e. aspect, elevation).
- The change in vegetation cover over time and in relation to ungulate activity was assessed using a GLMM with a beta distribution. Site characteristics (aspect, elevation) were included as predictors.

Results and discussion

- Tahr density (animals/km^2) decreased significantly over time in the two catchments with the highest densities (Arbor Rift, Zora), but increased significantly in the Hooker catchment. Tahr densities based on modelled estimates probably exceeded the intervention densities set in the *Himalyan Thar Control Plan* for all catchments in the last two monitoring periods.
- Meanwhile, ungulate activity (proportion of plots with ungulate pellets) significantly increased over time in six of the eight study catchments, but patterns in hare activity (proportion of plots with hare pellets) were more variable. There was no significant relationship between ungulate and hare activity. Tahr density increased significantly with ungulate activity, although the relationship is weak.
- Tussock height significantly decreased with increasing ungulate activity across all catchments. Tussock height was higher at intermediate live diameter, and showed a negative relationship with elevation but no relationship with crown death or aspect. In addition, tussock height showed a significant decline over time and across all catchments. This pattern suggests that snow tussocks have not been recovering and might still be affected by ungulate and hare activity.
- Conversely, vegetation cover increased across all catchments throughout the monitoring period, suggesting continuing vegetation recovery. However, we did not observe a significant relationship between vegetation cover and ungulate activity, and it is not known how other vegetation species are responding in these catchments. For example, it is possible that increasing vegetation cover is being driven by compensatory growth from other plant species that are less susceptible to ungulate browse.

Recommendations

- The current aerial survey method for estimating tahr density is designed for Management Unit or range-wide scales and is not designed for comparing densities in particular study catchments to the intervention thresholds in the *Himalayan Thar Control Plan*. We suggest that catchment-level density estimates using the double-count method be undertaken in conjunction with the vegetation monitoring. Introducing trail cameras alongside faecal pellet plots may enhance monitoring efforts by providing insights into the presence of other mammalian herbivores.
- Despite these limitations, the available data suggest that intervention densities have been exceeded in all catchments over the past decade, contributing to declines in tussock height. Further reduction of tahr densities appears to be required to mitigate ongoing vegetation impacts.
- While vegetation cover has increased since the previous report, it is unclear which plant species are driving this recovery. Additional information would need to be analysed to determine whether changes in vegetation cover are being driven by changes in tussock cover or by changes in other, less palatable plant species.
- Long-term monitoring in the eight study catchments should be continued to maintain the valuable dataset, but an alternative programme is needed to evaluate the effectiveness of intervention densities at maintaining ecological integrity within the tahr management units. Such a monitoring programme needs to ensure that tahr densities are measured robustly at the scale and location of the vegetation monitoring.

1 Introduction

Himalayan tahr (*Hemitragus jemlahicus*) were introduced to New Zealand in 1904 for game meat. Their populations grew rapidly, reaching densities of over 30 tahr/km^2 and spreading across approximately 6,150 km^2 of the Southern Alps (Forsyth & Tustin 2005; Parkes 2006). Within their range tahr mostly occupy shrublands and tussock grasslands above the treeline, but move to other vegetation types below the treeline both within and between seasons (Tustin & Parkes 1988). For example, male and female tahr typically occupy different habitats throughout most of the year, with females and juveniles present in high-altitude areas while males range more widely, often at lower altitudes. However, during the rut (late May to July), adult males move into areas primarily occupied by females and their offspring (Forsyth & Tustin 2005).

Snow tussocks (*Chionochloa* spp.) are an important component in the diet of tahr, especially in winter, while other grasses (*Poa colensoi* and *Rytidosperma setifolium*) and sedges (e.g. *Schoenus pauciflorus*) are more important in the summer (Tustin & Parkes 1988, Parkes & Forsyth 2008). Woody plants (particularly *Dracophyllum* spp.) and herbaceous species (e.g. *Celmisia* spp., *Aciphylla* spp., *Ranunculus lyallii*) are also important in their diet. Other mammalian herbivores, especially chamois (*Rupicapra rupicapra*), brown hares (*Lepus europaeus*), and red deer (*Cervus elaphus scoticus*), occupy the same habitats as tahr and consume many of the same native plant species (Forsyth et al. 2000). While their diets overlap, tahr tend to consume more grasses and fewer herbs and shrubs than chamois (Parkes & Forsyth, 2008). These dietary preferences meant that the high densities of tahr (and other browsing mammals) observed in the early 20th century negatively affected native alpine vegetation (Anderson & Henderson 1961; Burrows 1974), causing a shift from tall snow tussock species (*Chionochloa* spp.) to shorter tussock species (e.g. *Festuca* spp.) (Caughley 1970).

In response to these impacts, the government removed all legal protection from tahr in 1930 and began population control efforts. These initial efforts saw limited success until the introduction of aerial hunting by helicopter in the late 1960s. Between 1971 and 1982 over 90% of the tahr population was culled, reducing their numbers to a few thousand. At these lower densities the economic viability of harvesting tahr for game meat diminished. Also, recreational hunters were lobbying to maintain tahr as a hunting resource. The result was a moratorium on commercial hunting in 1983. This allowed the population to recover to around 10,000 animals over a contracted range of approximately 5,000 km^2, from the southern catchments of the Rakaia River in the north to the head catchments of Lake Hawea in the south (Parkes & Tustin 1985).

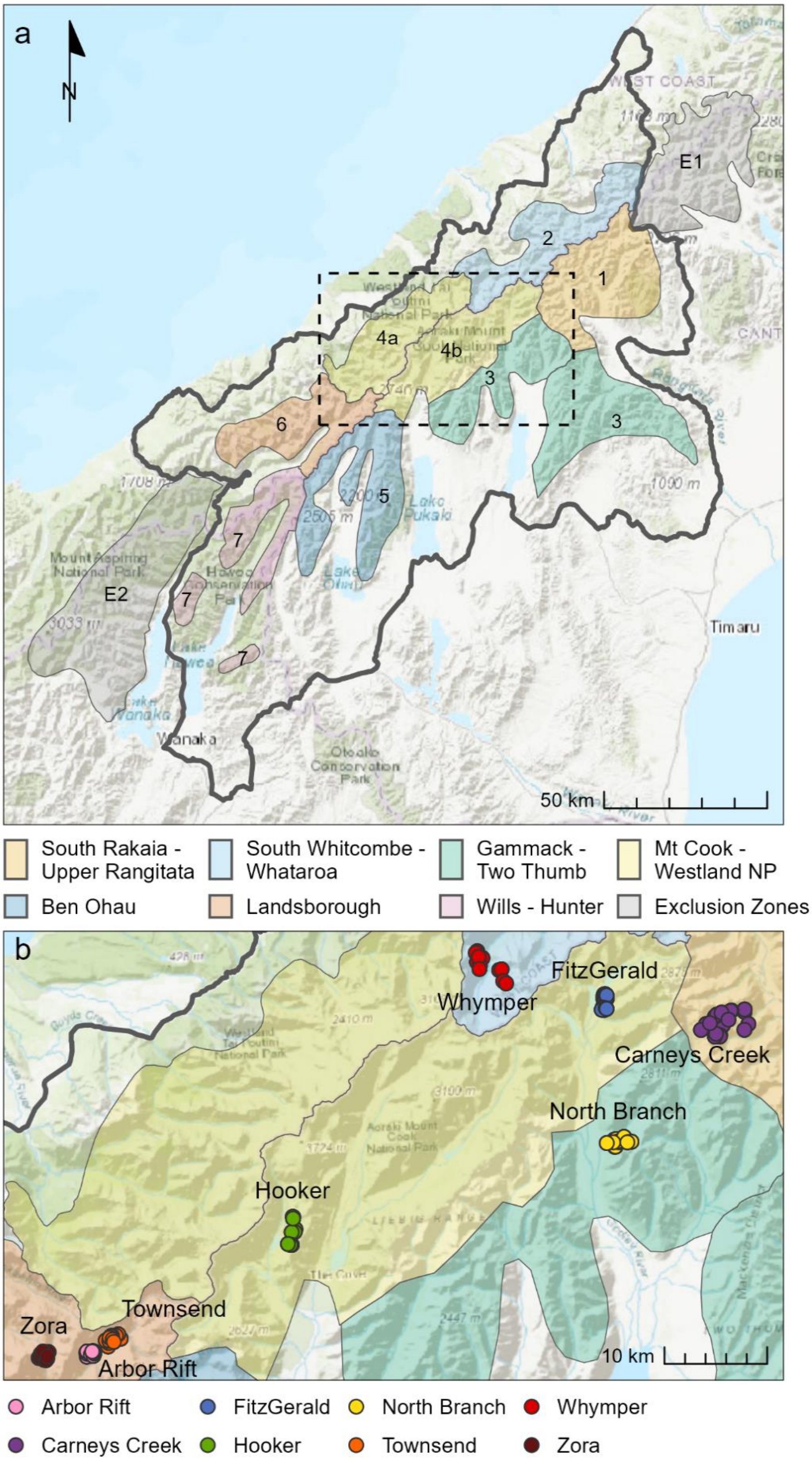
In 1984 the government solicited public comments on tahr management and developed a draft management strategy. Initially created under the New Zealand Forest Service's 'balanced use' mandates, this draft strategy was revised after the Department of Conservation (DOC) was established in 1987, which prioritised the protection of native biodiversity. The draft strategy favoured tahr eradication, but a 1988 DOC discussion document concluded that eradication was not feasible due to limited government access across land tenures (Parkes 1988). Consequently, the Minister of Conservation published the *Himalayan Thar Management Policy* (Department of Conservation 1991), which acknowledged the role of recreational hunters and set a range limit of 6,000 km^2 and a population cap of 10,000 animals. This cap, which was thought to represent about 20% of the carrying capacity, was intended to prevent vegetation decline by ensuring the population was not limited by food availability (Forsyth & Caley 2006). However, this assumption required further testing.

Following the publication of this policy, the *Himalayan Thar Control Plan* was developed (Department of Conservation 1993). The plan outlined how to maintain the population limit of 10,000 individuals across various management units (Figure 1a). It specified annual removal targets of c. 2,000 tahr (Parkes 2006) and density limits ranging from less than 1 to 2.5 tahr/km^2 across seven geographical management units (Table 1). Two exclusion zones with density targets of 0 tahr/km^2 were also identified to prevent the spread of tahr beyond their existing range. The plan stipulated that recreational, commercially guided, and game hunters would maintain tahr populations below the intervention densities, with DOC providing additional control if necessary. The plan also raised the question of whether these intervention densities were adequate to maintain alpine vegetation in an 'ecologically acceptable' state, with later research intended to define this state and adjust intervention densities accordingly.

The effects of tahr on snow tussock communities have been monitored in eight subjectively located study catchments in the Southern Alps since 1990 (Table 1). Tall snow tussocks, particularly *Chionochloa pallens*, *C. flavescens*, and *C. rigida*, were selected as key vegetation indicators in earlier analyses of tahr impacts (Parkes & Thomson 1999; Parkes et al. 2004; Cruz et al. 2014). This selection was based on several key factors. For a start, *Chionochloa* spp. dominate many of the habitats frequented by tahr, with animals spending c. 39% of their time in snow tussock communities (Tustin & Parkes 1988). *Chionochloa* spp. are also the largest component (30% by dried weight) of the tahr diet, and earlier work in Carneys Creek showed that snow tussocks were almost completely removed when tahr were at very high densities. However, tussock condition dramatically improved after tahr densities were reduced (see plates 1 and 2, page 8, of the *Himalayan Thar Control Plan*; Challies 1992; Department of Conservation 1993).

Although other introduced herbivores co-occur with tahr in snow tussock-dominated habitats, their impact on *Chionochloa* spp. varies. Research indicates that *Chionochloa* spp. make up only 2.3% of chamois diets overall, although tussocks are consumed more frequently in autumn and winter. In contrast, possums (*Trichosurus vulpecula*) do not consume *Chionochloa* spp. at all (Parkes & Forsyth 2008). These findings suggest that neither species exerts significant pressure on snow tussock communities. However, the impact of hares and red deer across the tahr range remains uncertain. Given that *C. pallens* is an important dietary component for both species in other alpine areas (Flux 1967; Mark 1989), it is likely that they also contribute to changes in snow tussock condition. Overall, *Chionochloa* spp. are central to the diet and habitat use of tahr, making them critical indicators for assessing tahr-related impacts on alpine vegetation.

In 2024 DOC commissioned Manaaki Whenua – Landcare Research to update the analyses of Cruz et al. (2014) using monitoring data collected from 1990 to 2023.



Tiles © Esri - Esri, DeLorme, NAVTEQ, TomTom, Intermap, iPC, USGS, FAO, NPS, NRCAN, GeoBase, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), and the GIS User Community

Figure 1. Maps of a) the tahr management units and exclusion zones, and b) the location of the vegetation plots within each study catchment (see Table 1). The dashed line in panel a) indicates the approximate location of panel b), while the bold solid line indicates the feral range of tahr as defined in the national *Himalayan Thar Control Plan* (Department of Conservation 1993).

Table 1. Study catchments in relation to the management units (MUs) and the associated intervention densities defined in the *Himalayan Thar Control Plan* (Department of Conservation 1993). The study catchments and management units are shown in **Error! Reference source not found.**.

Catchment	Area (km^2)	Management unit	Intervention density ($tahr/km^2$)	Dominant snow tussock
Arbor Rift	4.5	Landsborough (MU6)	1.5	*C. pallens*
Carneys Creek	19.0	S. Rakaia – Upper Rangitata (MU1)	2.5	*C. pallens*
FitzGerald	8.0	Mt Cook – Westland National Parks (MU4b)	<1.0	*C. pallens*
Hooker	17.5	Mt Cook – Westland National Parks (MU4b)	<1.0	*C. pallens*
North Branch	20.0	Gammack – Two Thumb (MU3)	2.0	*C. rigida*
Townsend	5.0	Landsborough (MU6)	1.5	*C. pallens*
Whymper	24.0	S. Whitcombe – Whataroa (MU2)	2.0	*C. pallens*
Zora	6.0	Landsborough (MU6)	1.5	*C. pallens*

2 Objectives

The overall aim of this report is to determine whether there have been changes in snow tussock height and vegetation cover from 1990 to 2023, and whether those changes correspond to changes in the activity index (measured as the proportion of pellet plots with faecal pellets) of tahr and other ungulates, or co-occurring hares.

Following the approach of Cruz et al. (2014), we have focused on tussock height as a proxy for tussock condition, because tahr at high densities can have an obvious effect on tussock height without increasing tussock mortality in the short term. Since 2016 DOC has collected data on tahr density (i.e. absolute abundance) using counts from helicopters on an 8 km grid of sampling locations (Department of Conservation 1993, 2018), and there is an opportunity to evaluate whether these data can be used to interpret changes in snow tussock height from the eight study catchments.

The specific objectives of this research were to:

1 evaluate whether the activity index of tahr and other ungulates (i.e. relative abundance) at the plot level can be related to the activity index of hares (i.e. relative abundance) and catchment-level estimates of tahr density (i.e. absolute abundance)

2 determine whether the activity index of tahr and other ungulates at the plot level is related to changes in snow tussock height (particularly *Chionochloa pallens, C. flavescens, C. rigida*), and overall vegetation cover since the sites were first measured

3 evaluate whether changes in snow tussock height and vegetation cover can be related to catchment-level estimates of tahr density to inform intervention densities for tahr that will maintain tussock condition and allow vegetation recovery.

3 Methods

3.1 Study areas

Eight study catchments were subjectively selected within the area of the Southern Alps occupied by tahr (Figure 1b). The catchments occur across five of the seven tahr management units (Table 1) and were typically located in areas permanently inhabited by adult female tahr and their young, including juveniles from the previous year (Forsyth & Tustin 2005). The impacts of the seasonal concentration of tahr in these alpine habitats may be more apparent. The dominant snow tussock species in seven of the eight catchments is *Chionochloa pallens*, with North Branch dominated by *C. rigida* (Table 1).

3.2 Vegetation plot design

Permanently marked plots (n = 117) were established by the Forest Research Institute and Landcare Research in five catchments between 1990 and 1993 and a further three catchments in 1999 (Rose & Allen 1990; Thomson, Parkes & Coleman 1997; Thomson, Parks, Coleman & McGlinchy 1997; Parkes & Thomson 1999). All plots have been remeasured at least three times since establishment (Figure 2; Table A3.1). The plots were subjectively located in areas dominated by snow tussock species (*Chionochloa* spp.; Table 2) and known to be used by tahr (Parkes et al. 2004). They were generally located on side slopes between 1,150 and 1,600 m above sea level (see photographs in Parkes et al. 2004).

Each permanent plot was described following the Recce method (Allen 1993; Department of Conservation 2019). Vegetation ground cover (percentage) over time, elevation (in metres) and aspect (in degrees) of each plot were recorded and used in our analysis. Each vascular plant species was identified and associated with a height tier, as follows (Allen 1993; Department of Conservation 2019):

- Tier 3 = 5–12 m
- Tier 4 = 2–5 m
- Tier 5A = 1–2 m
- Tier 5B = 0.3–1 m
- Tier 6A = 0.1–0.3 m
- Tier 6B = 0–0.1 m

and a cover class using a modified Braun-Blanquet scale:

- 1 = <1%
- 2 = 1–5%
- 3 = 6–25%
- 4 = 26–50%
- 5 = 51–75%
- 6 = 76–100%.

Plots were of variable area, ranging from 2 to 400 m^2 (Table 2), sufficient to include a minimum of 20 snow tussocks, usually *Chionochloa pallens*, *C. flavescens* or *C. rigida* and their hybrids, but with a small proportion (<15 %) of *C. crassiuscula* and *C. macra* (when they were mistaken for one of the other species) (Rose & Allen 1990). Each plot was subdivided into 1 m^2 contiguous quadrats in which all live snow tussocks were identified to species, mapped, and measured. Measurements for each individual plant included basal live diameter (cm), maximum height of the extended live leaves (cm), and the proportion of crown death estimated to the nearest 10%. Individual tussocks were assigned to an age class following Rose and Platt 1990:

- seedlings (≤1 cm live diameter)
- juveniles (1 to ≤5 cm live diameter)
- mature (>5 cm diameter and ≤50 % crown death)
- senescent (>5 cm diameter and >50 % crown death)

Table 2. Maximum number of surveyed plots, and number of plots with available plot size information and associated mean plot area (± SD) in each study catchment.

Catchment	Maximum number of plots	Mean plot area (m2)	Mean elevation (m)
Arbor Rift	18	13.78 ± 9.16	1146.02 ± 99.71
Carneys Creek	20	22.55 ± 18.81	1445.24 ± 169.76
FitzGerald	15	10.75 ± 5.65	1433.59 ± 93.98
Hooker	9	18.56 ± 3.05	1470.89 ± 134.58
North Branch	19	39.05 ± 17.72	1343.12 ± 261.72
Townsend	15	10.12 ± 4.43	1111.55 ± 63.10
Whymper	12	38.54 ± 108.73	1285.27 ± 107.10
Zora	15	10.40 ± 7.97	1247.95 ± 127.51

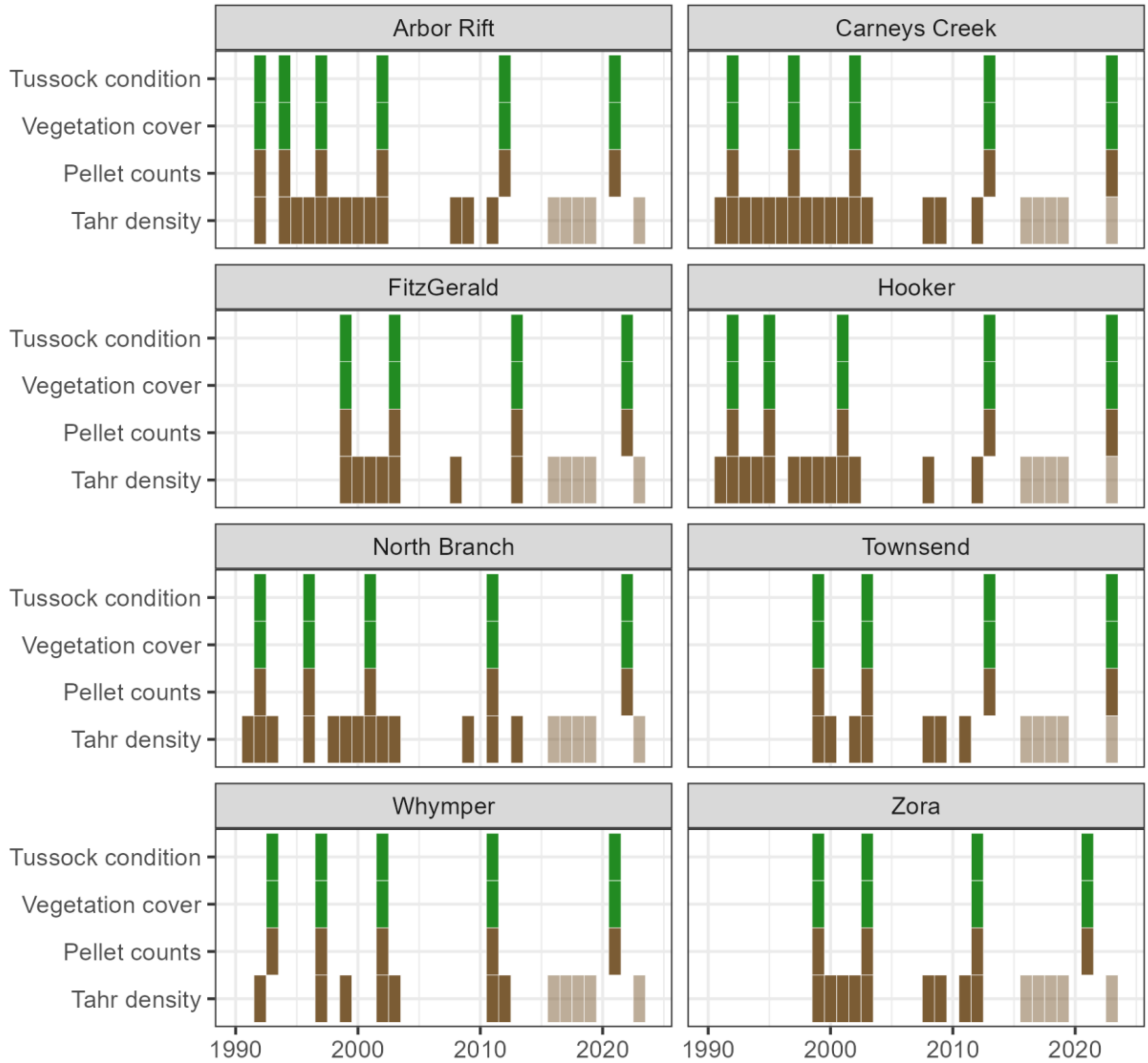


Figure 2. Monitoring of vegetation (green) and animal (brown) metrics over time in each of the eight study catchments. Light brown indicates the occurrence of tahr density monitoring within the tahr feral range that was not spatially aligned with the study catchments (see section 3.3).

3.3 Tahr and other herbivores

The number of tahr within each study catchment has been counted at irregular intervals since 1990 (Figure 2), although the method used has changed several times over the monitoring period (Figure 3). Most counts were made in late February to early March (i.e. before the start of the breeding season), before adult males disperse into the females' range. The earliest counts were attempts at a census, typically with two observers counting all visible animals using binoculars or spotting scopes from fixed viewing points, as described by Challies (1992). Later ground-based counts reduced the number of times each sub-area in the study catchments was assessed for each count, with counts representing the minimum number of tahr present (see Parkes et al. 2004).

A ground-based double-count method (Forsyth & Hickling 1997) was used at some study sites between 1998 and 2000 in an attempt to provide an estimate of the population size with a measure of variance. From 2008 to 2013 ground-based counts were replaced by irregular aerial counts using a single pass by a helicopter or counts made during aerial hunting. For all data collected before 2014, the area of observable habitat surveyed within each catchment was estimated and a density of tahr was calculated for each catchment (animals/km^2). However, the changing methods mean that these estimates of density are unlikely to be comparable.

Between 2016 and 2019 aerial surveys for tahr were undertaken at 117 × 4 km^2 monitoring plots situated at the vertices of an 8 km grid across the seven management units and two tahr exclusion zones. These aerial survey plots did not spatially align with the vegetation monitoring plots. Each 4 km^2 plot was surveyed three times by helicopter, with an observer counting the number of tahr present and identifying them to age class and sex, where possible (see Department of Conservation 2018 for a detailed methodology). The repeated counts at each plot were used to calculate tahr abundance and density, correcting for imperfect detection, using a dynamic N-mixture model for open populations (Ramsey et al. 2022). A second survey of a subset of 42 plots from the initial monitoring period was conducted in 2023 using the same approach (Dave Ramsey, Department of Energy, Environment and Climate Action, Victoria State Government, Australia, pers. comm., 15 May 2024).[2]

As pointed out by Sparrow and Kelly (2000), the vegetation plots in each catchment are pseudo-replicates if the 'treatment' variable is a catchment-level estimate of tahr density. Therefore, an index of ungulate activity at each plot was also measured to provide estimates of impact at a spatial scale matching the vegetation plots. This index was the proportion of 'pellet plots' containing ungulate faecal pellets. From 1994 to 1999 these pellet plots were the same 1 m^2 quadrats used for the vegetation monitoring, but thereafter the pellet plots were 40 or 64 circular plots (each 1 m^2) depending on terrain, set at 5 m intervals on eight transects radiating out from each vegetation plot. We pooled indices of ungulate activity from quadrats and circular plots in the analyses.

Other ungulate species (e.g. chamois, red deer) may be present in the study catchments (Bellingham et al. 2018), although little information is known about their distribution and abundance. A few chamois were seen in the Carneys Creek, Whymper, and North Branch study catchments in some years. However, since chamois rarely eat snow tussock (Yockney & Hickling 2000; Parkes & Forsyth 2008), we did not include them in the estimates of animal density. Any chamois or deer faecal pellets that may have been on the pellet plots could not be reliably distinguished from those of tahr and are therefore included in the ungulate activity index.

Other browsing herbivores are present in the study catchments, with the presence of hare and possum faecal pellets recorded on the pellet plots. Diet studies based on hare pellets and feeding observations have shown that *Chionochloa* species form an important part of hare diet (Flux 1967; Horne 1979; Perry 2003). Therefore, an index of hare activity was calculated using the same protocol as that used to determine ungulate activity. However, we

[2] Additional aerial monitoring for tahr density was conducted in MU1 and MU3 in 2021 (Ramsey & Forsyth, 2021) but this information was not available to MWLR at the time this report was prepared.

did not calculate an index of possum activity, as *Chionochloa* species have not been detected in diet studies of possums (e.g. Glen et al. 2012).

3.4 Statistical analyses

All analyses were conducted in R (R Core Team 2024, Version 4.4.0). A brief description of the general modelling approach used to develop and assess the statistical models generated for this report is described below, with specific model details described under each section.

For each response variable (described in more detail below), we first used the *fitdistrplus* package (Delignette-Muller 2015) to identify the most appropriate distribution to use for subsequent modelling. We then developed a candidate set of models that included all sensible combinations of the available predictor variables and random factors required to answer the specific question. Individual models were developed using the *lme4* or *glmmTMB* packages (Bates et al. 2015; Brooks et al. 2017), and the best model within the candidate set was identified as the model with the lowest AICc value using the *MuMIn* package (Bartoń 2024).

The best model for each response was assessed to ensure that it met assumptions of homoscedasticity, overdispersion, and zero-inflation using the *DHARMa* package (Hartig 2022). We identified significant covariates using a Wald chi-square test with the *Anova* function from the *car* package (Fox & Weisberg 2019). Model predictions for the significant fixed effects were generated using the *ggeffects* package (Lüdecke 2018) and plotted against the raw data to visualise the relationships.

3.4.1 Tahr density

Catchment-level estimates of tahr density were repeatedly made between 1990 and 2013 for the eight study catchments. However, the most recent counts (2016–2023) on the 4 km^2 grid did not spatially align with the vegetation monitoring plots, so we were not able to directly estimate the density of tahr within each study catchment over this period. Instead, we used random forest models (Breiman 1984, 2001; Cutler et al. 2007) to predict tahr density within each study catchment for each period (2016–2019, 2023).

We selected environmental predictors likely to be important in structuring tahr density through physical habitat provision and food availability (Table A1.1). These predictors described characteristics of the climate, topography and land cover in the landscape where the aerial monitoring occurred. A full description of the modelling approach is described in Appendix 1. To assess changes in the estimated catchment-level tahr density over the monitoring period (1990–2023), we developed a candidate set of generalised linear models (GLMs) using a gamma distribution, with year and catchment included as fixed effects.

3.4.2 Plot-level ungulate and hare activity

Hares are known to affect the growth and recovery of snow tussocks (Rose & Platt 1992) and they occur across the feral range of tahr. We used the two indices of ungulate and hare activity at the vegetation plots to assess the potential relative impact of these species on tussock height. The activity indices represented the proportion of pellet plots that contained faecal pellets of ungulates or hares at each vegetation plot. This approach allowed us to account for the changing number of pellet plots surveyed over time. The activity data were transformed to avoid zeroes and ones before analysis, using

$$\frac{y(n-1)+0.5}{n}$$

where y is the activity data and n is the total sample size, as per Smithson and Verkuilen (2006). We developed an initial candidate set of GLMs that used a binomial distribution to assess temporal trends in hare activity and ungulate activity, with catchment and year included as fixed effects.

We then fitted a second candidate set of models investigating the relationship between ungulate activity and hare activity, with catchment, year, and hare activity nested within catchment included as random effects.

3.4.3 Catchment-level ungulate activity and tahr density

The index of ungulate activity (based on the proportion of pellet plots with ungulate faecal pellets) provides a proximal indicator of the level of ungulate activity on each vegetation plot and has been monitored using relatively consistent methods over the duration of this monitoring programme. In contrast, measurements of tahr density (animals/km^2) have been undertaken at the scale of the study catchments or, more recently, at 4 km^2 plots across the feral range using several different methods. Tahr density is specified as the trigger for DOC intervention at the scale of management units (Table 1) under the national *Himalayan Thar Control Plan* (Department of Conservation 1993). However, the plan recommended testing the validity of the assumption that these intervention densities will allow vegetation recovery.

In order to test this assumption (i.e. relate changes in tussock height and vegetation cover to tahr densities during the monitoring period) and to evaluate this relationship against the intervention densities in the tahr management plan, we first needed to relate catchment-level measures of tahr density to the catchment-level ungulate activity index (calculated as the mean proportion of pellet plots across the catchment with ungulate faecal pellets).

We assessed the relationship between the catchment-level estimates of tahr density and ungulate activity using a candidate set of GLMM with a binomial distribution, where year and catchment were included in the model as random effects. This relationship could only be assessed using data where both metrics were collected within a catchment in the same year (e.g. where pellet count and tahr density boxes align in Figure 2).

Our analysis differs slightly from that presented in Cruz et al. (2014). In that report, the authors predicted ungulate activity from tahr density, whereas we predict tahr density from ungulate activity. This second approach means that the pellet count data that are collected during the routine monitoring could potentially be used to estimate tahr density within a catchment and allows comparison with appropriate intervention density for informing management decisions.

3.4.4 Mature tussock height

Tussock species were difficult to distinguish in the field and some hybrids were also present, so *Chionochloa* species were pooled for analysis. For comparability with Cruz et al. (2014), we focused our analyses on changes in the condition of mature tussocks only, where tussock condition was defined using plant height, live basal diameter, and the % of crown death.

We assessed the relationship between the height (cm) of mature tussocks and ungulate activity using GLMMs with a Gaussian distribution from the *lme4* package (Bates et al. 2015). We selected tussock height as the response variable for consistency with previous work done by Cruz et al. (2014). Tussock height was chosen rather than some combined index of tussock condition because ungulates (especially tahr) at high densities have an obvious effect on tussock height (see photographs of snow tussocks on page 8 in Department of Conservation 1993).

In addition to ungulate activity, we also included crown death (percentage), live diameter (centimetres), aspect (degrees), elevation (metres), and year of monitoring as fixed effects that may potentially influence tussock height. Diameter was included as a quadratic effect to allow for the non-linear relationship presented by Rose and Platt (1990). While Cruz et al. (2014) included aspect as a quadratic effect to allow for north-facing slopes, the cyclic component of aspect, whereby 0 is equivalent to 360, is better captured by calculating the cosine of aspect (Stage 1976; Brenning & Trombotto 2006). The cosine of aspect generates values between –1 (south-facing) and 1 (north-facing) and was included as a linear term.

In order to properly estimate the significance of the relationships, each numerical variable (i.e. ungulate activity, elevation, diameter, year, cosine of aspect, and quadratic terms) was scaled before running the GLMM models by subtracting the mean of the variable and dividing by 2 standard errors using the *arm* package (Gelman & Su 2024). In addition, we included plot ID within catchments as random effects to account for variable sampling effort between catchments and unaccounted differences between plots. Ungulate activity was also added to the models as a random coefficient to account for possible variation in the relationship between ungulate activity and tussock height across catchments (i.e. allows the slope of the relationship to vary by catchment).

Significant covariates were identified using a Wald chi-square test with the *Anova* function from the *car* package (Fox & Weisberg 2019). The fitted means of tussock height in relation to each significant fixed effect were predicted by keeping all other significant covariates at their mean values.

An additional mixed-effects model that included a random coefficient for year was also assessed (to account for possible differences between sites in changes in tussock height through time), but the small variance suggested it caused over-fitting (the data did not support differences in the relationship between height and year between sites) and so it was dropped from further analyses.

3.4.5 Vegetation cover

We assessed changes in overall vegetation cover (measured between 0 and 100%) using GLMMs with a beta distribution from the *glmmTMB* package (Brooks et al. 2017). This distribution is recommended when analysing proportion data (Damgaard & Irvine 2019). The proportion of overall vegetation cover was transformed to avoid zeroes and ones before analysis (Smithson & Verkuilen 2006). The vegetation cover was predicted from ungulate activity, the cosine of aspect, year of monitoring, and elevation, with plots within catchments included as random effects. All numerical variables were scaled before running the GLMMs by subtracting the mean of the variable and dividing by two standard errors.

4 Results

4.1 Tahr density

Overall, the random forest models of tahr density had satisfactory model performance when assessed against the criteria of Moriasi et al. (2015), with $R^2 = 0.35 \pm 0.01$, NSE = 0.34 ± 0.01, and PBias = 6.01 ± 1.47. However, the models tended to overpredict tahr density at low densities and underpredict tahr density at high densities (Figure A1.2). The most important predictor across all models was the percentage of alpine grass–herbfield within each 4 km^2 grid cell, with tahr density increasing with increasing levels of this vegetation class (Figure A1.3, Figure A1.4). Predicted tahr density decreased with increasing mean annual precipitation but increased at higher elevations. Monitoring period was the least important predictor but was retained in the models to allow prediction of tahr density for both periods. A full description of the results of the random forest modelling is provided in Appendix 1.

Mean catchment-level predictions of tahr density ranged from 2.90 to 5.82 animals/km^2 over the 2016–2019 and 2023 monitoring periods. There was greater variation in tahr density predicted in the Carneys Creek, North Branch, and Whymper catchments, where individual vegetation plots are located over a wide geographical area that encompasses a broad range of environmental conditions (Figure 1; Figure A1.5; Figure A1.6). However, there was little difference in the predicted tahr density between the two monitoring periods. Tahr densities in both periods in five of the eight catchments exceeded the intervention densities defined for their management unit under the national *Himalayan Thar Control Plan* (Figure A1.6; Department of Conservation 1993). The exceptions were the Carneys Creek, North Branch, and Whymper catchments, whose 95% confidence intervals overlapped with the intervention densities in at least one period.

The density of tahr within the eight study catchments has varied over time since 1990, with significant decreases estimated for the Arbor Rift and Zora catchments (Figure 3Figure 3; Table A2.1a; **Error! Reference source not found.**a). In comparison, the data suggest that tahr density has significantly increased within the Hooker catchment. No significant changes were estimated for the remaining five study catchments. Estimates of tahr density exceeded the intervention densities set in the tahr management plan (Department of Conservation 1993) for all catchments on some occasions, with densities consistently above intervention densities at the Arbor Rift and Zora catchments (Table 1; Figure 3Figure 3). However, the estimated decreasing trends in tahr density within these two catchments suggest that they may be approaching the limits for intervention. The estimated tahr densities for the two most recent monitoring periods, predicted from data collected using the 4 km^2 aerial monitoring method (Appendix 1), probably exceeded the intervention densities in all study catchments.

Table 3. Relationship between catchment and year (estimate ± SEM) for three response variables (tahr density, ungulate activity, hare activity). Shading indicates catchments with significant positive (orange) or negative (blue) relationships. Estimate ± SEM values for year are presented on the log scale for tahr density and the log odds ratio scale for the two activity responses.

Response	Catchment	Estimate ± SEM	t ratio	*P*-value
a) Catchment-level tahr density	Arbor Rift	-0.046 ± 0.017	-2.697	0.008
	Carneys Creek	0.003 ± 0.015	0.178	0.859
	FitzGerald	0.043 ± 0.024	1.791	0.077
	Hooker	0.082 ± 0.015	5.338	<0.001
	North Branch	-0.025 ± 0.015	-1.640	0.104
	Townsend	0.025 ± 0.025	0.995	0.322
	Whymper	0.026 ± 0.020	1.279	0.204
	Zora	-0.061 ± 0.024	-2.550	0.012
b) Plot-level ungulate activity	Arbor Rift	0.082 ± 0.005	16.470	<0.001
	Carneys Creek	0.106 ± 0.005	21.641	<0.001
	FitzGerald	0.054 ± 0.006	9.042	<0.001
	Hooker	0.044 ± 0.010	4.276	<0.001
	North Branch	0.001 ± 0.003	0.347	0.729
	Townsend	0.140 ± 0.007	18.897	<0.001
	Whymper	0.011 ± 0.008	1.353	0.176
	Zora	0.099 ± 0.006	17.571	<0.001
c) Plot-level hare activity	Arbor Rift	0.003 ± 0.005	0.625	0.532
	Carneys Creek	-0.012 ± 0.003	-3.573	<0.001
	FitzGerald	0.005 ± 0.005	1.097	0.272
	Hooker	0.073 ± 0.007	10.259	<0.001
	North Branch	-0.037 ± 0.004	-10.035	<0.001
	Townsend	-0.005 ± 0.005	-1.083	0.279
	Zora	0.042 ± 0.005	8.008	<0.001

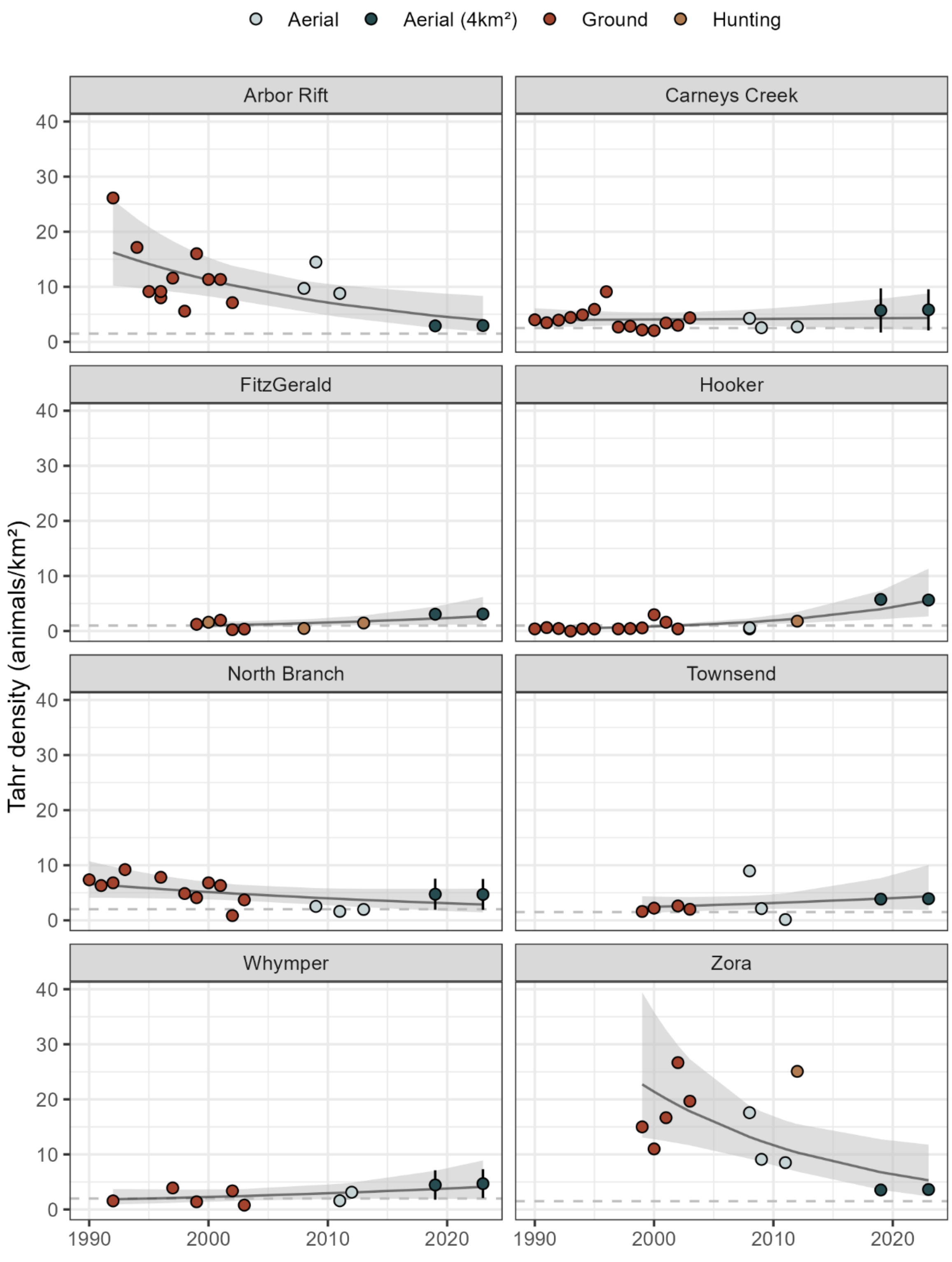


Figure 3. Estimates of tahr density (animals/km^2) since 1990 from ground counts, aerial counts or counts during aerial hunting, for the eight study catchments. Error bars for the 4 km2 aerial monitoring represent 95% confidence intervals for predictions from 1,000 random forest models. Lines show the mean (±95% confidence intervals) derived from a regression model with a gamma distribution. Dashed lines indicate the intervention density for each study catchment (Table 1; Department of Conservation 1993).

4.2 Plot-level ungulate and hare activity

Across the eight study catchments the index of ungulate activity at individual plots (calculated as the proportion of pellet plots with faecal pellets) ranged from 0 to 1 (mean ± SEM: 0.248 ± 0.11), with the lowest mean activity recorded in the Hooker catchment (Figure 4). Ungulate activity varied over time, and the best model included a significant interaction between year and catchment (Table A2.1a). There was no significant change in ungulate activity in North Branch or Whymper over the monitoring period. However, ungulate activity increased significantly over time in the remaining six catchments ($P < 0.001$, Table 3b).

The index of hare activity at individual plots also ranged from 0 to 1 (0.267 ± 0.011, Figure 4). Hare activity also varied over time, and the best model included a significant interaction between year and catchment (Table A2.1b). Significant increases were observed in the Hooker and Zora catchments and significant decreases in the North Branch and Carneys Creek catchments (Table 3c). Hare activity did not change significantly in the Arbor Rift, FitzGerald or Townsend catchments. The Whymper catchment was excluded from the analysis of hare activity over time because hare activity was recorded on only one pellet plot on one sampling occasion.

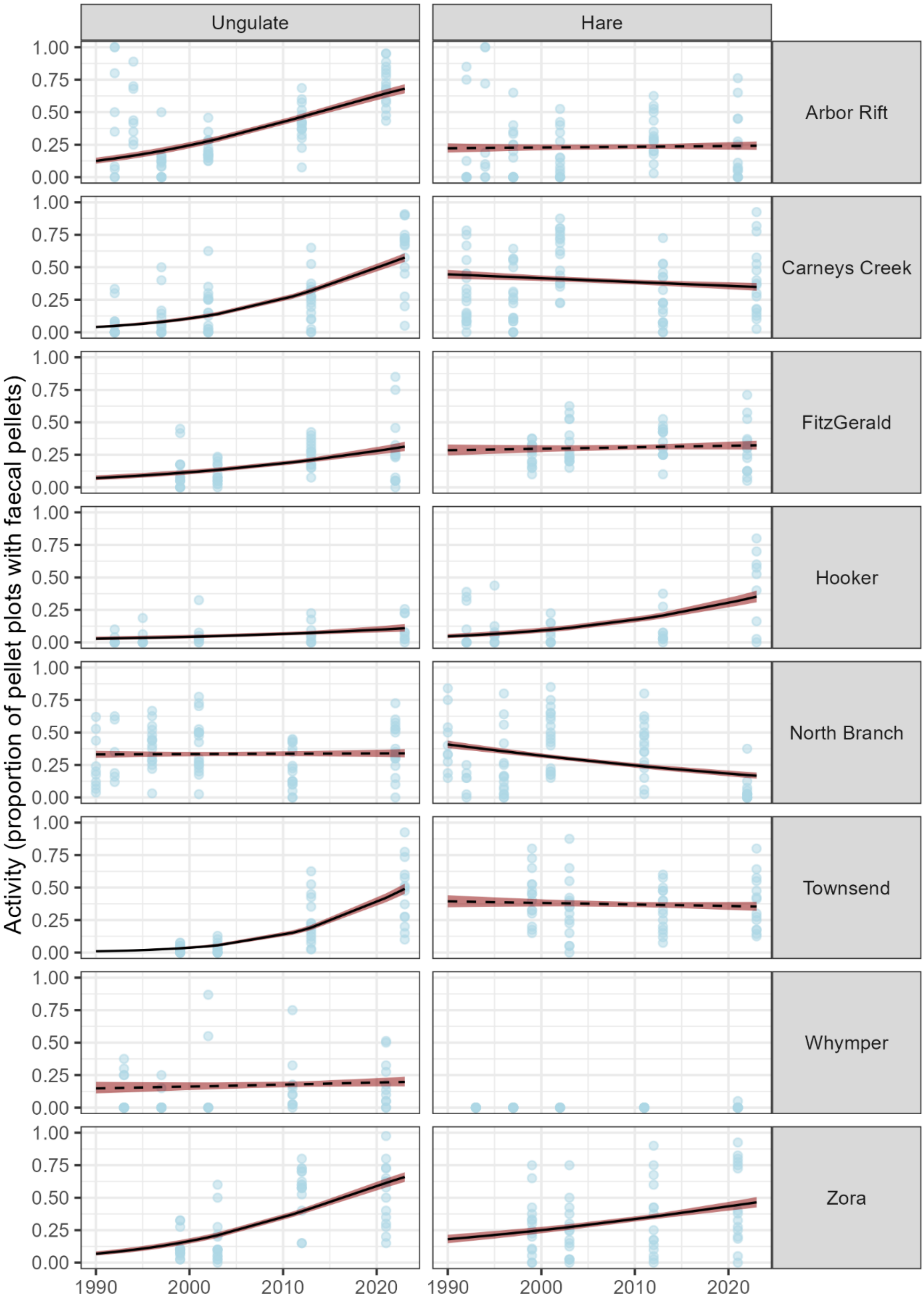


Figure 4. Observed ungulate and hare activity levels (defined as the proportion of pellet plots with faecal pellets) at each study catchment over the vegetation monitoring period. Lines show the mean (±95% confidence intervals) derived from binomial regression models for each species, while blue points represent the raw data for each plot. Solid lines indicate a significant slope, while dashed lines indicate a non-significant slope at α = 0.05. Whymper was excluded from the hare activity model due to hare pellets only occurring in one pellet plot in one sampling period.

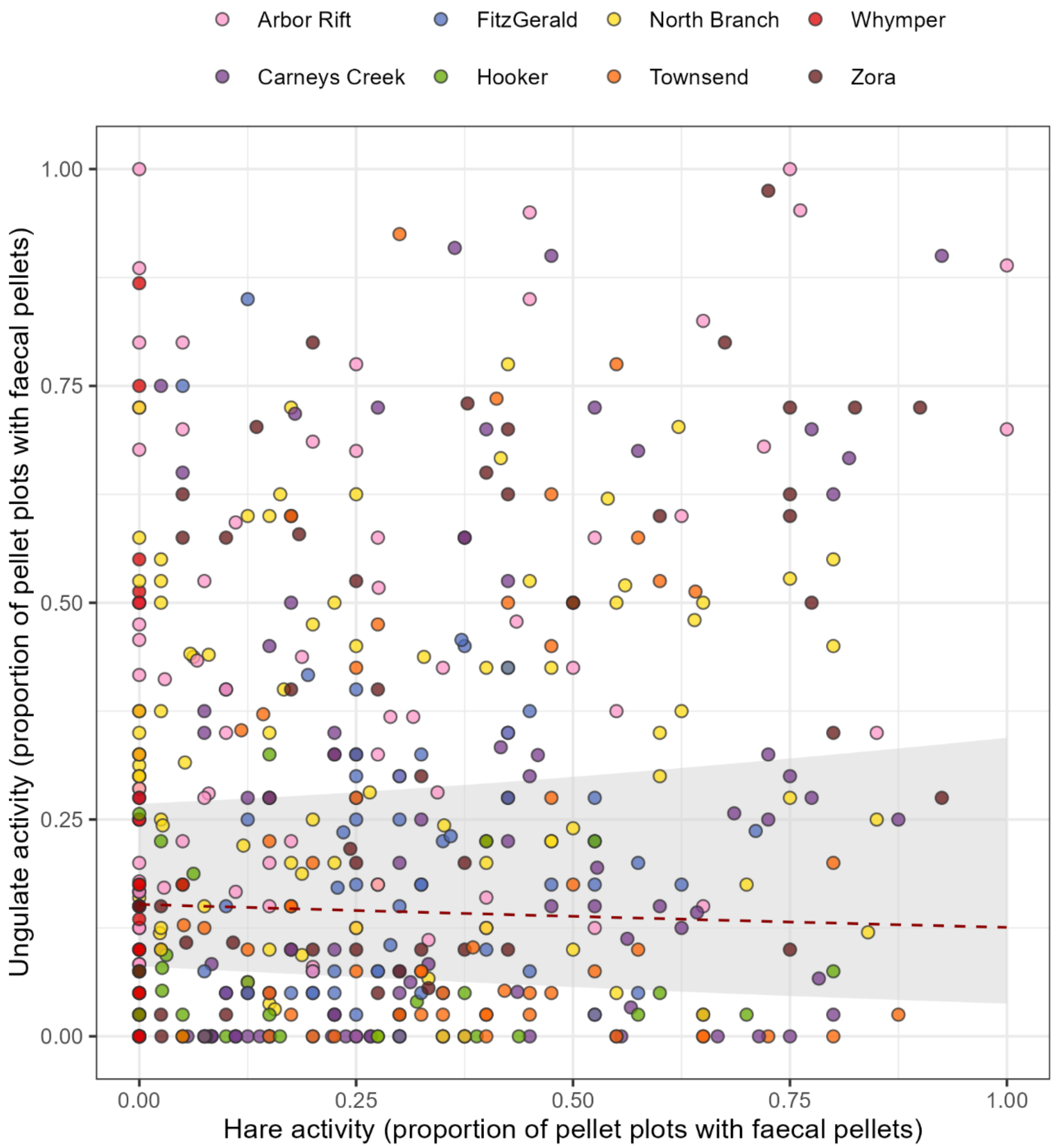


Figure 5. Predicted mean (±95% confidence intervals) relationship between ungulate and hare activity (defined as the proportion of pellet plots with faecal pellets). The relationship was derived from a GLMM with a binomial distribution, including hare activity nested within catchment, plot, and year as random factors. The dashed line indicates a non-significant slope at α = 0.05. Points represent all raw data, coloured by catchment.

There was no significant relationship between hare and ungulate activity (Table A2.2, Figure 5, beta = –0.11 ± 0.19, P = 0.564).

4.3 Catchment-level ungulate activity and tahr density

Mean catchment-level estimates of ungulate activity were associated with a high level of uncertainty (as indicated by the horizontal 95% confidence intervals in Figure 6). Overall, tahr density increased significantly as the mean catchment-level ungulate activity increased (estimate = 1.69 ± 0.69, P = 0.015, Figure 6), with the best model including year and catchment as random effects (Table A1.3). However, the mean catchment-level ungulate activity for a given density of tahr was highly variable, with considerable overlap in mean ungulate activity values across a range of tahr densities. For example, tahr densities below the maximum intervention density of 2.5 animals/km^2 were associated with mean catchment-level ungulate activity values that ranged from 0.002 to 0.247, while tahr densities from 2.5 to 10 animals/km^2 were associated with mean catchment-level ungulate activity values ranging from 0.002 to 0.623. The Arbor Rift and Zora catchments had particularly high tahr densities relative to their recorded ungulate activity (Figure 6). Overall, while there was a significant relationship between tahr density and ungulate activity, the high uncertainty means that ungulate activity is not a very accurate predictor of tahr density.

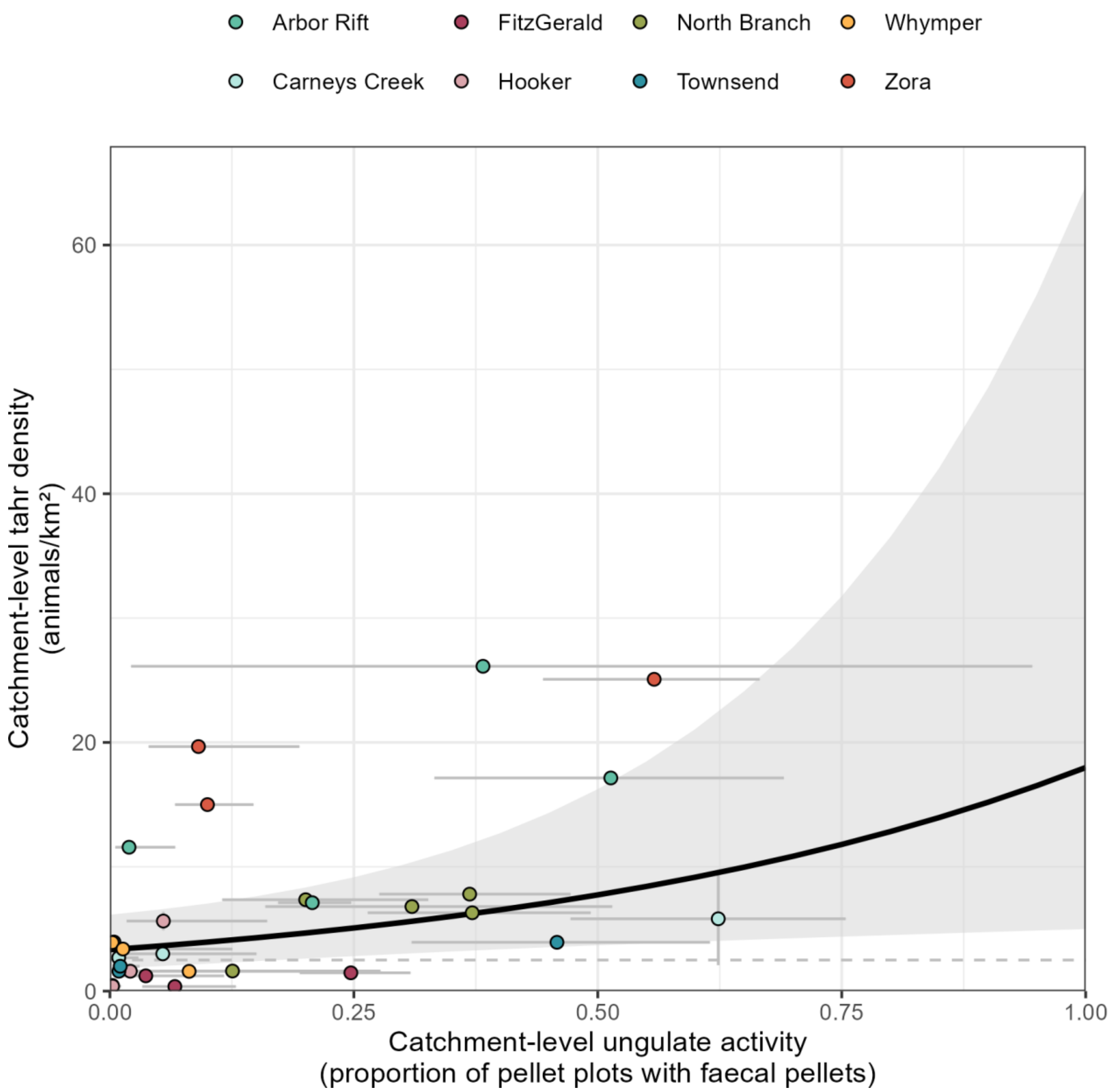


Figure 6. Predicted mean (±95% confidence intervals) relationship between mean catchment-level ungulate activity (proportion of pellet plots with faecal pellets) and tahr density (animals/km^2). Points show the raw data coloured by catchment, with error bars representing the 95% confidence intervals. The significant relationship was derived from a GLMM with a binomial distribution and included catchment and year as random effects. The dashed vertical line indicates the maximum intervention density (2.5 animals/km^2) from the *Himalayan Thar Control Plan* (Table 1; Department of Conservation 1993).

4.4 Mature tussock height

Overall, the model predicting tussock height showed similar trends to the previous report covering the 1990–2013 period (Cruz et al. 2014). In our analysis tussock height was significantly associated with live diameter, year of monitoring, elevation, and ungulate activity (Table 4, Figure 7). Despite using a different method to consider plot aspect, aspect did not show a significant relationship with tussock height, which is consistent with previous findings (Table 4).

Tussock height significantly decreased with higher ungulate activity (Figure 7e) with a similar relationship observed across all catchments (Figure 8). This result aligns with previous findings, suggesting a significant impact of ungulates on tussocks. Greater tussock height was associated with intermediate live diameter (Figure 7a). We found no relationship between tussock height and the percentage of crown death (Figure 7b). Tussock height declined with increasing elevation (Figure 7c).

Despite including more recent measurements (2021–2023; Table A3.1), tussock height still showed a negative relationship with year of measurement across all catchments, suggesting that tussocks have not been recovering (Table 4; Figure 7; Figure 9; Table A3.2). Although trends were similar across catchments, the decline in mean height of tussocks in relation to ungulate activity or year varied by catchment. For instance, plots in Arbor Rift showed a 60% decline in tussock height over the whole study period, with mean tussock height going from 35 cm in 1992 to 14 cm in the last survey done in 2021, while plots in Hooker valley showed a 30% decline of tussock height over time, with mean tussock height dropping from 86 cm in 1990 to 60 cm in 2022 (Figure 9; Table A3.2). Focussing on changes over the last decade (i.e., between the last two measurements in each catchment), the greatest decline in mean tussock height was observed in the Townsend catchment (51%). Mean tussock height declined by more than 20% in the Arbor Rift (39%), North Branch (24.%) and Zora (21%) catchments (Table A3.2).

Table 4. Relationships between tussock height and tussock live diameter (cm), year, elevation (m asl), ungulate activity (proportion of pellet plots with faecal pellets), cosine of aspect (–1 = south-facing, 1 = north-facing), and crown death (%), with associated degrees of freedom (df), chi-squared values, and *P*-values. The model included plot nested within catchments as a random factor, with ungulate activity as a random intercept. diameter^2 = the term representing the quadratic effect of diameter.

Fixed effects	df	chi-sq.	*P*-value
Diameter	1	2643.73	<0.001
Diameter^2	1	316.77	<0.001
Year	1	281.67	<0.001
Elevation	1	13.07	<0.001
Ungulate activity	1	12.40	<0.001
Aspect	1	2.54	0.111
Crown death	1	1.58	0.209

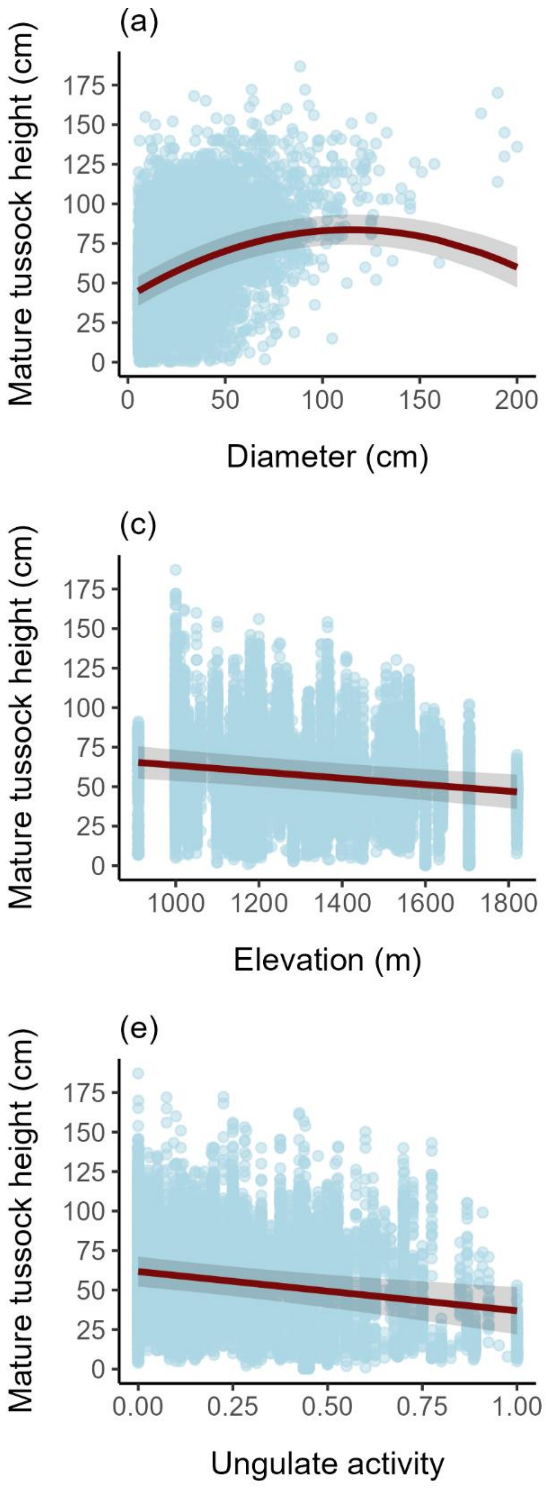


Figure 7. Predicted mean (±95% confidence interval) relationship between tussock height (cm) and (a) tussock live diameter (cm), (b) crown death (%), (c) elevation (m), (d) year, and (e) ungulate activity (proportion of pellet plots with faecal pellets). Each relationship was predicted with the other fixed effects at their mean values. Blue points represent all raw data. See Table 4 for detailed outputs.

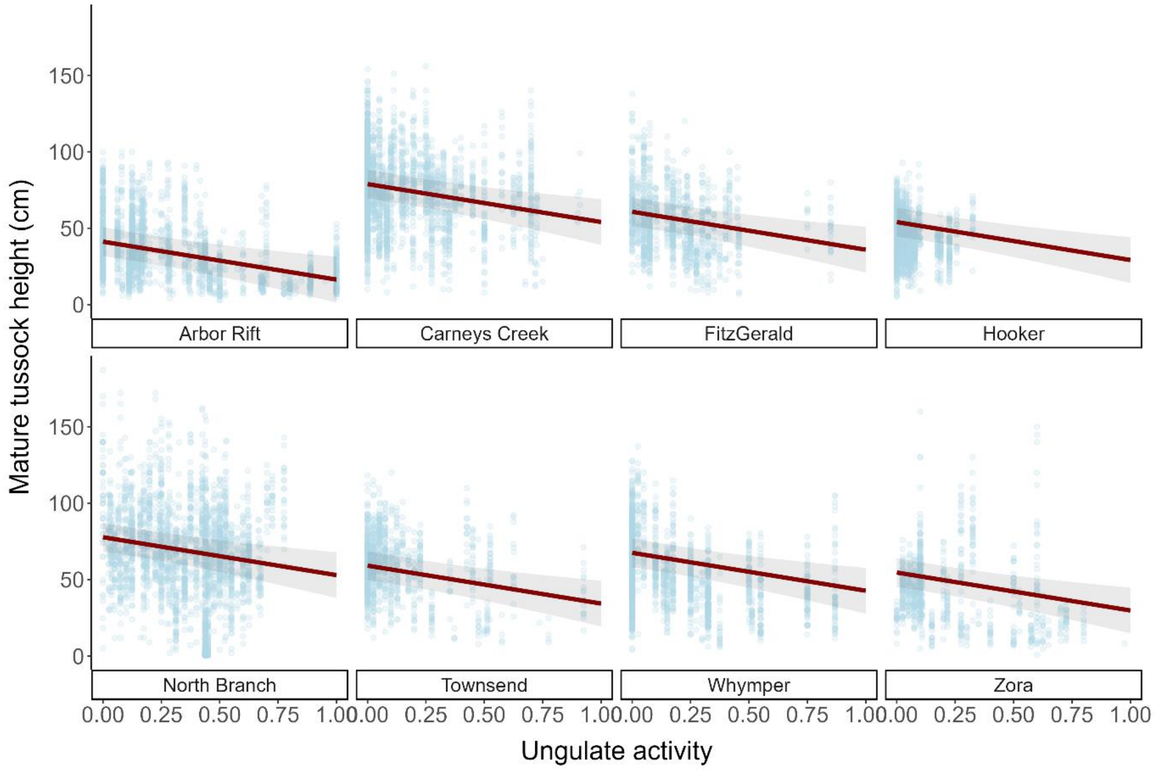


Figure 8. Predicted mean (±95% confidence intervals) relationship between tussock height and ungulate activity (proportion of pellet plots with faecal pellets) per catchment. Blue points represent the raw data (see Table A3.2 for raw means per catchment).

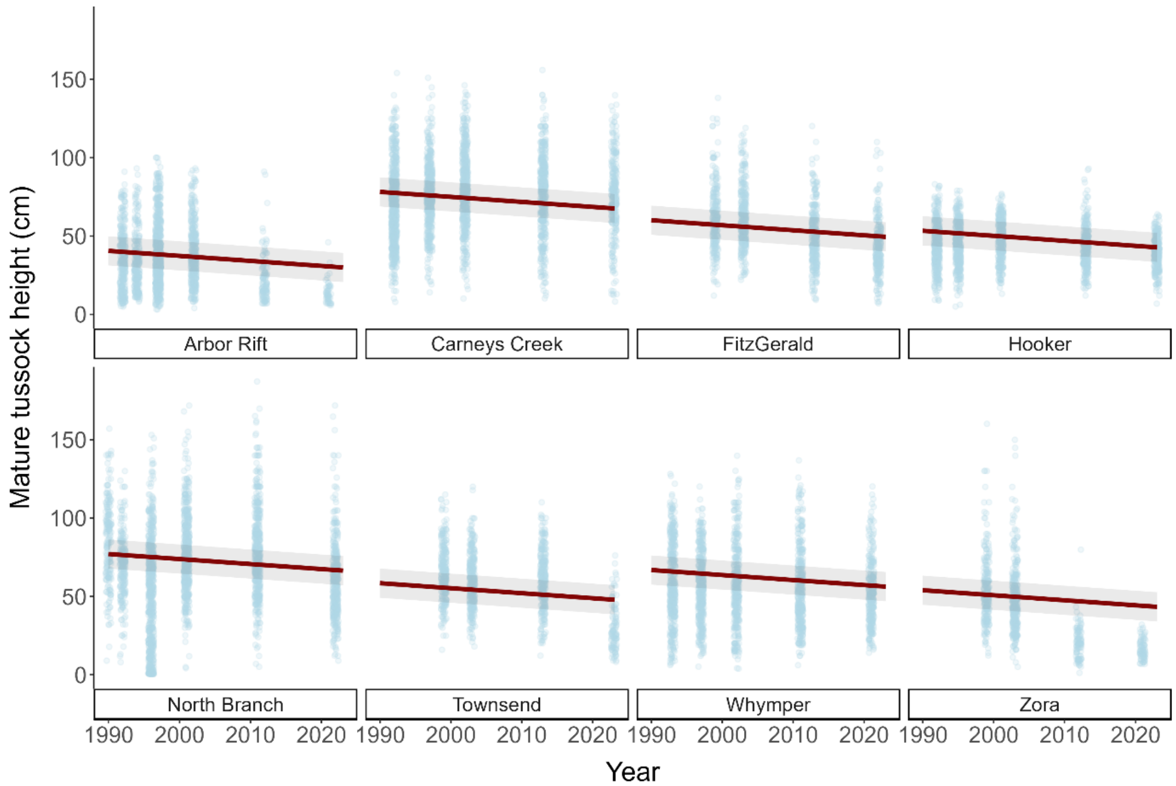


Figure 9. Predicted mean (±95% confidence intervals) relationship between tussock height and year, per catchment. Blue points represent the raw data (see Table A3.2 for raw means per catchment, per year).

4.5 Vegetation cover

We ran two types of model to assess changes in vegetation cover, with the first including aspect (in degrees) as a quadratic effect (see Table A3.2 for outputs) to directly compare with the previous findings of Cruz et al. (2014), and the second including the cosine of aspect, which is the statistically more appropriate approach. The first model that included aspect (in degrees) as a quadratic effect generated an inaccurate relationship with overall vegetation cover, whereby fitted means that should have been relatively close (0° and 360° are equivalent) were different. For instance, an aspect of 11° had a fitted mean of 86% cover and an aspect of 347° had a fitted mean of 32% cover (Figure A3.1; Table A3.3).

For the second model, which included the cosine of aspect, only year of measurement and aspect were significantly associated with vegetation cover (Table 5). As in the previous report, vegetation cover increased throughout the monitoring period across all catchments (Figure 10b; Table A3.2). For instance, plots in the Zora catchment had a raw mean vegetation cover increasing from 56% to 66% between 1999 and 2012 (Table A3.2).

Consistent with the previous report, overall vegetation cover was higher on south-facing slopes (Figure 10c). No relationship was found between ungulate activity and vegetation cover, suggesting no or very low impact of ungulate activity on overall vegetation cover, in contrast with the previous study (Table 5, Figure 10a).

Table 5. Relationship between overall vegetation cover and cosine of aspect (–1 = south-facing, 1 = north-facing), year, and ungulate activity (proportion of pellet plots with faecal pellets), with associated degrees of freedom (df), chi-squared values, and P-values. The model followed a beta regression and included plot nested within catchment as a random factor.

Fixed effects	df	chi-sq.	*P*-value
Year	1	17.54	<0.001
Aspect	1	9.001	0.002
Ungulate activity	1	0.01	0.910

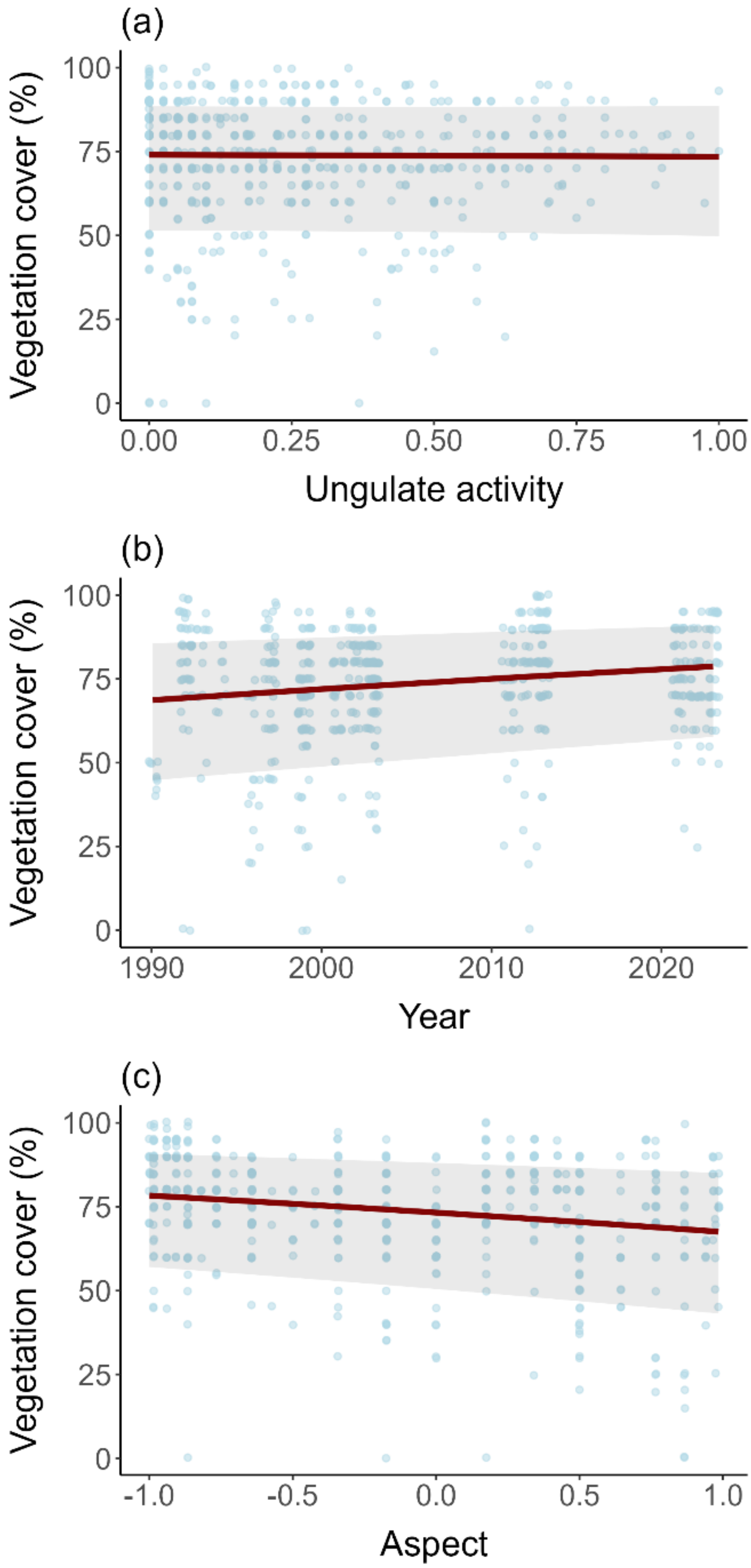


Figure 10. Predicted mean (±95% confidence interval) relationship between overall vegetation cover (percentage) and (a) ungulate activity (proportion of pellet plots with faecal pellets), (b) year, and (c) aspect as a cyclic variable (–1 = south-facing, 1 = north-facing). Blue points represent the raw data. See Table 6 for detailed outputs and Table A3.2 for raw means.

5 Discussion

Before the significant reduction of the tahr population in the 1970s, high densities of tahr had a noticeable impact on snow tussock condition, with declines in percentage cover and a shift towards communities dominated by fescue and blue tussock *(Poa colensoi*), particularly at lower altitudes (Caughley 1970; Department of Conservation 1993). Although the evidence suggesting that the reduced size of the tahr population led to substantial improvements in snow tussock condition is primarily anecdotal, it was supported by some limited photographic evidence (Department of Conservation 1993). By the early 1990s, when this study commenced, tussock condition had already greatly improved (Department of Conservation 1993). The key question now is whether the densities of tahr since then have resulted in continued improvement, decline, or stability in tussock height and/or vegetation cover.

The condition of vegetation in the absence of tahr remains unknown for the study catchments, so we have no definitive ecological benchmark or management target to compare against. Comparative data from vegetation plots beyond the tahr range (e.g. Tier One monitoring plots [Bellingham et al. 2018] and other historical monitoring plots in tussock grasslands [e.g. Rose & Platt 1990; Rose & Platt 1992; Holdaway et al. 2014]) could be used to extrapolate vegetation composition and structure, and tussock height, growth, recruitment, and mortality rates in the absence of tahr. Such an approach would build on the one used to understand deer impacts in forest ecosystems, where long-term permanent plot data from areas with varying densities of deer have been interpreted alongside diet studies, paired control and exclosure plots, and management experiments.

However, this may be challenging for two reasons. First, vegetation composition and condition are highly variable, both within and between plots and catchments in this study, let alone compared to sites outside the tahr feral range, with differences potentially driven by differing environmental conditions (e.g. altitude, aspect, slope, rainfall, geology). Even within the tahr feral range, Bellingham et al. (2018) showed that the subjectively located plots analysed for this report are not representative of the vegetation and environmental conditions (based on Tier 1 plots) and may not represent the true impacts of tahr on vegetation communities. Second, it is important to recognise that other non-native browsers (e.g. chamois, red deer, possums, hares) co-occur at different densities, both within the study catchments and across the wider Southern Alps (Bellingham et al. 2018). These multi-species browser communities complicate our ability to attribute vegetation impacts to particular browsing species and, therefore, to evaluate the likely vegetation condition in the absence of any browsers (Forsyth et al. 2000). Fenced exclosures could go some way towards untangling these dynamics, but maintaining them in alpine habitats has generally been considered impractical.

The available data indicate contrasting trends in tahr density across the eight study catchments since 1990. Catchments with historically higher densities (Arbor Rift, Zora) have seen a significant decrease in tahr density since 1990, driven in part by large declines since 2013. Conversely, the Hooker catchment has seen a significant increase in tahr density over this period, with recent density estimates an order of magnitude higher than those recorded before 2013. However, caution needs to be taken when considering these trends, as methodological changes in the estimation of tahr density may affect the comparability of the data.

The movement patterns and habitat preferences of tahr can complicate density estimation, regardless of monitoring method. Tahr are patchily distributed across the landscape, influenced by high spatial variation in food availability and other environmental and behavioural factors. They tend to form large groups that make daily vertical migrations –from lower elevations at night to higher elevations during the day – and often seek refuge midday in tall vegetation or rocky outcrops (Tustin & Parkes 1988; Watson 2007), where detectability may decrease. Habitat variability across their range may further affect density estimates: western areas with taller, denser vegetation could reduce detectability compared to open areas or shorter vegetation. Also, in areas with high helicopter hunting pressure, tahr may exhibit avoidance behaviour, potentially leading to underestimates during aerial surveys (Forsyth & Tustin 2021).

Methods for estimating tahr density have evolved significantly over time. Early estimates used the 'largest-count' method, in which observers conducted at least two ground-based surveys with binoculars and spotting scopes, recording the 'largest and most confident classification' of tahr groups (Challies 1992). Later ground-based methods introduced double-counting to estimate minimum tahr numbers with a measure of uncertainty (Forsyth & Hickling 1997). Recently, aerial surveys have incorporated a more rigorous protocol, aiming to maximize detection probability on 4 km^2 plots by conducting three counts at intervals of at least 10 days, allowing density estimates with calculated uncertainties (Ramsey et al. 2022). However, this aerial survey method was designed for Management Unit or range-wide scales and the surveyed plots did not spatially align with the eight study catchments. The use of random forest modelling in this study to estimate catchment-level densities from density estimates from the aerial surveys may have introduced additional uncertainty in the density estimates.

Despite these limitations, the recent density data indicate that tahr densities in five of the eight study catchments (excluding Carneys Creek, North Branch, and Whymper) exceed intervention density levels for their respective management units (Figure A1.6). These findings align with Ramsey et al.'s (2022) conclusions, showing that tahr densities exceed intervention thresholds in six of the seven management units, as well as in both exclusion zones.

In contrast to tahr density, which is assessed at the catchment level, ungulate activity, which is measured at the plot level, has significantly increased in six of the eight catchments since 1990. While density and activity are both indicators of tahr pressure, their differing trends within catchments may initially seem counterintuitive. These differences could stem from changes in density estimation methods, as described above, potentially affecting the reliability of the observed density trends. Alternatively, the observed increase in ungulate activity may reflect rising numbers of other ungulate species (e.g. chamois, red deer) in the vegetation plots, although no data are available to support this hypothesis. Despite these differences, we found that catchment-level tahr density was positively associated with mean catchment-level ungulate activity, although the relationship was not strong. This weak association may be partly attributable to the mismatch in measurement scales between these two metrics. Moreover, the considerable variation in plot-level ungulate activity within catchments probably reflects the patchy spatial distribution typical of tahr.

Regardless, the high uncertainty about the relationship between tahr density and ungulate activity means that it is not appropriate to use ungulate activity at the plot level as a surrogate to determine if catchment-level tahr densities are below the required intervention density within a given catchment or management unit. For example, catchment-level tahr densities below the maximum intervention density of 2.5 animals/km^2 were associated with mean catchment-level ungulate activities ranging from 0.002 to 0.247 (proportion of plots with ungulate faecal pellets).

In addition, it is worth considering the spatial scale at which intervention densities are calculated and applied for management purposes. The patchy distribution of tahr across the landscape means that the local density of tahr may be quite high relative to the density calculated for, and applied at, the scale of management units under the *Himalayan Thar Control Plan* (Department of Conservation 1993). This may result in a mismatch between the tahr management goals and conservation objectives specified for each management unit at different spatial scales. Identifying the appropriate scale for estimating and managing tahr density requires a better understanding of tahr movement patterns across the landscape and the vulnerability of different plant communities to browsing pressure from tahr. Ideally, this would include the measurement of tahr density, ungulate activity, and vegetation condition at the same locations.

Earlier analyses of data from the vegetation plots used in this study, covering the 1990–2013 period, showed no overall recovery of mature tussocks over the two decades of monitoring (Cruz et al. 2014). Additional data from remeasurement of the plots 10 years later indicates that tussock condition (as measured by tussock height) is still declining with no signs of recovery, particularly in the Arbor Rift, Townsend, and Zora catchments (Table A3.2), where ungulate activity has significantly increased. Our findings suggest that these results might be at least partly due to the ongoing impact of ungulates rather than the legacy of a historical impact by ungulates.

Tussock height has continued to decline over time, with ungulate activity increasing significantly in most catchments over the same period. The intervention densities proposed in the *Himalayan Thar Control Plan* (Department of Conservation 1993) were probably exceeded in all catchments over the past decade, and it appears that the average tahr densities have been too high to allow improvement in tussock height in any of the study catchments. Snow tussocks are extremely slow growing and may live in excess of 20 years (Rose & Platt 1990), meaning that it may take a long time for recovery in response to management to become evident. For example, it is too early to tell whether the removal of a large number of tahr in 2022/23 will result in improvements in tussock height. Assessing other metrics of snow tussock condition (e.g. recruitment, age-class structure, density) collected at the vegetation plots may provide additional strands of evidence to assess the effectiveness of the intervention densities at maintaining snow tussock communities. However, these analyses were out of scope for the current report.

Hares can also significantly affect snow tussock communities and they co-occur with tahr in seven of the eight study catchments, complicating our ability to attribute changes in tussock height to tahr alone. Both species preferentially graze on snow tussocks, which can lead to intensified browsing pressures. However, hares exhibit a distinctive browsing behaviour by selectively nibbling on the more nutritious parts of tussocks, typically clipping vegetation at a characteristic 45° angle and leaving the tops of leaves intact (Flux 1990). Unlike ungulates, which graze tussocks more evenly, hares tend to consume only a few leaves from each plant before moving on, often leaving clipped vegetation behind (Flux 1967; Wong & Hickling 1999). This selective foraging can create patterns of grazed tillers in a semi-circle, which may differ from the uniform grazing patterns observed with other herbivores. Rose and Platt (1992) found that heavy browsing by hares in the absence of other herbivores hindered tussock recovery, with damage to nearly all snow tussocks resulting in low seed production and high seedling mortality. However, snow tussocks showed pronounced recovery after 10 years, with tussocks >5 cm in diameter nearly twice as tall as those on the stand grazed only by sheep.

The potential for cumulative browsing pressure from both hares and tahr may further compromise the resilience and long-term survival of snow tussock communities, limiting their ability to regenerate and thrive. It also makes it more difficult to attribute the effects of tahr alone on snow tussock communities. While we found evidence of increasing ungulate activity in six of the eight study catchments, hare and ungulate activity were not significantly correlated when considered across all catchments. Indeed, only two catchments (Hooker and Zora) had significant increasing trends of both hare and ungulate activity over time. Therefore, it is likely that ungulate activity is the primary factor driving the observed declines in tussock height and vegetation cover within the study catchments. However, more information is needed on the preferred species and dietary overlap between hares, tahr, and other ungulates in these alpine habitats, as well as the relative browsing pressure exerted by these species.

Like the previous report (Cruz et al. 2014), we found that overall vegetation cover significantly increased across the monitoring period. However, we found no significant relationship with ungulate activity. While we have not investigated which species contributed to the increasing vegetation cover, we can assume that it is unlikely to be tussocks, as these have significantly declined in condition. Therefore, as noted by Cruz et al., changes in vegetation cover may reflect a shift in the vegetation community towards non-palatable species due to browsing pressure on species preferred by tahr. An analysis of the detailed information on vegetation composition would be needed to identify why vegetation cover has increased over time and whether this is related to ungulate activity within the catchment.

The vegetation monitoring undertaken in the eight study catchments was designed to report on tahr impacts on snow tussocks and other dominant vegetation, as well as relating tussock height to tahr densities, to support the setting of meaningful intervention densities. The wider goal for this monitoring was to provide the data to ensure maintenance of ecological integrity ('the full potential of indigenous biotic and abiotic features and natural processes, functioning in sustainable communities, habitats, and landscapes', McGlone et al. 2020), which includes:

- maintaining ecosystem composition (which includes the demography of functional groups, and the abundance of common and widespread taxa)
- maintaining ecosystem processes
- preventing declines and extinctions.

Tussocks are a structural dominant in many alpine ecosystems (Wardle 1991; Day et al. 2023), and because they can dominate above- and below-ground vegetation biomass, they contribute significantly to ecosystem processes and ecosystem function (e.g. litter inputs and nutrient cycling, seed rain, and food web complexity, Grime 1998).

In this study, tussock condition is measured using tussock height (the extended length of the longest leaf). This measure has two key advantages: it relates directly to the leaf tissues that tahr browse, and it can be measured easily, probably with low measurement error. A shortcoming of relying on tussock height is that it does not relate to tussock crown death (Figure 7b; section 4.4.) and so may not tell us about maintenance of the population (i.e. maintenance of the number and sizes of individuals). In addition, it is not possible to easily distinguish between different mammalian browsers, making it difficult to attribute the cause of declines in tussock height. Population maintenance of dominant species is crucial for maintaining ecological integrity (McGlone et al. 2020; Wright et al. 2020). In an extreme scenario, the mean height of tussocks could remain constant over time while the population size declines from many hundreds to a few remaining plants.

Because the remit of this report was to update the earlier analysis of Cruz et al. (2014), we did not include measures based on population size or age structure; we recommend including these in future analyses to determine population trajectories, and to test for sufficient recruitment of juvenile plants across sites. Population persistence is determined by the net effects of recruitment, growth, and mortality, and methods of doing this for tussocks are available (e.g. Rose & Platt 1992; Holdaway et al. 2014).

Lastly, we recommend including an analysis of vascular plant composition on the plots to determine whether vegetation composition is being maintained across these sites. However, we acknowledge that these plots were located to target tussock species, so they cannot be expected to reflect the full compositional variation (Bellingham et al. 2018).

6 Recommendations

Based on the outcomes of this report, we suggest that DOC may wish to consider the following recommendations.

1 The methods used in this project to estimate tahr densities within the eight study catchments do not appear to be sufficiently reliable to compare them with the intervention densities in the *Himalayan Thar Control Plan*. The new aerial helicopter method may be more accurate at estimating densities but did not align spatially or temporally with the remeasurement of the vegetation plots, making it difficult to estimate and compare densities within these catchments directly. We echo the recommendation of Cruz et al. (2014) that faecal pellet plots continue to be measured as an index of ungulate activity, although caution that these do not appear to be an appropriate proxy for the density of tahr. The addition of trail cameras as a monitoring tool within each study catchment may both enable the estimation of tahr density and provide information about other browsing species (e.g. chamois, deer, hares) that may be influencing vegetation recovery (Hickling et al. 2024). We suggest that catchment-level density estimates following the double-

count method of Forsyth & Hickling (1997) continue to be undertaken at the same time and in the same location as the vegetation monitoring to enable evaluation and calibration of any new monitoring tools. However, it is important to ensure that the presence of people camped within the study area does not unduly influence these estimates.

2 Despite the potential limitations in accurately estimating tahr density within the study catchments, the available data suggest that the intervention densities were probably exceeded in all catchments over the past decade. Moreover, tussock height continued to decline across all catchments, with strong effects noted in those catchments with high tahr densities (e.g. Arbor Rift and Zora). Further reduction of tahr densities appear to be required to mitigate ongoing vegetation impacts.

3 Vegetation analyses have focused on the height of snow tussock species. Although tussock height is a good indicator of browse, it does not measure whether populations are being maintained. Additional field data are available on tussock demography (i.e. growth, recruitment, mortality, number and size of individuals), and analysis and inclusion of these data would provide a more complete understanding of tussock population maintenance. Likewise, analyses of full vascular plant composition within the plots would allow a more complete assessment of tahr impacts on other vulnerable plant species.

4 We echo the recommendations of Bellingham et al. (2018) that monitoring should continue within the eight study catchments discussed in the current study to maintain the long-term data set, but that an alternative monitoring programme also be established to better assess the effectiveness of the intervention densities at maintaining ecological integrity within the tahr management units. Such a monitoring programme needs to ensure that tahr densities are measured robustly at the scale and location of the vegetation monitoring.

7 Acknowledgements

We thank Ella Hayman for assistance with data extraction from the National Vegetation Survey databank; Duane Peltzer for peer review within Manaaki Whenua – Landcare Research; Kathrin Affeld, Ingrid Gruner, Tom Brookman, Cielle Stephens and Claire Newell for peer review within the Department of Conservation; and Ray Prebble for editing the final report.

8 Glossary of abbreviations and terms

AICc	Corrected Akaike's Information Criterion.
DOC	Department of Conservation.
feral range	Area defined under the Wild Animal Control Act 1977 as 'the area that is from time to time occupied by a free ranging population of wild animals of that species, excluding transient wanderers from the main herd and from the range of the main herd'.
exclusion zones	Areas within the breeding range of tahr where populations are to be reduced to a zero density under the national *Himalayan Thar Control Plan* (Department of Conservation 1993; Figure 1), providing a barrier to their further dispersal.
GLM	Generalised linear model – a regression model that does not include random effects.
GLMM	Generalised linear mixed effects model – a regression model that includes random effects.
hare activity	An index of the proportion of pellet plots containing hare faecal pellets.
LCDB	Land Cover Database (Manaaki Whenua – Landcare Research 2020).
management units (MU)	Seven areas within the breeding range of tahr where populations are to be managed to specified levels under the *Himalayan Thar Control Plan* (Department of Conservation 1993; Figure 1).
MSE	mean square error – a measure of model performance.
MWLR	Manaaki Whenua – Landcare Research.
NSE	Nash-Sutcliffe efficiency – a measure of overall model performance by indicating how closely a plot of observed versus predicted values lies to the 1:1 line, whereby 1 corresponds to a perfect match.
PBias	A measure of model performance – the sum of the differences between the observations and predictions divided by the sum of the observations.
SD	Standard deviation.
SEM	Standard error of the mean.
ungulate activity	An index of the proportion of pellet plots containing ungulate faecal pellets.

9 References

Allen RB 1993. A permanent plot method for monitoring changes in indigenous forests: a field manual. Manaaki Whenua – Landcare Research.

Anderson J, Henderson J 1961. Himalayan thar in New Zealand: aspects of life history and assessment of management problems. New Zealand Deerstalkers Association Special Publication 2.

Bartoń K 2024. MuMIn: Multi-Model Inference. R package version 1.48.4. http://cran.r-project.org/package=MuMIn

Bates D, Mächler M, Bolker B, Walker S 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67(1): 1–48.

Bellingham PJ, Wiser SK, Burge O, Easdale TA, Richardson S 2018. Potential of Tier One and alternative monitoring networks to assess the ecological integrity of alpine vegetation exposed to tahr grazing Manaaki Whenua – Landcare Research contract report LC3328.

Breiman L 1984. Classification and regression trees. Belmont, CA, Wadsworth International Group.

Breiman L 2001. Random forests. Machine Learning 45(1): 5–32.

Brenning A, Trombotto D 2006. Logistic regression modeling of rock glacier and glacier distribution: topographic and climatic controls in the semi-arid Andes. Geomorphology 81(1): 141–154.

Brooks ME, Kristensen K, Benthem KJ, van Magnusson A, Berg CW, Nielsen A, et al. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9(2): 378.

Burrows CJ 1974. A botanist's view on the thar problem. Tussock Grasslands and Mountain Lands Institute Review 28: 5–18.

Caughley G 1970. Eruption of ungulate populations, with emphasis on Himalayan thar in New Zealand. Ecology 51(1): 53–72.

Challies CN 1992. Thar monitoring in Carneys Creek, Rangitata catchment: a plan for small catchment surveys. Unpublished report to the Department of Conservation.

Cruz J, Thomson C, Parkes JP 2014. Impact of Himalayan tahr (*Hemitragus jemlahicus*) on snow tussocks in the Southern Alps, New Zealand. Landcare Research contract report LC1900.

Cutler DR, Edwards TC, Beard KH, Cutler A, Hess KT, Gibson J, et al. 2007. Random forests for classification in ecology. Ecology 88(11): 2783–2792.

Damgaard CF, Irvine KM 2019. Using the beta distribution to analyse plant cover data. Journal of Ecology 107(6): 2747–2759.

Day N, Barratt B, Christensen B, Curran T, Dickinson K, Lavorel S, et al. 2023. Predicting ecological change in tussock grasslands of Aotearoa New Zealand. New Zealand Journal of Ecology 47(1): 3549.

Delignette-Muller MLD, Christophe 2015. fitdistrplus: an R package for fitting distributions. Journal of Statistical Software 64(4): 1–34.

Department of Conservation 1991. Himalayan thar management policy. Wellington, Department of Conservation.

Department of Conservation 1993. Himalayan Thar Control Plan. Canterbury Conservancy Conservation Management Series No 3. Wellington, Department of Conservation.

Department of Conservation 2018. Field protocols for DOC Tier 1: Himalayan tahr abundance monitoring protocol, version 4.0. Wellington, Department of Conservation.

Department of Conservation 2019. Field protocols for DOC Tier 1 inventory & monitoring and LUCAS plots, Version 14. Wellington, Department of Conservation.

Flux JEC 1967. Hare numbers and diet in an alpine basin in New Zealand. Proceedings of the New Zealand Ecological Society 14: 27–33.

Flux JEC 1990. Brown hare. In: King CM ed. The handbook of New Zealand mammals. Auckland, Oxford University Press. Pp. 138–174.

Forsyth DM, Caley P 2006. Testing the irruptive paradigm of large-herbivore dynamics. Ecology 87(2): 297–303.

Forsyth DM, Hickling GJ 1997. An improved technique for indexing abundance of Himalayan thar. New Zealand Journal of Ecology 21(1): 97–101.

Forsyth DM, Parkes JP, Hickling GJ 2000. A case for multi-species management of sympatric herbivore pest impacts in the central Southern Alps, New Zealand. New Zealand Journal of Ecology 24(1): 97–103.

Forsyth DM, Tustin KG 2005. Himalayan tahr. In: King CM ed. The handbook of New Zealand mammals. 2nd edn. Melbourne, Oxford University Press. Pp. 351–360.

Fox J, Weisberg S 2019. An R companion to applied regression. 3rd edn. Thousand Oaks, CA, Sage.

Gelman A, Su Y-S 2024. arm: data analysis using regression and multilevel/hierarchical models. R Package version 1.14-4. https://CRAN.R-project.org/package=arm

Glen AS, Byrom AE, Pech RP, Cruz J, Schwab A, Sweetapple PJ, et al. 2012. Ecology of brushtail possums in a New Zealand dryland ecosystem. New Zealand Journal of Ecology 36(1): 29–37.

Greenwell BM 2017. pdp: an R package for constructing partial dependence plots. The R Journal 9(1): 421–436.

Grime JP 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. Journal of Ecology 86(6): 902–910.

Hartig F 2022. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.4.6. https://CRAN.R-project.org/package=DHARMa

Hickling GJ, Warburton B, Sweetapple PJ 2024. Wild animal monitoring methods for the Department of Conservation's Inventory and Monitoring Toolbox. Manaaki Whenua – Landcare Research contract report LC4465.

Holdaway RJ, Rose AB, Newell CL, Carswell FE 2014. Demographic drivers of biomass carbon recovery in degraded perennial tussock grassland, with and without domestic grazing. New Zealand Journal of Ecology 38(2): 29–37.

Horne RSC 1979. Seasonal and altitudinal variations in diet and abundance of the European hare (*Lepus europapeus* Pallas) in Tongariro National Park, New Zealand. Unpublished MSc thesis, Massey University, Palmerston North, New Zealand.

Liaw A, Wiener M 2002. Classification and regression by randomForest. R News 2(3): 18–22.

Lüdecke D 2018. ggeffects: tidy data frames of marginal effects from regression models. Journal of Open Source Software 3: 722.

Manaaki Whenua – Landcare Research 2020. Land Cover Database (LCDB v5.0). 5.0 edn. LRIS Portal.

Mark AF 1989. Responses of indigenous vegetation to contrasting trends in utilization by red deer in two south-western New Zealand national parks. New Zealand Journal of Ecology 12: 103–114.

McCarthy J, Leathwick J, Roudier P, Barringer J, Etherington T, Morgan F, et al. 2021. New Zealand Environmental Data Stack (NZEnvDS): a standardised collection of spatial layers for environmental modelling and site characterisation. New Zealand Journal of Ecology 45(2): 3440.

McGlone M, McNutt K, Richardson S, Bellingham P, Wright E 2020. Biodiversity monitoring, ecological integrity, and the design of the New Zealand Biodiversity Assessment Framework. New Zealand Journal of Ecology 44(2): 3411.

Moriasi D, Gitau M, Pai N, Daggupati P 2015. Hydrologic and water quality models: performance measures and evaluation criteria. Transactions of the ASABE 58(6): 1763–1785.

Parkes JP 1988. A review of the options to manage Himalayan thar (*Hemitragus jemlahicus*) in New Zealand. Unpublished Forest Research Institute Report to the Department of Conservation.

Parkes JP 2006. Does commercial harvesting of introduced wild mammals contribute to their management as conservation pests? In: Allen RB, Lee WG eds. Biological Invasions in New Zealand. Berlin, Heidelberg, Springer. Pp. 407–420.

Parkes JP, Tustin KG 1985. A reappraisal of the distribution and dispersal of female Himalayan thar in New Zealand. New Zealand Journal of Ecology 8: 5–10.

Parkes JP, Forsyth DM 2008. Interspecific and seasonal dietary differences of Himalayan thar, chamois and brushtail possums in the central Southern Alps, New Zealand. New Zealand Journal of Ecology 32(1): 46–56.

Parkes JP, Thomson C 1999. Impact of Himalayan thar (*Hemitragus jemlahicus*) on snow tussock in the Southern Alps. Science for Conservation 132.

Parkes JP, Thomson C, Newell CL, Forrester G 2004. Impacts of Himalayan thar (*Hemitragus jemlahicus*) on snow tussocks in the Southern Alps. Landcare Research contract report LC0304/077.

Perry ME 2003. The browsing impact and abundance of European brown hares *(Lepus europaeus*) in the central North Island, New Zealand. Unpublished MSc thesis, Massey University, Palmerston North, New Zealand.

R Core Team 2024. R: a language and environment for statistical computing. Version 4.4.0. Vienna, Austria, R Foundation for Statistical Computing.

Ramsey DSL, Forsyth DM 2021. Abundance of Himalayan tahr in the South Rakaia/Upper Rangitata and Gammack/Two Thumb management units. Heidelberg, Victoria: Arthur Rylah Institute for Environmental Research, Department of Environment, Land, Water and Planning.

Ramsey DSL, Forsyth DM, Perry M, Thomas P, McKay M, Wright EF 2022. Using helicopter counts to estimate the abundance of Himalayan tahr in New Zealand's Southern Alps. The Journal of Wildlife Management 86(6): e22252.

Rose AB, Allen RB 1990. Impact of Himalayan thar on vegetation of the North Branch, Godley Valley, Canterbury. Forest Research Institute Contract Report FEW 90/32.

Rose AB, Platt KH 1990. Age-states, population structure, and seedling regeneration of *Chionochloa pallens* in Canterbury alpine grasslands, New Zealand. Journal of Vegetation Science 1(1): 89–96.

Rose AB, Platt KH 1992. Snow tussock (*Chionochloa*) population responses to removal of sheep and European hares, Canterbury, New Zealand. New Zealand Journal of Botany 30(4): 373–382.

Smithson M, Verkuilen J 2006. A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. Psychological Methods 11(1): 54–71.

Sparrow A, Kelly D 2000. Thar density and vegetation condition. Conservation Advisory Science Notes No. 281. Wellington, Department of Conservation.

Stage AR 1976. An expression for the effect of aspect, slope, and habitat type on tree growth. Forest Science 22(4): 457–460.

Thomson C, Parkes JP, Coleman MC 1997. Impact of Himalayan thar on alpine tussock grasslands in Carneys Creek, Rangitata catchment. Landcare Research contract report LC9798/38.

Thomson C, Parkes JP, Coleman MC, McGlinchy A 1997. Impact of Himalayan thar on alpine tussock in the Hooker Valley and the North Branch of the Godley Valley Landcare Research contract report LC9697/97.

Tustin KG, Parkes JP 1988. Daily movement and activity of female and juvenile Himalayan thar (*Hemitragus jemlahicus*) in the eastern Southern Alps, New Zealand. New Zealand Journal of Ecology 11: 51–59.

Wardle P 1991. Vegetation of New Zealand. Cambridge, U.K, Cambridge University Press.

Watson MB 2007. Aspects of the feeding ecology of Himalayan tahr (*Hemitragus jemlacicus*), some comparisons with chamois (*Rupicapra rupicapra rupicapra*) and implications for tahr management in New Zealand. Unpublished thesis, Lincoln University, Lincoln, New Zealand.

Wong V, Hickling GJ 1999. Assessment and management of hare impact on high-altitude vegetation. Science of Conservation 116. Wellington, Department of Conservation.

Wright EF, Bellingham PJ, Richardson SJ, McKay M, MacLeod CJ, McGlone MS 2020. How to get a national biodiversity monitoring programme off the ground: lessons from New Zealand. Parks 26.2: 67–78.

Yockney IJ, Hickling GJ 2000. Distribution and diet of chamois (*Rupicapra rupicapra*) in Westland forests, South Island, New Zealand. New Zealand Journal of Ecology 24(1): 31–38.

Appendix 1 – Modelling the density of tahr

This appendix outlines the modelling approach used to predict the density of tahr in the eight study catchments for the 2016–2019 and 2023 monitoring periods, along with key outputs. This modelling was necessary because counts of tahr made during these periods were undertaken on 4 km^2 grids that did not align with the study catchments (Ramsey et al. 2022). The predictions of tahr density were used to inform the relationship between catchment-level tahr density and ungulate activity (section 3.4.3).

Methods

The 4 km^2 aerial survey grid used for the most recent tahr counts (2016–2023) did not spatially align with the vegetation monitoring plots (Figure A2.1; Ramsey et al. 2022), so we were not able to directly use these estimates of tahr density in our analyses. In order to estimate catchment-level tahr density in our study catchments, we used these data to model tahr densities for this period as a function of relevant environmental variables using random forest models (Table A2.1; Breiman 1984, 2001; Cutler et al. 2007). We first predicted the likely density of tahr across the seven tahr management units and exclusion zones, and then used these predictions to estimate tahr density within each study catchment for each monitoring period (2016–2019, 2023).

We selected environmental predictors likely to be important in structuring tahr density through physical habitat provision and food availability (Table A1.1). These predictors described characteristics of the climate, topography, and land cover in the landscape where the aerial monitoring occurred. Because the aerial monitoring plots had an area of 4 km^2, we resampled the environmental variables to the same resolution. Layers representing climate and topography were sourced from the New Zealand Environmental Data Stack (McCarthy et al. 2021), while land-cover data were acquired from the Land Cover Database (LCDB5; Manaaki Whenua – Landcare Research 2020) and converted to represent the proportion of each 4 km^2 grid cell covered by each land-cover class.

We modelled tahr density as a function of the environmental predictors with 1,000 random forest models (Breiman 1984, 2001; Cutler et al. 2007) using the *randomForest* and *pdp* packages (Liaw & Wiener 2002; Greenwell 2017). For each model iteration, the density value for each 4 km^2 monitoring plot was drawn from a random truncated normal distribution based on the mean ± 95% confidence intervals predicted by Ramsey et al (2022) and subsequent work. This approach allowed us to incorporate the uncertainty associated with the density estimates.

A random forest model is a flexible, machine-learning algorithm based on an ensemble of decision trees (Breiman 2001). Unlike linear models, random forest models cannot be expressed as equations. However, the relationships between predictor and response variables identified by random forest models can be represented by importance measures and partial dependence plots (Breiman 2001; Cutler et al. 2007). Variable importance is a measure of the significance of each predictor in predicting the response and is calculated by assessing the loss in model performance (i.e. the increase in the mean square error; MSE) when predictions are made using randomly permuted observations. The differences in MSE between trees fitted with the original and permuted observations are averaged over all trees and normalised by the standard deviation of the differences (Cutler et al. 2007).

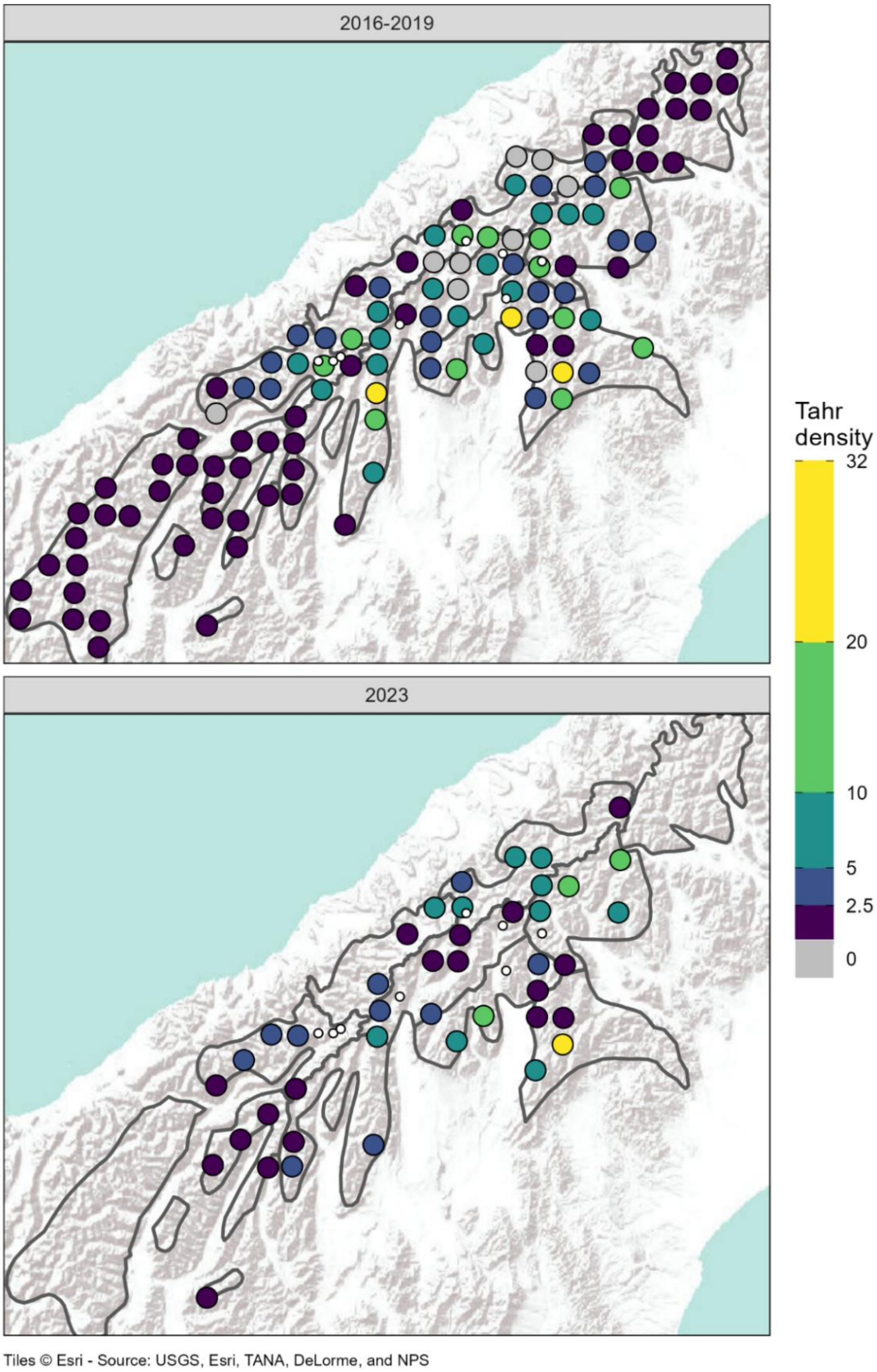


Figure A1.1. The mean predicted density of tahr (animals/km^2) estimated from aerial helicopter monitoring in 4 km^2 plots over two periods from 2016–2019 and 2023. Densities greater than 2.5 animals/km^2 exceed the maximum intervention density (Table 1). Note that the plot size is exaggerated for ease of visualisation, with the study catchment locations shown by white dots. Density data are from Ramsey et al. 2022 and DSL Ramsey, Department of Energy, Environment and Climate Action, Victoria State Government, Australia, pers. comm., 15 May 2024.

Table A1.1. Predictors used in random forest models of tahr density. Climate and topography predictors were sourced from McCarthy et al. 2021, while the land-cover predictors were calculated from LCDB5 (Manaaki Whenua – Landcare Research 2020).

Group	Predictor	Description	Unit
Climate	Mean annual temperature	Based on Land Environments of New Zealand data from 1950 to 1980.	°C
	Annual temperature variability	Based on the standard deviation of monthly temperature means from 1950 to 1980.	°C
	Mean annual precipitation	Based on Land Environments of New Zealand data from 1950 to 1980.	mm
	Precipitation seasonality	Annual precipitation variability for the years 1950–1980 based on the ratio of the standard deviation of the monthly total precipitation to mean monthly precipitation.	%
	Annual potential incoming solar radiation	Annual sum of daily potential solar radiation accounting for elevation, surface orientation, influences (shading) of surrounding topography, and (to a certain extent) atmospheric conditions.	$MWh/m^2/yr$
Topography	Elevation	Elevation above sea level generated from a 25 m digital elevation model	m
	Slope	Slope in degrees generated from a 25 m digital elevation model	°
Land cover	Alpine grass – herbfield	Percentage of 4 km^2 cell containing alpine grass – herbfield (LCDB5: Class 15)	%
	Tall tussock grassland	Percentage of 4 km^2 cell containing tall tussock grassland (LCDB5: Class 43)	%
	Permanent snow & ice	Percentage of 4 km^2 cell containing Permanent snow & ice (LCDB5: Class 14)	%
	Sub-alpine shrubland	Percentage of 4 km^2 cell containing Sub-alpine shrubland (LCDB5: Class 55)	%
	Indigenous forest	Percentage of 4 km^2 cell containing indigenous forest (LCDB5: Class 69)	%
Survey	Monitoring period	The monitoring period over which tahr density data were collected (2016–2019 & 2023).	Factor

The relationships between tahr density and the environmental predictors were visualised using partial dependence plots, which provide a graphical representation of the marginal effect of a predictor on the response when the values of all other predictors are held constant. Partial dependence plots do not perfectly represent the effects of each predictor, particularly if predictors are highly correlated or strongly interacting, but they do provide an approximation of the modelled predictor–response relationships that are useful for model interpretation (Cutler et al. 2007).

Model performance was assessed by comparing observations with independent predictions (i.e. sites that were not used in fitting the model), which were obtained from the out-of-bag samples. We summarised the models using three statistics: regression R^2, Nash–Sutcliffe efficiencies (NSE), and percent bias (PBias). Model predictions were evaluated to be very good, good, satisfactory or unsatisfactory, following the criteria proposed by Moriasi et al. (2015).

Predictions were made with each random forest model by 'running' new cases down every tree in the fitted forest and averaging the predictions made by each tree (Cutler et al. 2007). For each monitoring period (2016–2019 & 2023) we predicted tahr density for every 4 km^2 grid cell within the tahr management units and exclusion zones. These predictions were then used to estimate the tahr density at the location of each vegetation monitoring plot and then summarised to produce catchment-level mean (±95% confidence interval) predictions of tahr density.

Results

The average model performance was satisfactory when assessed against the criteria of Moriasi et al. (2015), with $R^2 = 0.35 \pm 0.01$, NSE = 0.34 ± 0.01, and PBias = 6.01 ± 1.47. However, the models tended to overpredict tahr density at low densities and underpredict tahr density at high densities, as indicated by the slope of the blue line in Figure A1.3 relative to the 1:1 line.

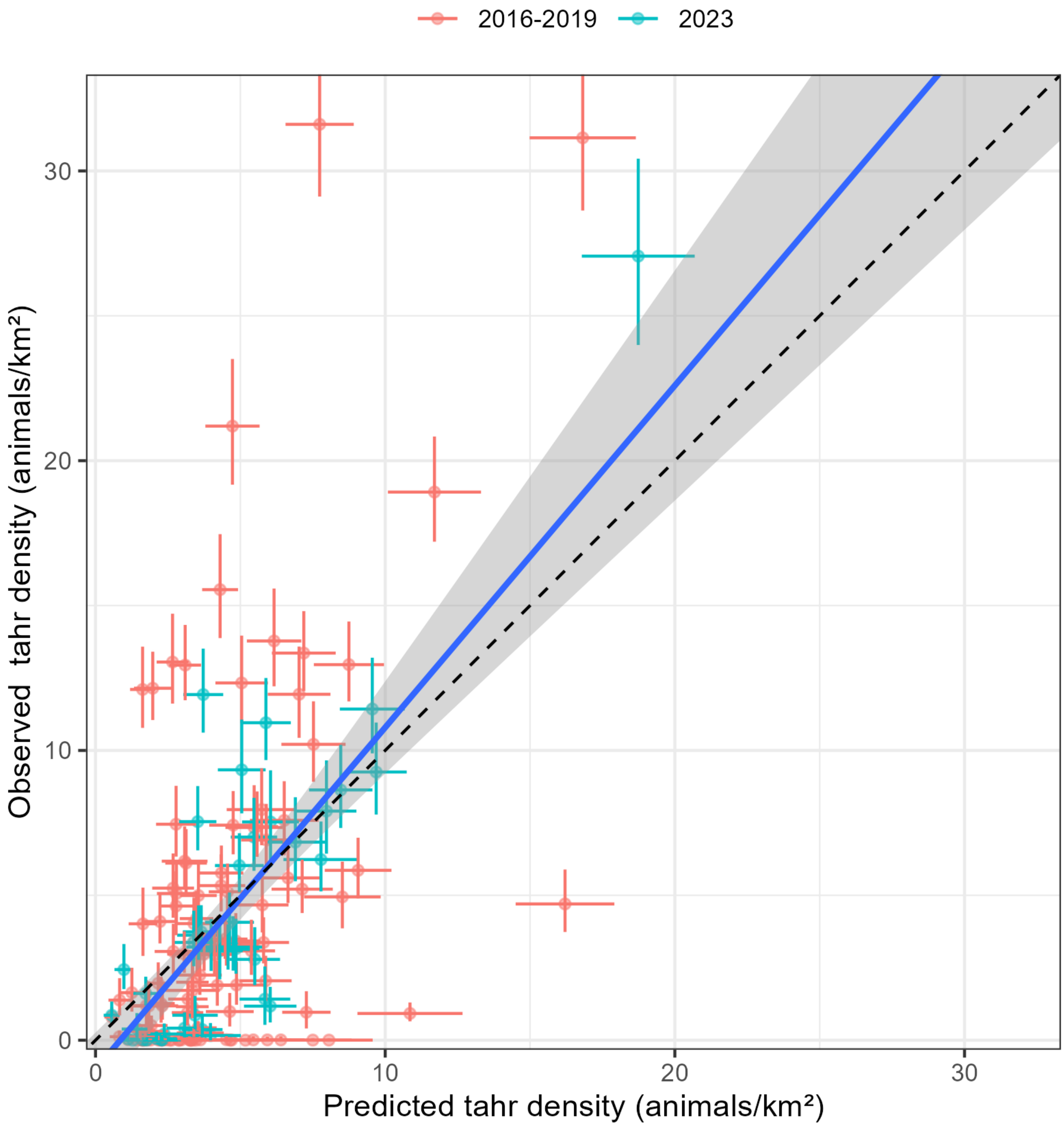


Figure A1.2. Comparison of predicted mean (±95% credible interval) tahr density (animals/km^2) within the 4 km^2 monitoring plots (Ramsey et al. 2022) versus mean (±95% confidence interval) tahr density (animals/km^2) predicted by 1,000 random forest models for each monitoring period. The observed values from Ramsey et al. 2022 are plotted on the y-axis and predicted values on the x-axis, following Piñeiro et al. (2008). Blue solid line: best fit linear regression of the observed and mean predicted values; black dashed line: one-to-one line.

The predictors with high importance reflected strong associations between tahr density and land cover, climate, and topography (Figure A1.2, Figure A1.3). The most important predictor in all models was the percentage of alpine grass–herbfield within each 4 km^2 grid cell, with tahr density increasing with increasing levels of this vegetation class. Tahr density decreased with increasing mean annual precipitation, but increased at higher elevations. Monitoring period was the least important predictor but was retained in the models to allow prediction of tahr density for both periods.

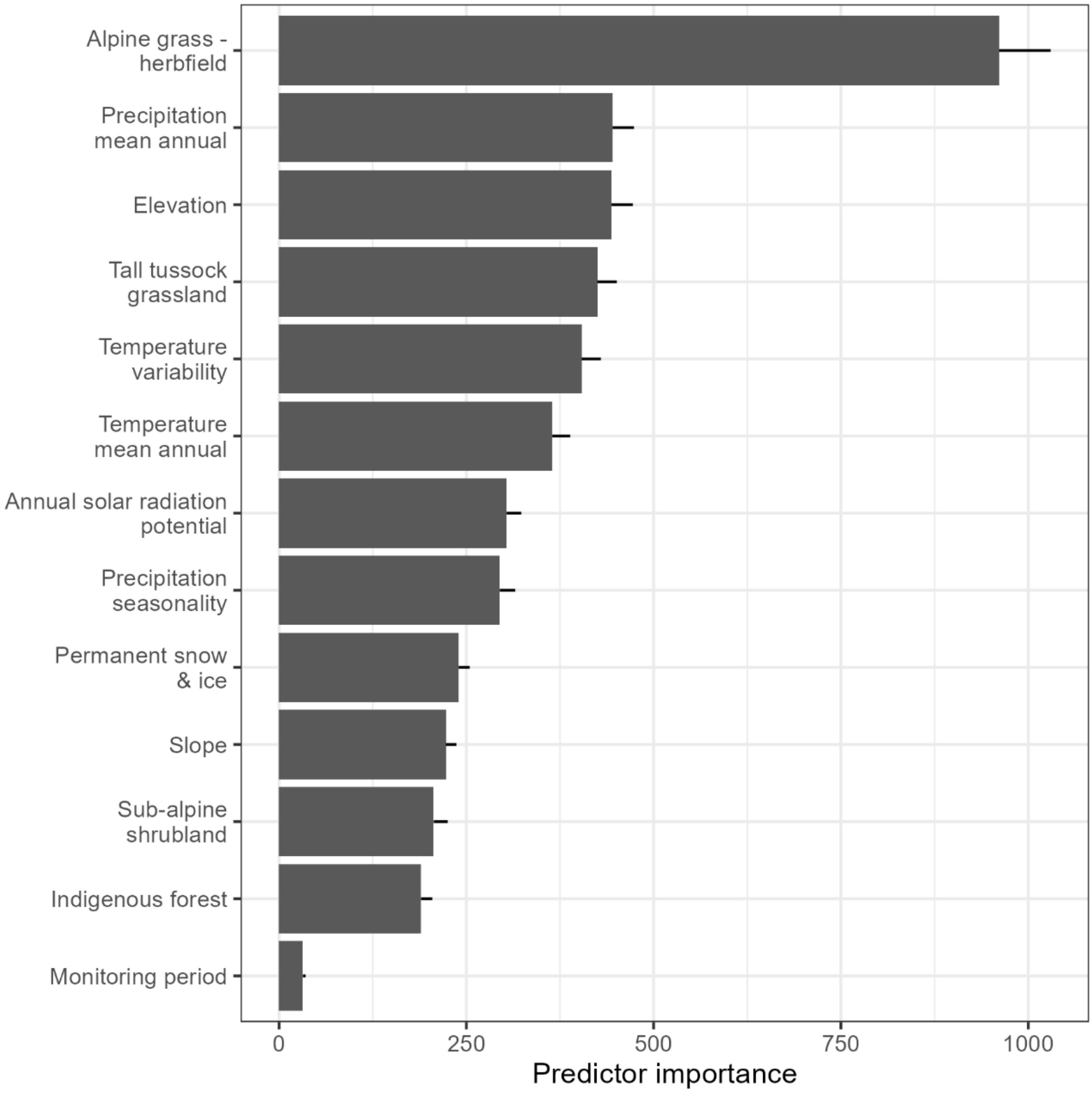


Figure A1.3. Mean relative importance of predictors of tahr density based on 1,000 random forest models. Error bars represent the standard deviation.

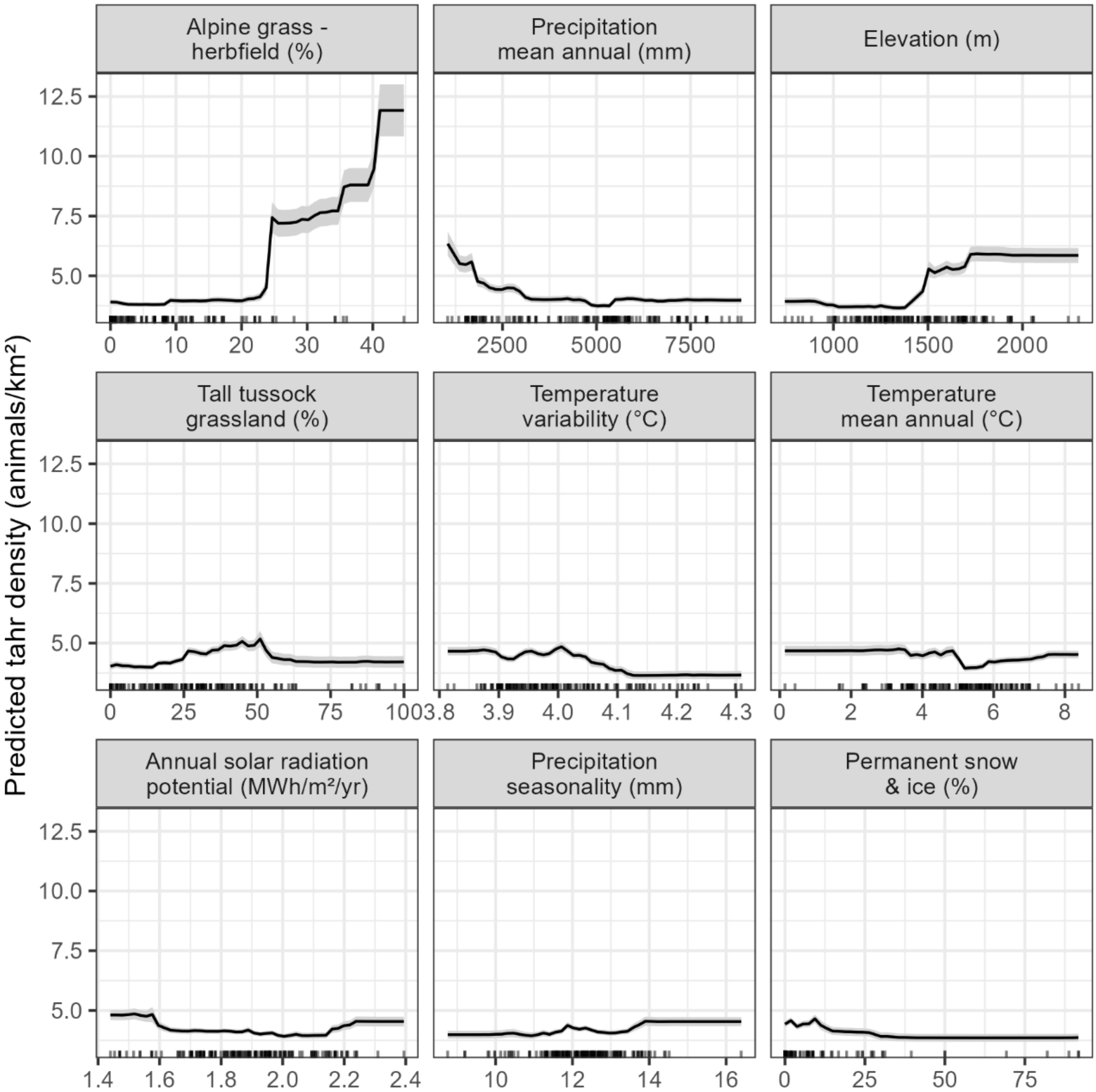


Figure A1.4. Partial dependence plots for the nine most important predictors of tahr density (animals/km^2) based on 1,000 random forest models, with panels ordered by predictor importance (Figure A1.3). Each panel represents the mean (±95% confidence intervals) predicted density of tahr when all other predictors are held at their mean value. The plot amplitude (the range of the response on the y-axis) is directly related to a predictor's importance (i.e. a larger amplitude for predictors with higher importance). Vertical marks on the x-axes show the distribution of the 4 km^2 aerial monitoring plots along each environmental gradient.

The predicted density of tahr across the tahr management units and exclusion zones ranged from 0.24 to 25.57 animals/km^2 (Figure A1.5). The highest mean densities were predicted to occur in the eastern regions, particularly in the Two Thumb–Gammack and Ben Ohau management units. However, prediction uncertainty (expressed as the standard deviation of predictions from 1000 random forest models) was also highest in these areas, suggesting the models are less reliable when predicting higher densities. These patterns strongly reflect the patterns of uncertainty associated with the density data used to parameterise the random forest models (Ramsey et al. 2022).

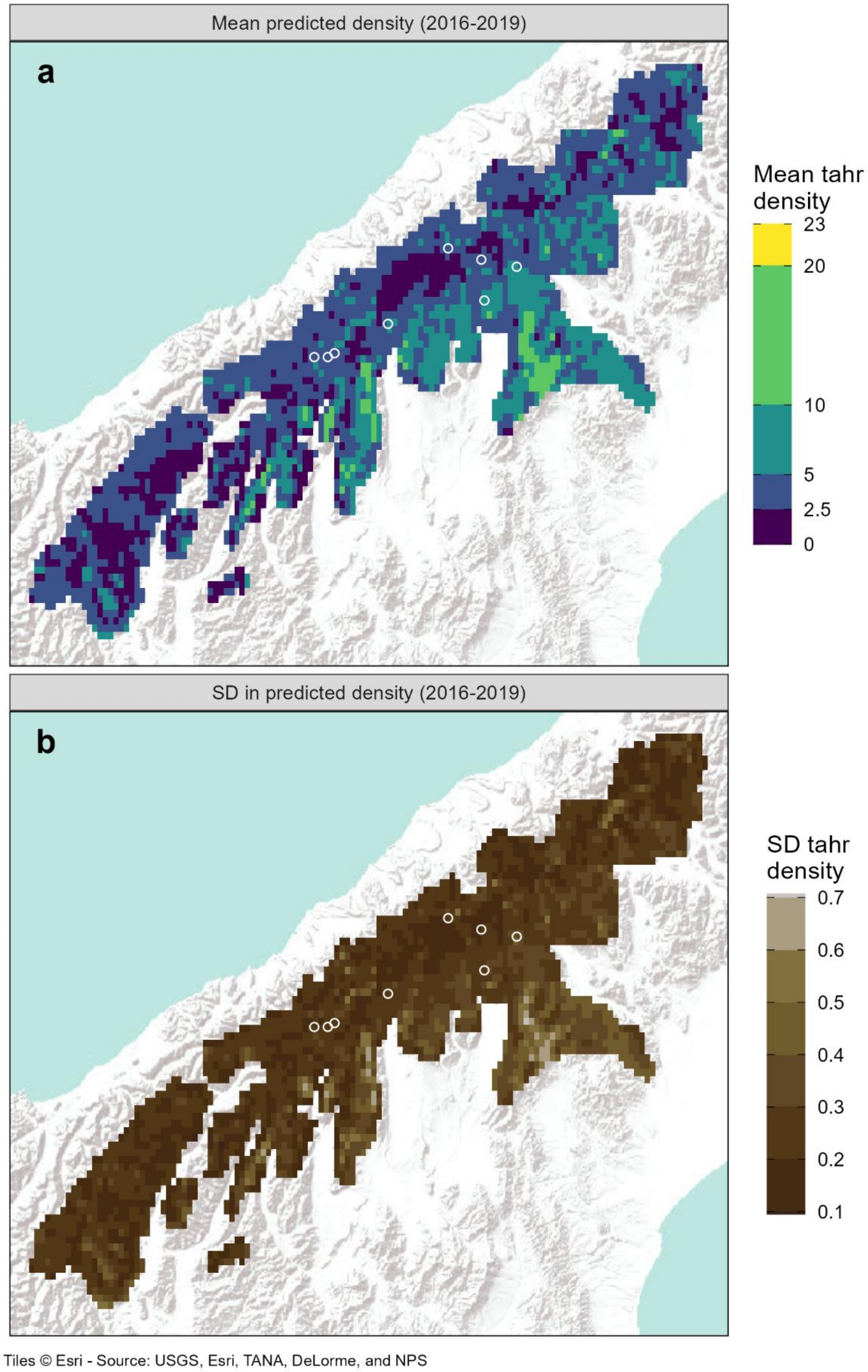


Figure A1.5. Predicted tahr density (animals/km^2) across the tahr management units and exclusion zones for the 2016–2019 monitoring period. a) Predicted mean tahr density, where values >2.5 animals/km^2 exceed the maximum intervention density across all management units (Table 1). b) Prediction uncertainty expressed as the standard deviation of the predictions, where lighter colours reflect a higher uncertainty in the predicted mean tahr density shown in panel a). Notes: white circles show the location of the study catchments (Table 1, Figure 1b).

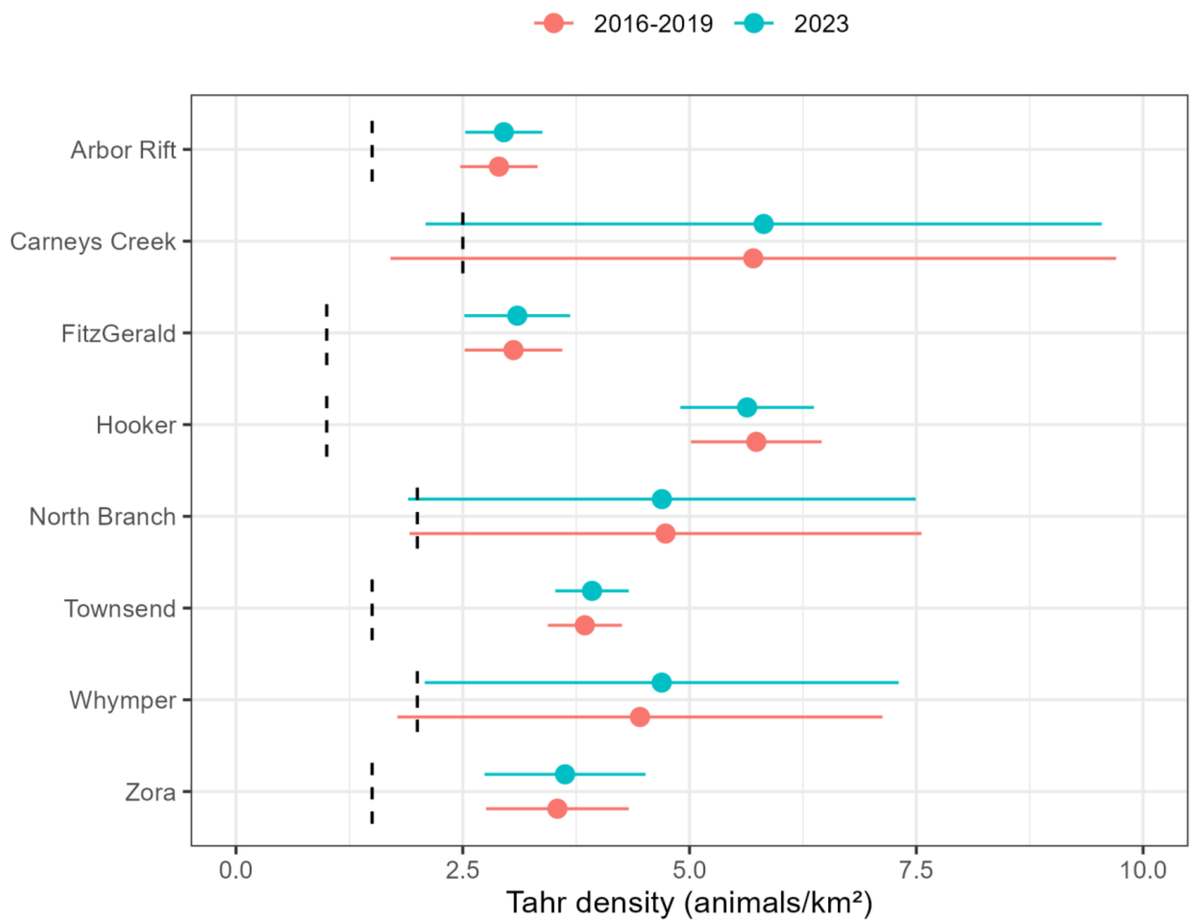


Figure A1.6. Predicted mean (±95% confidence intervals) tahr density (animals/km^2) for the study catchments over the two periods where tahr were monitored within 4 km^2 plots by helicopter. Predictions are based on 1,000 random forest models. Vertical dashed lines indicate the intervention density within each associated management unit (Department of Conservation 1993).

Mean catchment-level predictions of tahr density ranged from 2.90 to 5.82 animals/km^2, with greater variation observed in the Carneys Creek, North Branch, and Whymper catchments, where individual vegetation plots are located over a wide geographical area that encompasses a broad range of environmental conditions (Figure A1.6; Figure 1). However, there was little difference in the predicted tahr density between the two monitoring periods. Tahr densities in both periods in five of the eight catchments exceeded the intervention densities defined for their management unit under the national *Himalayan Thar Control Plan* (Figure A1.6; Department of Conservation 1993). These mean predictions of tahr density were subsequently used in statistical analyses to assess changes in tahr density over time (section 3.4.1) and the relationship between ungulate activity (expressed as the proportion of pellet plots with ungulate faecal pellets) and tahr density (section 3.4.3)

Appendix 2 – Model selection for ungulate and hare activity models

Table A2.1. Candidate model sets for tahr density, hare activity, and ungulate activity, as evaluated by comparing corrected Akaike's Information Criterion (AICc). Models for tahr density used a gamma error distribution, while the models for the hare and ungulate activity used a binomial error distribution. The log likelihood (logLik) differences in model AICc value from the best model (ΔAICc), degrees of freedom (df), and Akaike weights are shown for each model. The best model (in bold) for each response variable was identified using ΔAICc and model diagnostics.

Model	logLik	AICc	dAICc	df	Weight
a) Catchment-level tahr density (animals/km^2)					
year * catchment	**–216.52**	**474.00**	**0.00**	**17**	**1.00**
year + catchment	–239.15	500.61	26.61	10	0.00
catchment	–241.17	502.22	28.23	9	0.00
1 (intercept only)	–285.76	575.64	101.65	2	0.00
year	–285.47	577.17	103.17	3	0.00
b) Plot-level ungulate activity (proportion of plots with ungulate pellets)					
catchment * year	**–2,419.08**	**4,871.22**	**0.00**	**16**	**1.00**
catchment + year	–2,749.20	5,516.75	645.53	9	0.00
year	–3,327.84	6,659.71	1,788.49	2	0.00
catchment	–3,339.51	6,695.29	1,824.07	8	0.00
1 (intercept only)	–3,803.76	7,609.52	2,738.3	1	0.00
c) Plot-level hare activity (proportion of plots with hare pellets)					
catchment * year	**–2,922.19**	**5,873.29**	**0.00**	**14**	**1.00**
catchment	–3,077.36	6,168.97	295.68	7	0.00
catchment + year	–3,076.95	6,170.21	296.93	8	0.00
1 (intercept only)	–3,241.70	6,485.41	612.13	1	0.00
year	–3,241.59	6,487.21	613.92	2	0.00

Table A2.2. Candidate model sets for ungulate activity (proportion of pellet plots with faecal pellets), as evaluated by comparing corrected Akaike's Information Criterion (AICc). All models used a binomial error distribution. The log likelihood (logLik), differences in model AICc value from the best model (ΔAICc), degrees of freedom (df), and Akaike weights are shown for each model. The best model (in bold) was identified using ΔAICc and model diagnostics. hare_scale = hare activity (proportion of pellet plots with hare pellets), scaled by subtracting the mean divided by 2 SD.

Model	logLik	AICc	dAICc	df	weight
hare_scale + (1 + hare_scale | catchment) + (1 | catchment_plot) + (1 | year)	**–1,782.69**	**3,579.60**	**0.00**	**7**	**1.00**
hare_scale + (1 + hare_scale | catchment) + (1 | year)	–2,326.39	4,664.93	1,085.33	6	0.00
hare_scale + (1 | year)	–2,705.89	5,417.83	1,838.24	3	0.00
hare_scale + (1 + hare_scale | catchment) + (1 | catchment_plot)	–2,739.10	5,490.36	1,910.76	6	0.00
hare_scale + (1 | catchment_plot)	–2,834.59	5,675.22	2,095.62	3	0.00
hare_scale + (1 + hare_scale | catchment)	–3,255.32	6,520.74	2,941.15	5	0.00
hare_scale	–3,729.71	7,463.44	3,883.84	2	0.00
1 (Intercept only)	–3,809.93	7,621.86	4,042.26	1	0.00

Table A2.3. Candidate model sets for catchment-level tahr density (animals/km^2), as evaluated by comparing corrected Akaike's Information Criterion (AICc). All models used a gamma error distribution. The log likelihood (logLik), differences in model AICc value from the best model (ΔAICc), degrees of freedom (df), and Akaike weights are shown for each model. The best model (in bold) was identified using ΔAICc and model diagnostics. activity_mean = mean catchment-level ungulate activity (mean proportion of pellet plots with ungulate faecal pellets).

Model	logLik	AICc	dAICc	df	weight
Catchment-level tahr density (animals per km^2)					
activity_mean + (1 | catchment)	**–73.52**	**156.71**	**0.00**	**4**	**0.807**
activity_mean + (1 | year) + (1 | catchment)	–73.52	159.65	2.94	5	0.185
activity_mean	–79.76	166.47	9.76	3	0.006
activity_mean + (1 | year)	–79.76	169.18	12.47	4	0.002
1 (intercept only)	–84.20	172.86	16.16	2	0.000

Appendix 3 – Estimating tussock height and vegetation cover

Table A3.1. Number of surveyed plots (total and plots with vegetation cover measured) and number of mature tussocks surveyed, by year. Columns highlighted in green indicate data that are new to the current report and have not previously been analysed.

Catchment		1990	1992	1993	1994	1995	1996	1997	1999	2001	2002	2003	2011	2012	2013	2021	2022	2023
Total plots		**9**	**44**	**12**	**8**	**9**	**16**	**48**	**45**	**28**	**47**	**45**	**29**	**32**	**56**	**42**	**32**	**42**
Arbor Rift	Plots		9		8			18			18			17		16		
	Veg cover		9		8			9			17			16		16		
	Mature		346		258			795			390			127		204		
Carneys Creek	Plots		20					18			18				18			18
	Veg cover		20					18			17				18			17
	Mature		761					585			567				476			288
FitzGerald	Plots								15			15			14		15	
	Veg cover								15			14			15		15	
	Mature								251			332			310		272	
Hooker	Plots		9			9				9					9			9
	Veg cover		9			-				9					9			9
	Mature		446			434				356					314			318
North Branch	Plots	9	6				16			19			18				17	
	Veg cover	13	6				16			18			18				16	

Catchment		1990	1992	1993	1994	1995	1996	1997	1999	2001	2002	2003	2011	2012	2013	2021	2022	2023
	Mature	203	228				950			552			526				442	
Townsend	Plots								15			15			15			15
	Veg cover								13			16			16			14
	Mature								275			331			303			112
Whymper	Plots			12				12			11		11			11		
	Veg cover			12				12			9		11			11		
	Mature			447				449			379		387			317		
Zora	Plots								15			15		15		15		
	Veg cover								30			30		15		15		
	Mature								246			376		116		85		

Table A3.2. Summary of number of surveyed plots, by catchment and year, with the number of tussock species, the mean height (cm), mean live diameter (cm), mean crown death (%), mean vegetation cover (%), mean ungulate activity (proportion of quadrats with faecal pellets). Values are mean ± standard deviation calculated across each catchment within a given year.

Catchment	Year	No. plots	No. species	Height (cm)	Diameter (cm)	Crown death (%)	Vegetation cover (%)	Ungulate activity
Arbor Rift	1992	9	3	34.62 ± 18.8	14.46 ± 8.9	20.71 ± 15.9	77.28 ± 7.0	0.43 ± 0.4
	1994	8	3	33.90 ± 18.2	17.17 ± 10.5	21.18 ± 16.8	73.35 ± 6.4	0.56 ± 0.2
	1997	17	3	38.23 ± 20.2	15.58 ± 11.1	8.18 ± 12.8	76.89 ± 8.7	0.1 ± 0.1
	2002	17	2	38.89 ± 18.9	17.72 ± 14.2	12.37 ± 13.9	79.25 ± 7.4	0.23 ± 0.1
	2012	15	1	22.87 ± 14.7	11.69 ± 8.1	22.40 ± 15.8	83.00 ± 17.8	0.48 ± 0.1
	2021	10	2	14.00 ± 7.0	8.74 ± 3.4	25.79 ± 19.1	80.95 ± 8.9	0.74 ± 0.1
Carneys Creek	1992	20	3	67.92 ± 23.9	20.96 ± 16.4	7.60 ± 10.9	84.46 ± 17.1	0.03 ± 0.1
	1997	18	2	75.85 ± 19.8	24.22 ± 17.4	13.24 ± 13.0	66.54 ± 19.2	0.08 ± 0.1
	2002	18	3	80.46 ± 23.4	29.68 ± 18.6	15.54 ± 12.4	78.01 ± 13.2	0.16 ± 0.2
	2013	17	2	76.73 ± 24.8	34.44 ± 23.5	20.81 ± 17.1	84.85 ± 16.3	0.20 ± 0.2
	2023	13	2	75.01 ± 24.8	30.58 ± 20.3	22.16 ± 14.5	73.02 ± 14.5	0.51 ± 0.2
FitzGerald	1999	15	4	61.55 ± 20.4	22.69 ± 17.3	27.27 ± 13.5	74.22 ± 12.1	0.12 ± 0.2
	2003	15	2	62.11 ± 18.8	20.83 ± 16.1	14.71 ± 11.9	77.24 ± 13.6	0.11 ± 0.1
	2013	14	2	49.70 ± 18.6	27.12 ± 17.8	21.58 ± 16.0	79.15 ± 9.1	0.25 ± 0.1
	2022	15	3	41.88 ± 17.0	26.11 ± 20.0	26.23 ± 13.6	76.96 ± 11.3	0.28 ± 0.2
Hooker	1992	9	2	44.00 ± 13.8	16.31 ± 9.1	10.79 ± 9.6	76.26 ± 27.5	0.01 ± 0
	1995	9	2	44.57 ± 12.9	17.05 ± 10.0	10.42 ± 10.1	-	0.03 ± 0.1
	2001	9	1	48.01 ± 12.7	23.96 ± 13.0	10.53 ± 11.6	80.73 ± 8.9	0.04 ± 0.1
	2013	9	2	43.04 ± 13.1	23.76 ± 12.6	10.34 ± 18.5	87.68 ± 4.5	0.07 ± 0.1
	2023	9	3	39.14 ± 10.1	23.00 ± 13.0	17.86 ± 13.3	78.73 ± 8.8	0.08 ± 0.1

Catchment	Year	No. plots	No. species	Height (cm)	Diameter (cm)	Crown death (%)	Vegetation cover (%)	Ungulate activity
North Branch	1990	9	3	85.67 ± 26.4	33.23 ± 26.2	35.30 ± 14.4	46.56 ± 3.7	0.22 ± 0.2
	1992	6	1	68.95 ± 20.6	27.64 ± 18.9	17.53 ± 13.9	76.73 ± 3.1	0.35 ± 0.2
	1996	15	2	51.91 ± 33.6	35.33 ± 22.0	12.89 ± 16.2	49.6 ± 16.9	0.41 ± 0.1
	2001	19	5	77.73 ± 24.5	37.60 ± 25.7	14.30 ± 14.2	61.38 ± 18.1	0.38 ± 0.2
	2011	18	3	78.33 ± 27.3	37.25 ± 26.3	14.81 ± 14.7	64.00 ± 14.6	0.21 ± 0.2
	2022	17	3	59.58 ± 23.8	35.20 ± 25.8	24.26 ± 15.2	67.77 ± 14.5	0.41 ± 0.2
Townsend	1999	15	2	65.13 ± 17.4	17.36 ± 10.7	30.38 ± 12.6	73.62 ± 16.0	0.03 ± 0
	2003	15	2	60.10 ± 17.0	17.96 ± 12.5	20.70 ± 13.7	77.87 ± 10.6	0.04 ± 0
	2013	15	2	60.73 ± 18.1	22.18 ± 16.5	32.95 ± 14.4	81.86 ± 17.0	0.24 ± 0.2
	2023	12	2	29.83 ± 14.6	15.97 ± 12.4	31.43 ± 15.6	82.92 ± 11.6	0.44 ± 0.3
Whymper	1993	12	2	58.29 ± 25.4	15.84 ± 11.8	24.66 ± 12.3	78.67 ± 17.0	0.06 ± 0.1
	1997	12	2	56.16 ± 21.1	16.53 ± 12.3	20.28 ± 12.8	83.64 ± 6.8	0.04 ± 0.1
	2002	11	2	57.10 ± 25.7	22.29 ± 17.0	13.81 ± 12.2	86.15 ± 6.6	0.33 ± 0.4
	2011	11	2	56.00 ± 24.6	24.26 ± 16.9	17.67 ± 13.3	81.64 ± 5.9	0.25 ± 0.2
	2021	11	1	52.20 ± 20.4	22.54 ± 17.1	21.59 ± 16.3	88.49 ± 6.5	0.25 ± 0.2
Zora	1999	15	2	54.30 ± 21.7	15.85 ± 11.2	33.94 ± 11.9	56.18 ± 23.7	0.13 ± 0.1
	2003	15	2	47.01 ± 20.7	16.64 ± 12.5	14.36 ± 14.0	65.56 ± 14.8	0.16 ± 0.2
	2012	15	3	20.59 ± 10.3	11.94 ± 6.5	24.56 ± 16.8	66.16 ± 24.9	0.54 ± 0.2
	2021	14	2	16.35 ± 6.1	9.86 ± 6.5	32.73 ± 14.9	66.00 ± 19.4	0.44 ± 0.2

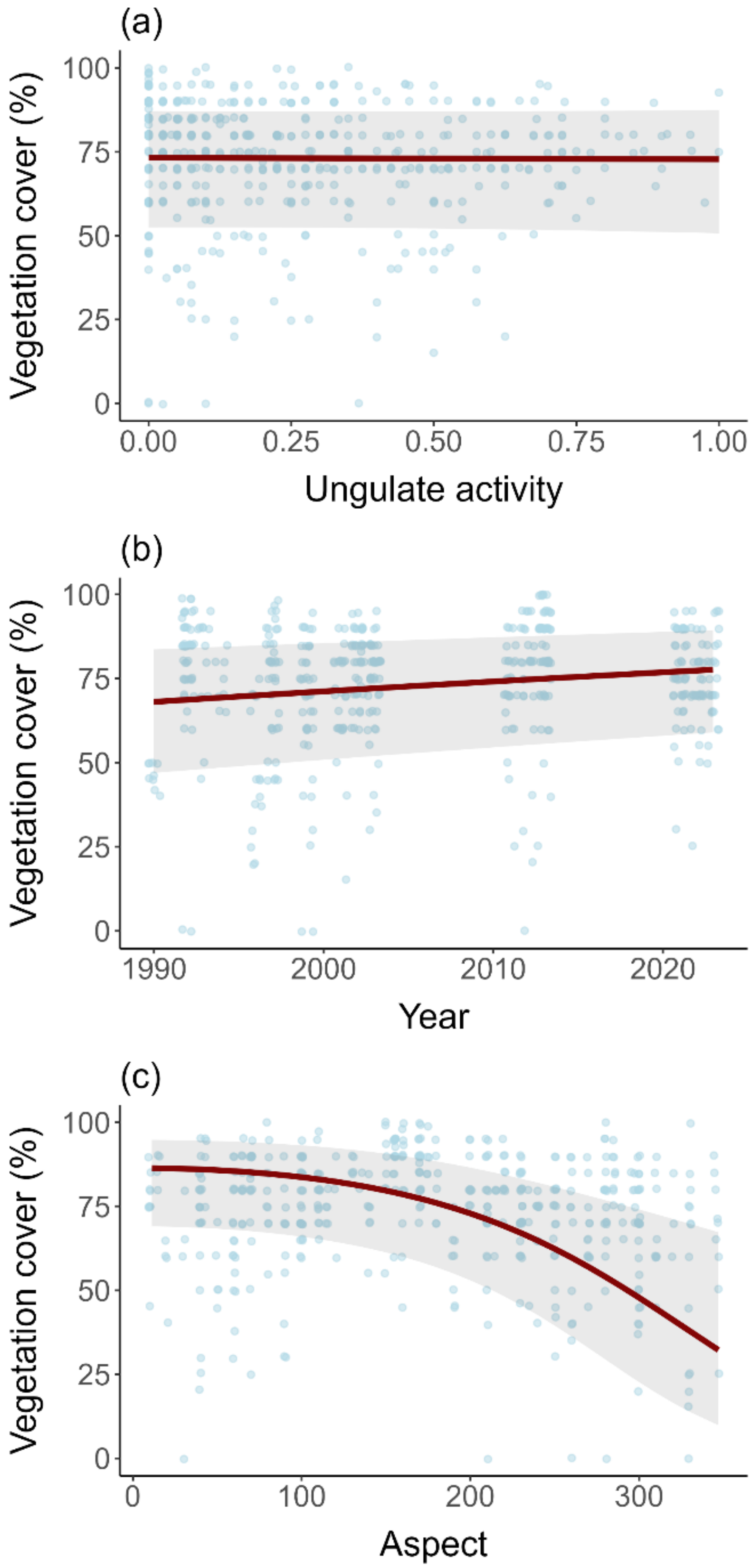


Figure A3.1. Predicted mean relationship between overall vegetation cover (in %), ungulate activity (a), year of monitoring (b), and aspect (°) with quadratic term (c). The model also included year, elevation, and ungulate activity as predictors, followed a beta regression, and included plot nested within catchment as random factors. All the other fixed effects included in the model were set at their mean values. Grey areas represent 95% confidence intervals. See Table A3.3 for detailed outputs.

Table A3.3. Relationships between overall vegetation cover and elevation (m), aspect (°), year, and ungulate activity, with associated degree of freedom (df), chi-sq. values, and *P*-values. The model followed a beta regression and included plot nested within catchment as random factors. aspect^2 = the term representing the quadratic effect of aspect.

Fixed effects	Relationship	df	chi-sq.	*P*-value
year	increase	1	13.05	<0.001
aspect^2	negative	1	8.34	0.004
aspect	positive	1	5.25	0.022
elevation	ns	1	2.44	0.119
ungulate activity	ns	1	0.004	0.948