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RESEARCH ARTICLE

Hunting of sika deer over six decades does not restore forest regeneration

Sean W. Husheer[1] | **Andrew J. Tanentzap**[2]

[1]New Zealand Forest Surveys, Hastings, New Zealand
[2]Ecosystems and Global Change Group, School of the Environment, Trent University, Peterborough, Ontario, Canada

Correspondence
Andrew J. Tanentzap
Email: atanentzap@trentu.ca

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Abstract

1. High densities of native and introduced deer hamper the regeneration of temperate forests worldwide. Sport hunting is often the sole means of deer control, but whether it can restore forest regeneration remains uncertain.
2. We assessed the potential to restore forest regeneration using unrestricted sport hunting alongside commercial harvesting and government-funded culling of introduced sika deer (*Cervus nippon*) across a 594 km^2 landscape in North Island, New Zealand. We used six decades of repeated measurements of forest regeneration and deer presence, alongside monitoring of tagged stems in a 20-year paired exclosure experiment, to determine whether deer control restored regeneration.
3. In our exclosure experiment, mountain beech (*Fuscospora cliffortioides*) seedling and sapling density, growth and survival were variable but consistently higher when deer were excluded by fencing. Sapling counts in unfenced plots were ≈3–10 times lower after 60 years of deer control compared with unfenced plots, before sika colonisation and other mountain beech forests without sika deer. This result suggests canopy replacement remains at risk despite government-funded culling and encouragement of sport hunting.
4. Individual-based demographic models show that mountain beech is unlikely to regenerate following canopy gap formation in our study landscape unless deer impacts are reduced from current levels. These demographic models predicted present-day forest regeneration far better than two widely used proxies of deer impact: plot-based counts of saplings and estimates of deer densities from faecal pellet counts.
5. *Synthesis and applications*. Here, we show that intensive culling beyond that achievable by sport hunting is needed to reduce deer densities enough to assure canopy regeneration. These interventions will be necessary in the many places worldwide where sport hunting is being relied upon to protect forests but appears to be failing. Given the controversy associated with deer culling, and the need for clear evidence to justify its implementation, we suggest managers could strengthen the evidence base for their interventions by collecting data to build demographic models.

KEYWORDS
browsing, disturbance, forest management, hunting, restoration, seedling regeneration, ungulates, wildlife management

1 | INTRODUCTION

Overabundant deer populations have modified temperate forests in North and South America, Europe, Asia and Oceania (e.g. Ramirez et al., 2019; Russell et al., 2001). At high densities ($>4\,\text{km}^{-2}$), deer shift competitive advantage towards browse-tolerant herbs and small-leaved woody shrubs by preferentially browsing palatable grasses and seedlings (Royo & Carson, 2006). Trampling and browsing of seedlings can further inhibit canopy regeneration and permanently alter forest succession (Hidding et al., 2013; Thrippleton et al., 2018).

Methods to reduce deer densities and restore forest condition include removal of restrictions for sport hunters, commercial harvesting, government-funded culling and predator reintroductions where they were previously present (Nilsen et al., 2007; Redick & Jacobs, 2020). Despite these options, sport hunting is often the sole means of deer population control, because pressure from hunting organisations, landowners, animal rights organisations and wildlife conservationists restricts the use of alternate techniques (Hampton & Hyndman, 2019). Sustained sport hunting can reduce deer abundance, but it is largely unknown if the reduced abundances from sport hunting translate into improvements in forest condition (Reed et al., 2022). Deer abundance and impacts are nonlinearly related, and it can take decades for seedlings to grow into forest canopies once deer impacts are reduced (Tanentzap et al., 2012). One of the best known examples of large-scale managed sport hunting found that browse pressure declined over a 3-year period corresponding to reductions in deer populations, but the long-term outcomes for forest condition were unknown (Hothorn & Müller, 2010). Other studies that suggest sport hunting may be effective at improving forest condition have only tracked seedlings and not their progression into the canopy (Lesser et al., 2019), or only studied understorey plants (Chollet et al., 2016; Jenkins et al., 2014). Even when deer populations are reduced, they can be replaced by other browsers, or the course of succession can be irreversibly altered by browsing (Beguin et al., 2016; Gerhardt et al., 2013; Simard et al., 2013; Tanentzap et al., 2011). To our knowledge, no study has explicitly tracked how sport hunting at the landscape scale directly influences forest regeneration from seedling to canopy, likely because it requires decades of study.

In addition to uncertainty over the effectiveness of sport hunting, interest groups often require unequivocal proof of long-term deer impacts before they will allow reductions in deer densities (Dandy et al., 2012). This requirement is reasonable, because although deer impacts on tree regeneration are generally negative, other factors, such as climate and disturbance, may be more important for forest condition (Spake et al., 2020; Stokely & Betts, 2020). Results from deer impact monitoring are also often ambiguous and can be interpreted differently by different groups, hampering decision-making. Indirect measurements of deer impacts, such as deer counts, faecal pellet surveys, changes in seedling counts, browse indices or summaries of plant cover and composition, are pervasive in management (Côté et al., 2004; Fuller & Gill, 2001; Husheer & Frampton, 2005; Takatsuki, 2009). Sapling and faecal pellet count data are useful for showing trends in forests and deer populations, but may be influenced by confounding factors, such as seasonal rainfall, and so can be unconvincing to sceptics. Ideally, observations of regeneration in forests with little hunting pressure and high deer densities would be compared with forests with high hunting pressure and low or zero deer densities. Data on size-specific survival, abundance and growth rates from tagged seedlings, saplings and trees remeasured over decades could then be used to construct predictive models of forest regeneration along hunting gradients, but these approaches have seldom been implemented (Chollet et al., 2021; Stroh et al., 2008; Tanentzap et al., 2013).

New Zealand offers opportunities to test deer population control methods at temporal and spatial scales that are unavailable in other countries. Because New Zealand lacks any native land mammals, deer are considered a pest by forest conservationists. Restrictions on sport and commercial hunting can be completely removed, encouraged or subsidised. Government-funded culling using aerial shooting can be applied over large areas and for long periods of time ($>100\,\text{km}^2$ and >40 years, Tanentzap et al., 2009). Although introduced red deer (*Cervus elaphus*) populations have been reduced across all of New Zealand by ≈75% by commercial harvesting using aircraft, sika deer (*Cervus nippon*) populations have remained at high densities (Forsyth et al., 2011; Husheer et al., 2006; Husheer & Robertson, 2005). Sika deer have modified forests and prevented canopy regeneration in New Zealand (Husheer et al., 2003), in their native range in eastern Asia (McCullough et al., 2008), and where they have been introduced into Britain, western Europe and the USA (Bartoš, 2009; Feldhamer & Demarais, 2009; Pérez-Espona et al., 2009). Even at low densities (<4 deer km^{-2}), sika deer browsing and trampling can prevent the recruitment of trees into canopy gaps (Iijima & Ueno, 2016; Tamura & Nakajima, 2017). Since their introduction into New Zealand, sika deer have progressively increased their range, replacing the more widespread and commercially valuable red deer, and now occupy >5% of the North Island's area (>6000 of $113{,}729\,\text{km}^2$; Davidson & Fraser, 1991). Sika deer browsing has reduced the density and height of palatable indigenous seedlings (e.g. kāmahi, *Weinmannia racemosa*; three finger, *Raukaua simplex* and broadleaf, *Griselinia littoralis*) and suppressed the regeneration of indigenous beech forest (mountain, red and silver beech; *Fuscospora cliffortioides*, *F. fusca*, *Lophozonia menziesii*, family Nothofagaceae; Husheer et al., 2006).

Here, we tested whether six decades of unrestricted sport hunting, commercial harvesting and government-funded culling of sika deer can restore forest regeneration across a mountain beech-dominated landscape in New Zealand. We first compared changes in counts of saplings and trees of mountain beech with deer population densities estimated from faecal pellet surveys over 58 years. From 1998 to 2018, sampling was focussed at open canopy sites where we expected mountain beech regeneration would be most likely to occur and would reflect the effects of long-term deer hunting on seedling recruitment and establishment. We then tested the dependency of regeneration on parent seed sources and canopy disturbance by constructing a demographic model with two decades of individual seedling, sapling and tree stem measurements in 40 paired fenced–unfenced plots. We predicted nil or very low deer densities would be required before sapling growth and survival rates were high enough for trees to fill canopy gaps (Wright et al., 2012). Alternatively, if canopy regeneration had been permanently suppressed by sika deer, there would be no evidence of differential regeneration in fenced plots. We aim to highlight the value of using long-term forest demographic data for advancing decision-making on deer control.

2 | MATERIALS AND METHODS

2.1 | Kaweka Forest Park study area

Kaweka Forest Park (F.P., 39° S, 176° E, 594 km^2) is located ≈15 km south of the 1905 New Zealand liberation point of sika deer (Map S1). Mountain beech is the most common forest type (≈140 km^2), often forming mono-specific stands from ≈1000 m to tree line at ≈1400 m a.s.l. (Figure S1). Restrictions on sport hunting were removed in 1930, and from 1957 to 1973, a hut and track network was established to aid government cullers (Hunter, 2009; Map S2). Deer culling by government-employed foot hunters was undertaken from 1958 to 1988, when kill rates exceeded one deer per hunter day (mean 563 red and sika deer killed annually; Davidson & Fraser, 1991). From 1965, aircraft were used to shoot from, to recover deer for sale and to transport hunters. A trial of helicopter-based deer culling in ≈110 km^2 commenced in 1998 and ceased in 2015 (mean 251 deer killed annually; Husheer & Robertson, 2005; Latham et al., 2017). Deer kill rates were initially high (>5 deer per flying hour). Rates declined when sport hunters successfully lobbied for the exclusion of stags from culling, effort halved and was undertaken in the austral winter (June–November vs. September–January pre-2009). From 2016, sport hunting has been the sole means of deer control in Kaweka F.P., due to pressure from hunting organisations and reductions in funding for culling. Further details are given in the Methods section of Supporting Information. All data were collected by employees and contractors of the New Zealand Forest Service (1958–1987) and the Department of Conservation (1987–2018, DOC). Permission to use these data was obtained with DOC contract 5419678. Our study did not require ethical approval.

2.2 | Mountain beech count plots

2.2.1 | Permanent plots

Vegetation monitoring plots have been measured in Kaweka F.P. from 1960 to 2018 (Table 1). In 1960, five permanently marked 404 m^2 plots were established in mountain beech forest in eastern Kaweka F.P. Trees (≥2.54 cm diameter at breast height [DBH], that is measured at 135 cm along stems) were counted in 2.54 cm diameter classes. Mountain beech saplings (<2.54 cm DBH and >30 cm high) were counted in twenty 1.14 m radius subplots. Plots were remeasured in 1965 using the same protocols and again during a 1980–1982 survey. In the 1980–1982 survey, an additional 38 permanently marked 20 m × 20 m plots were established throughout mountain beech forest in Kaweka F.P. These plots were remeasured between November 1998 and February 2001. Tree stems (≥2.5 cm DBH) were identified by species, tagged and their diameters measured. Mountain beech saplings (<2.5 cm DBH and ≥45 cm high) were counted in each plot. The change in definitions of trees and saplings arose because of the switch from imperial to metric measurement systems in New Zealand and was inconsequential for our results (see in Supporting Information for discussion along with further description of measurement protocols).

2.2.2 | Low basal plots located in canopy gaps

In the austral summer of 2005–06, tree basal area was estimated at 189 sites systematically located on a 660 m square grid in Kaweka F.P. mountain beech forest using a prism gauge (Map S3). Thirty of those sites (16%) were classed as low basal area (<44 m^2 ha^{-1}) and deemed to be canopy gaps, where increased sapling density would be expected (Wright et al., 2012). At these low basal sites, mountain beech saplings were counted in 10 m × 10 m plots. Measurements were repeated between November 2012 and January 2013, when 207 randomly selected sites were assessed for low basal area. At the 78 sites with low basal area (37%), plots were remeasured using the same protocols as in the 2005 survey. During 2018, 32 of these 78 low basal area sites were remeasured.

2.3 | Estimation of deer densities

To understand how forest regeneration has varied with deer abundance, we estimated deer densities in Kaweka F.P. Faecal pellet surveys have regularly recorded the number or frequency of occurrence of deer faecal pellet groups within subplots of either 1, 1.14 and 2.2 m radius (Table 1). Deer densities at any given time should then be directly proportional to the observed number of faecal pellets, the number of defecations per deer and the time until pellets decay beyond detection:

$$\text{Pellet counts}\left(\text{groups km}^{-2}\right)=\text{Deer}\left(\text{deer km}^{-2}\right)\times\text{Defecation rate}\left(\text{groups day}^{-1}\ \text{deer}^{-1}\right)\times\text{Decay rate (days)}. \quad (1)$$

As faecal pellet counts were directly observed, and both the rate of defecation and pellet decay could be estimated from known values, we fitted the model described by Equation (1) to estimate deer densities along each line j in each survey year k from 1960 to 2018. We modelled pellet group density from a Gaussian prior distribution with estimated mean μ_{jk} and standard deviation σ, where:

$$\mu_{jk} = deer_k \times defecation_k \times decay_{jk}. \quad (2)$$

Deer densities were sampled from a gamma distribution with shape and rate parameters of 2 and 0.125, respectively (2–45 deer km^{-2}), corresponding with a mean of ≈16 deer km^{-2} (estimated by Husheer & Robertson, 2005). Defecation rates $defecation_k$ were sampled from a Gaussian distribution with a mean set at 30 pellet groups per day per deer for the first three surveys (1960, 1965, 1974) with a standard deviation (SD) of 6. After 1981, the mean for the defecation rate prior increased to 40 to allow for the increasing dominance of sika deer in the landscape (Davidson & Fraser, 1991). Pellet $decay_{jk}$ rate priors also followed a Gaussian distribution with a mean of 3 months and a SD of 1 month until pellet groups decayed beyond a defined condition for the surveys until 1974 and then a mean of 6 months and a SD of 3 months for surveys until 2005 because of changing definitions. Because definitions of pellet validity were even less restrictive from 2005, the prior for the mean time until decay occurred was set at 18 months with a SD of 6 months (details in Supporting Information).

Deer food intake and activity, and therefore defecation rates, as well as pellet decay rates, can vary with seasonal changes in weather. We therefore obtained daily rainfall and temperature data for each sampling line j and included mean daily rainfall r_{jk} in the 6 months prior to pellet counting and mean daily temperature t_{jk} in the 3 months prior to faecal pellet counting in our model. We chose these time periods because they align with mean decay rates and this combination of time periods was the least intercorrelated (Table S1). We then multiplied $defecation_k \times decay_{jk}$ from Equation (1) by a value between 0 and 1 θ_{jk} to scale rates proportionally by r_{jk} and t_{jk}:

$$\text{logit}\left(\theta_{jk}\right) = \beta_1 + \beta_2 \times r_{jk} + \beta_3 \times t_{jk}, \quad (3)$$

where the β's were estimated from a relatively uninformative zero-mean Gaussian distribution with SD of 1 and both r_{jk} and t_{jk} were scaled to a mean of 0 and SD of 1.

The model was fitted with Hamiltonian Monte Carlo sampling, with four Markov chains, a warm-up of 2000 iterations and 4000 iterations using RStan 2.19 (Stan Development Team, 2020). Model convergence was assessed by visually inspecting chain traces and

TABLE 1 Numbers of mountain beech forest plots and faecal pellet monitoring lines measured between 1960 and 2018 in Kaweka F.P.

	1960	1965	1974	1980–1982	1995	1998	1997–2005	2006	2007	2008	2009–2012	2013–2017	2018
Mountain beech forest plots													
Permanent 404 m^2 plots subjectively located	5	5		5									
Permanent 400 m^2 plots randomly located				38			38						
Paired 100 m^2 deer exclosure plots in gaps							40						40
Low basal area 100 m^2 plots								189			207		32
Faecal pellet lines													
Presence on 1.14 m radius	66	66	97	56	22	56							
Counts on 2.2 m and presence on 1.14 m radius							15						
Counts on 1 m radius									50	71	120	60–208	37

Note: Tree diameters of all species were measured, and all saplings were counted in permanent vegetation plots. Mountain beech stems ≥15 cm high were individually tagged in 40 paired exclosure plots. Concurrently, the presence of faecal pellets was recorded in 1.14 m radius plots spaced at 20-m intervals along subjectively (1960–1965) and randomly located lines (1974, 1981, 1995 and 1998). Faecal count plots (2.2 m radius) on lines were remeasured annually between 1997 and 2005 at paired exclosure plots. From 2007, pellet count lines with thirty 1 m radius plots spaced at 5-m intervals were located on a grid in mountain beech forest. From 2013, line locations changed annually (2013 = 208, 2014 = 60, 2015 = 150, 2016 = 60 and 2017 = 150 lines).

with posterior predictive checks. Model effects were inferred by calculating 95% credible intervals. Bayesian R^2 was calculated to summarise model fit.

We tested whether deer densities declined with deer culling by compiling all available data from published and historical records. From 1958 until 1988, government-funded deer culling was undertaken by ground hunters throughout Kaweka F.P. Commercial harvesting using aeroplanes and helicopters to recover deer carcasses began in 1965 and permitted harvesting ceased in 1975. Commercial harvesting and government-funded culling did not occur again until 1998, when aerial culling occurred up until 2015.

2.4 | Exclosure experiment

2.4.1 | Paired 10 m × 10 m plots

Two decades of size-specific mountain beech growth, survival and recruitment data were obtained from 40 paired fenced and unfenced plots (Map S4). Plots were established between November 1997 and March 1999 at 20 subjectively selected mountain beech forest stands where regeneration was expected to occur. Plot pairs were placed within conspicuous canopy gaps large enough to include both plots, and where a 12 m × 12 m, 1.8 m high deer exclusion fence could be constructed around one plot. Established mountain beech seedlings (15–135 cm high) and saplings (≥135 cm high and <3.0 cm DBH) were individually tagged and their heights measured in permanently marked 10 m × 10 m plots. All trees (≥3.0 cm DBH) were tagged and their DBH measured. Plots were remeasured between February and December 2018 using the same protocols. Surviving tagged mountain beech seedlings and saplings were relocated and their heights measured. The heights of all untagged stems ≥15 cm high were also measured to provide data on size-specific recruitment. The heights of a subset of mountain beech trees were measured with a hypsometer (Figure S2). Saplings of all species were counted in each plot, and the presence of all other vascular plant species recorded.

2.4.2 | Demographic analysis of paired plots

Two separate integral projection models (IPMs) were used to calculate mountain beech population rates of change over 20 years for fenced and unfenced plots. Briefly, we constructed separate growth, survival and reproduction matrices using the R package IPMpack (Metcalf et al., 2014) with estimated coefficients from mixed-effects models of size-specific survival, growth and fecundity (described in detail in Supporting Information). Trees were assumed to contribute to the seedling bank in each plot in proportion to their basal area. Growth, survival and fecundity matrices were then integrated into separate matrices for fenced and unfenced plots, and eigen analysis was used to decompose the matrices into a population rate of increase (λ).

As large tree survival can be high for both fenced and unfenced plots, because episodic disturbance events that result in canopy mortality are unlikely over the two-decade time span of our study, we simulated the effect of future gap increase on λ. We used the IPM models to estimate λ along a gradient of large tree survival rates from a rate of survival of 0.2 (simulating canopy gap creation) to 0.95 (where little canopy thinning occurs). In this procedure, large trees were progressively removed from data for each plot. Survival, growth and seedling bank models were then re-estimated for each iteration of large tree survival (n = 100 iterations). Results from each bootstrap iteration were used to construct separate IPM matrices and then estimates of λ along the simulated large tree survival gradient.

3 | RESULTS

3.1 | Mountain beech counts in monitoring plots 1960–2018

Where sika deer are present, sapling and canopy occupancy are lower than would be expected in a forest with unhindered regeneration (Figure 1). A fully occupied mountain beech stand is

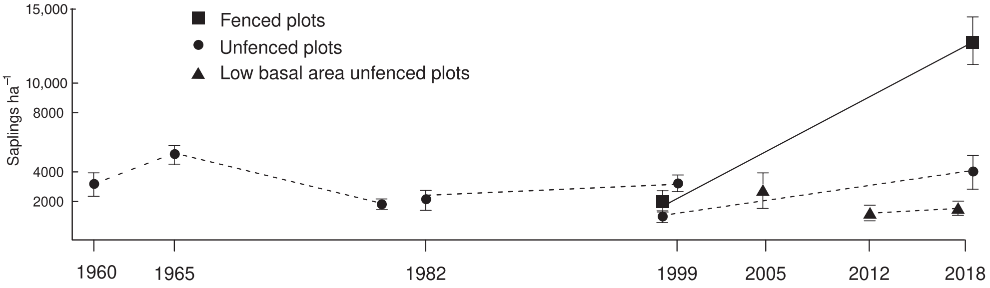

FIGURE 1 Density of mountain beech saplings in Kaweka F.P. Points are means ±95% confidence intervals. The 1960, 1965 and 1980 (n = 5), and the 1998 and 2018 (n = 40) paired plot surveys are remeasurements of the same subjectively located plots. The 1982 and 1999 surveys are remeasurements of 20 m × 20 m plots (n = 38) on randomly selected lines. The 2005 (n = 189) and 2012 (n = 207) surveys are measurements of low basal area 10 m × 10 m plots (<44 $\text{m}^2\,\text{ha}^{-1}$, ▲). Points are linked for fenced (■ ——) and unfenced (●- - -) plots that were remeasured. Saplings were >30 cm high and <2.54 cm DBH in 1960 and 1965 and ≥45 cm high and <2.5 cm DBH in 1980–2018 permanent and low basal plot surveys. For visualisation, only data from saplings ≥45 cm high and <3.0 cm DBH were plotted from paired exclosures.

expected to have basal area of >44 m^2 ha^{-1} (Wardle, 1984), but many Kaweka F.P. stands are below this level. The proportion of plots with low basal area measured using the prism gauge method more than doubled between the 2005 and 2012 surveys (16% vs. 37%, $\tilde{\chi}^2 = 12.9$, $p < 0.001$, Table S2). The increase suggests that canopy gaps are becoming more common with suppressed regeneration. This finding was supported by low mountain beech stem counts. In the 1960 and 1965 surveys, mountain beech counts exceeded 3000 sapling ha^{-1} (plants <2.5 cm DBH). By the 1980s when sika deer had colonised most of Kaweka F.P., densities were under 3000 versus >20,000 ha^{-1} in comparable regions without sika deer (Husheer et al., 2006). Counts remained low up to 2018 (<4000 ha^{-1}), except in fenced plots where they approached 15,000 saplings ha^{-1}.

3.2 | Deer faecal pellet monitoring 1960–2018

Our modelling estimated that deer densities remained between 4 and 40 deer km^{-2} between 1960 and 2018 in Kaweka F.P. (Figure 2; model Bayesian R^2 95% credible interval = 0.49–0.56). Deer densities appeared to decline from >30 deer km^{-2} in the 1960s to <10 deer km^{-2} in 1980 and then returned to >30 deer km^{-2} by 2018 despite unrestricted sport hunting. This pattern is consistent with other New Zealand studies, which have shown similar trends, and have been associated with changes in the intensity of commercial harvesting and government-funded culling (Moloney et al., 2021). Although our model explained much of the variation among lines and surveys in pellet counts, predictions for individual surveys were relatively imprecise. The 5%–95% credible intervals exceeded ±10 deer km^{-2} for most surveys, suggesting that six decades of pellet data collection has not substantially improved upon our prior understanding of deer densities in Kaweka F.P. (Figure S3).

Estimated deer densities relied on variation in pellet defecation, decay and climate and not on pellet counts themselves. The 95% credible interval for the Bayesian R^2 was only 0.087–0.090 in a null model of deer densities that excluded both defecation and decay rates as well as climate variables. Estimated deer densities also appeared unrelated to the trend for increasing occurrence of canopy gaps (Table S2) and changes in sapling density (Figure 1). Finally, deer densities were not related to government-funded culling. The mean correlation between the number of deer culled annually and each iteration across the posterior distribution of model-estimated deer densities was −0.08 (95% credible interval for $r = -0.52$ to 0.31).

3.3 | Paired fenced and unfenced plots 1998–2018

Mountain beech grew 5–10 cm year^{-1} between 1998 and 2018 inside fenced plots through all height classes >15 cm high (Figure S4). Outside fenced plots, seedling and sapling growth rates were lower until 5 m in height (≈5 cm year^{-1}). Once above 5 m in height, trees in fenced and unfenced plots grew at similar rates (Figure S4). Within fenced plots, survival of seedlings from 1998 to 2018 was higher than in unfenced plots (Figure S5). In comparison, where deer were present, the probability of a stem <5 m high surviving over the same period was <0.5 for most sites. Inclusion of a random effects term of site improved fit for height, growth, survival and seedling bank counts, confirming high spatial variability in mountain beech regeneration (Table S3).

The IPM models predicted mountain beech can recover in canopy gaps by doubling in stem density within two decades, due to higher growth and survival of seedlings, but only without sika deer (Figure 3). As disturbance is increased, that is, reduced survival of canopy trees, the probability of regeneration occurring within 20 years declined (Figure 3). Some stands required more than 20 years for stem replacement to occur, even in the absence of deer.

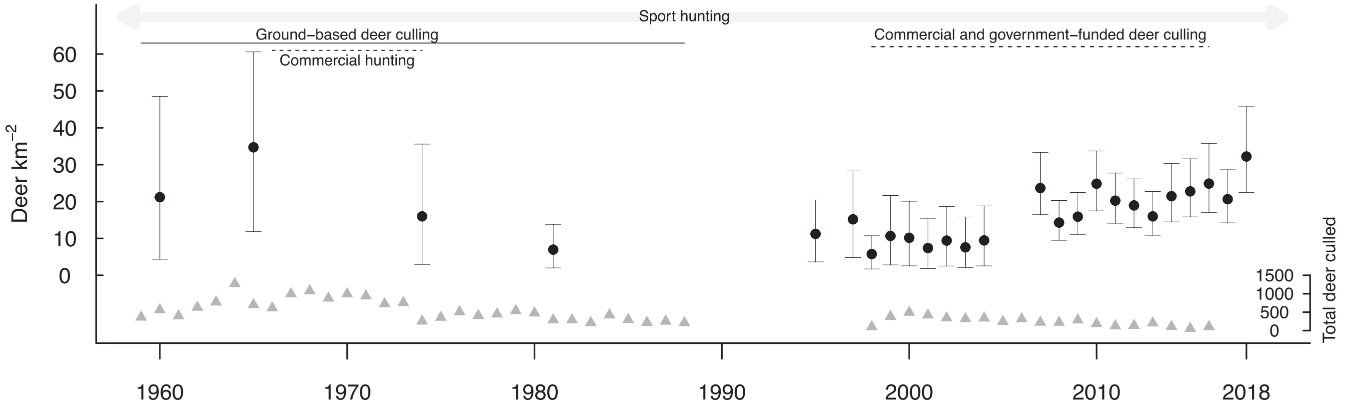

FIGURE 2 Deer density in Kaweka F.P. estimated from faecal pellet survey data (left axis). Data were from 1960 to 1965 in eastern Kaweka F.P., along randomly located lines in 1974, 1981–1982, 1995, 1998–2000, from paired exclosure plot sites in mountain beech forest from 1997 to 2005 and from randomly located lines in mountain beech forest from 2007 to 2018 (Maps S3–S5). Estimated means (●) are presented with 5%–95% Bayesian credible intervals. Total numbers of deer shot each summer season by government-funded cullers are displayed (▲, 58–1271 deer season^{-1}, right axis). All sampling lines were established in areas in Kaweka F.P. where unrestricted sport hunting and government-funded culling occurred. Commercial harvesting using aircraft for recovery began in 1965, but was not permitted from 1975 to 1998. Data on numbers of deer shot by sport hunters and commercial harvesters are unavailable.

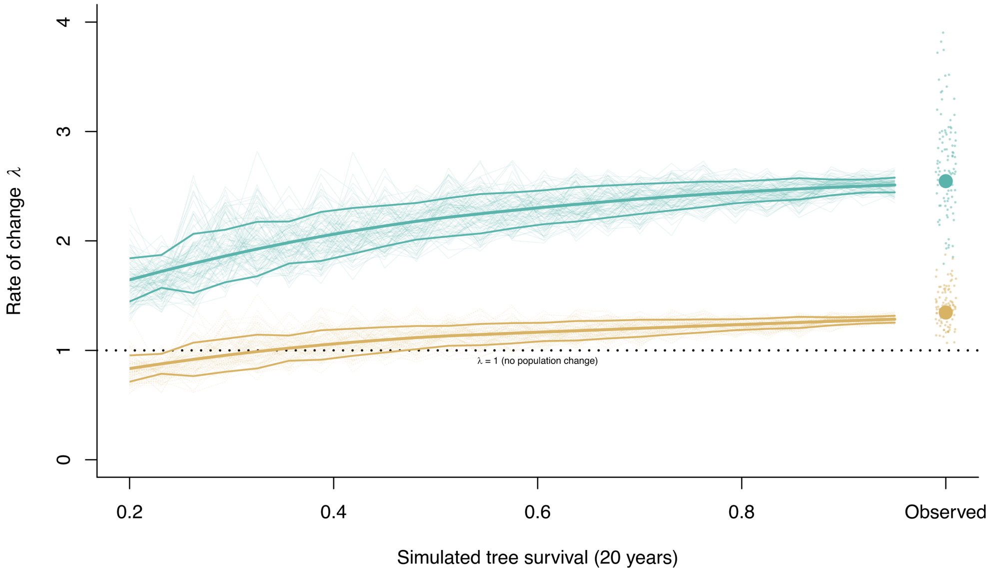

FIGURE 3 Predicted change in mountain beech stem numbers (λ) over 20 years. Predictions were generated from 40 paired fenced (—) and unfenced (—) plots located in canopy gaps in Kaweka F.P. IPM demographic modelling was undertaken on observed data from fenced ● and unfenced ● plots, with points from a bootstrap procedure ($n=100$ iterations, fenced = •, unfenced = •). A randomised simulation procedure ($n=100$ iterations) was used to predict λ following further canopy tree death (survival of large trees from 0.2 to 0.95). Fitted means, standard deviation and results from individual iterations are displayed as thickest, moderately thick and thinnest lines, respectively.

With sika deer browsing and increased large tree mortality, eventual regeneration failure becomes almost inevitable ($\lambda < 1$).

Consistent with the predictions of the IPM, mountain beech sapling counts only increased after 20 years of complete deer exclusion. Fenced plots contained >10,000 saplings ha^{-1}, which was about three times greater than in unfenced plots (Figure 1). Sapling counts of other species present, which were mostly small-leaved shrubs of low palatability, were also higher in fenced plots (paired $t_{19}=3.031$, $p=0.007$; Table S4). Two species avoided by deer (*Coprosma pseudocuneata* and *Phyllocladus alpinus*) had higher counts in unfenced plots. Species preferentially selected by deer were almost absent outside fenced plots as saplings (Table S4). No exotic species were present as saplings at either exclosure plot sites or randomly located plots. Exotic grasses and composite herbs were only present in 11 of 40 exclosure plots. Most of those plots ($n=8$) had basal area <10 m^2 ha^{-1}, suggesting that disturbance was an important factor in exotic species colonisation. Only three plots had more than one exotic species present.

4 | DISCUSSION

4.1 | Sport hunting cannot be relied upon to restore forest regeneration where deer are overabundant

Our study demonstrates that unrestricted sport hunting alongside commercial harvesting and government-funded culling for six decades could not reverse the inhibition of forest regeneration caused by overabundant sika deer across a 594 km^2 landscape. Hunter organisations favour high deer numbers and sport hunter satisfaction. In New Zealand, hunter organisations have successfully opposed the reductions in sika deer populations required for successful forest regeneration (Leathwick & Byrom, 2023), making it difficult to rely on even unrestricted sport hunting as an effective forest management strategy. Following consensus that a deer population's impact on forests needs to be reduced, restrictions on hunting are often relaxed for sika and other deer species (Gerhardt et al., 2013; Kaji et al., 2010; Milner et al., 2006). However, improving access for sport hunters has not substantially reduced deer populations and has provided little evidence of benefit for forest regeneration in New Zealand. North American, European and Australian studies have shown that overabundant deer populations need to be reduced by at least 50% before browsing impacts are noticeably reduced (Holsman, 2000; Mysterud et al., 2016). Where commercial harvesting of red deer has been subsidised or unrestricted in New Zealand, deer populations have been halved, and there have been increases in canopy seedling densities (Tanentzap et al., 2009). To restore forest regeneration, New Zealand forest managers need to increase government culling of sika deer and subsidise commercial harvesting. These methods could also be considered in other countries where sport hunting has not restored tree regeneration (Vercauteren et al., 2011).

4.2 | Deer impacts remain reversible despite hunting not reducing densities to low enough levels to restore regeneration

Our simulation modelling provides new insight into the widespread empirical observation that browsing-induced regeneration failure can be irreversible after population reductions or even the complete removal of deer (George & Bazzaz, 1999; Nuttle et al., 2011). Regeneration in many temperate forests, including New Zealand beech stands, relies on exogenous disturbance from drought, earthquakes and storms to reduce large tree survival and create stand-scale canopy gaps (Veblen et al., 1996; Wright et al., 2012). These canopy gaps facilitate mountain beech seedling and sapling growth by reducing competition for nutrients and light, allowing the recruitment of saplings into tree size classes, eventually refilling gaps in forest canopies (Hurst et al., 2011; Wardle, 1984). In Kaweka F.P., our monitoring plots demonstrate that browsing by introduced sika deer on indigenous mountain beech has disrupted this process by reducing the survival and especially growth of seedlings and saplings. Six decades of commercial harvesting, government-funded culling and unrestricted sport hunting have not reduced deer numbers to low enough levels to reduce browsing on seedlings in canopy gaps and allow forest regeneration. When large tree replacement fails due to browsing, seed production and the long-term seedling bank declines—placing regeneration at further risk. In the case of mountain beech, its seed also persists poorly in soil, has poor dispersal and may be unavailable after canopy collapse (Jane, 1986). Soil compaction from hoof trampling and changes in soil biotic and abiotic properties can further reduce or prevent seed germination (Kardol et al., 2014). Once canopy tree occupancy is reduced, pollination and seed-fall are likely to be reduced (Kelly et al., 2001). Regeneration failure over large areas will also become more likely in Kaweka F.P. with climate change if extreme temperature and windstorm events become more common and increase gap formation (Stott, 2016). Coupled with deer-induced regeneration failure, large tree biomass will inevitably decrease. Fewer large trees will have far-reaching effects on hydrological processes, nutrient cycling, soil ecology and bird communities (Kardol et al., 2014). For example, because most forest carbon is stored in large trees, which are only replaced after decades of successful regeneration, deer will also limit the full potential of forests to combat climate change (Tanentzap & Coomes, 2012) and potentially act as an additive feedback for gap formation.

Using two decades of tree demographic data from Kaweka F.P., we discovered that browse-induced regeneration failure was actually reversible, and we were able to attribute this potential to the presence of large-seeding trees. Following deer exclusion by fencing, we found that increases in mountain beech survival and particularly growth were rapid at most sites, and recruitment of seedlings into tree size classes occurred independent from tree survival rates. Simulation modelling showed that most seeding-sized trees in a stand need to be removed before depletion of seedling banks is sufficient to delay regeneration beyond 20 years. Invasive species were also not advantaged by deer browsing on native species. Nor did the presence of introduced plants alter canopy regeneration (Blossey & Gorchov, 2017 provide contrasting examples). Although unpalatable small-leaved shrubs and larger-leaved palatable plants also increased within fenced plots, they did not prevent mountain beech regeneration and may even have been synergistic or facilitative (Bee et al., 2009). Managers therefore need to focus on conserving and expanding seed sources alongside reducing deer impacts.

4.3 | Faecal pellet surveys unreliable

Monitoring in Kaweka F.P. illustrates that following the fates of individual seedlings and trees is more informative in determining the impacts of deer than attempts at measuring deer abundance. Managers often set, monitor and try to achieve a deer population density or biomass threshold where forest regeneration is expected to occur. For example, thresholds of 115 kg km^{-2} and between 4 and 8 deer km^{-2} have been suggested for northern hemisphere deer populations in temperate forests (DeCalesta & Stout, 1997; Putman et al., 2011; Russell et al., 2017). Such approaches require cost-effective and reliable estimates of deer density, which can then be linked to forest regeneration. Deer faecal pellet surveys are unlikely to provide reliable enough estimates of deer abundance, because they rarely detect differences of <10 deer km^{-2} in populations which are <40 deer km^{-2} (i.e. <25% change, Forsyth et al., 2022). In Kaweka F.P., estimates of deer density from faecal pellet monitoring from 1960 to 2018 are erratic and imprecise. Although formerly reported deer densities and rates of annual harvest are consistent with these estimates (>16 deer km^{-2} and <1000 deer shot year^{-1} in Kaweka F.P. by sport hunters; Husheer & Robertson, 2005), large 5%–95% credible intervals in deer density estimates suggest that few Kaweka F.P. faecal pellet surveys estimated deer populations with precision better than 10 deer km^{-2}, despite accurate model predictions and good estimates of faecal pellet detection, defecation and decay.

An effective monitoring method should be able to detect anticipated changes in what is being measured. Ideally, managers would know deer densities within 1 deer km^{-2}, which our faecal pellet surveys and estimates did not provide. This precision is critical because commercial harvesting, government-funded culling and sport hunting in Kaweka F.P. combined probably removed <2 deer km^{-2} annually (Husheer & Robertson, 2005). If estimating deer density and biomass is essential, a combination of methods may prove more reliable than faecal pellet surveys (see Discussion in Supporting Information). Managers could then set arbitrary thresholds (e.g. <1 deer per helicopter hour and <1 deer per ground-based deer culler night) and monitor the response of tagged seedlings to an index of deer biomass to guide future interventions. Ultimately, browsing impacts are unlikely to be linearly related to deer density (Tanentzap et al., 2012). Deer may need to be eliminated from a forest for decades to restore forest regeneration and, once that is achieved, only a deer population controlled to low density may be compatible with ongoing regeneration (Tanentzap et al., 2009). For these reasons, monitoring vegetation responses may be more informative of ecosystem pressures than monitoring animal densities (Morellet et al., 2007).

5 | CONCLUSIONS

For the past century, regeneration failure and arrested forest succession has been commonly observed in temperate forests following increases in deer populations (Aldous, 1944; Beguin et al., 2016;

Leopold et al., 1947; Walsh, 1892). Hunters oppose reductions in overabundant deer populations, even when deer suppress regeneration, reduce harvests of valuable timber and transmit diseases to humans and livestock (Gill, 1992; Riley et al., 2003; Vaske & Miller, 2019). Conflict can then occur between forest managers who may see even low deer numbers as a liability and sport hunting organisations who desire high deer numbers to improve the success of ageing and increasingly sedentary hunters (Apollonio et al., 2010; Austin et al., 2013; Diefenbach et al., 2021; Lovelock et al., 2022). Managers often rely on indices of deer abundance, which at best only approximate the impacts of deer (Morellet et al., 2007). In the absence of reliable information on deer abundance, managers can present convincing results from seedling, sapling and tree demographic analysis. Effects of deer browsing on forest biomass can take decades to determine without these demographic approaches (Allen et al., 2023). Our study illustrates the value of combining forest demographic modelling with long-term vegetation monitoring to infer deer impacts, in contrast to unreliable indices of deer abundance and ephemeral measures like browsing indices and seedling counts.

Managers of New Zealand forests where sika deer are present need to reduce deer impacts to levels that enable forest regeneration (i.e. $\lambda > 2$ in canopy gaps). Given that the New Zealand flora is also poorly adapted to the impacts of browsing mammals (Lee et al., 2010), deer densities should be lowered as much as technically feasible. Such reductions can be achieved through commercial harvesting and government-funded culling, which have been successful in restoring forest regeneration elsewhere in New Zealand (Leathwick & Byrom, 2023; Tanentzap et al., 2009). If sport hunting continues to be used to control sika deer in Kaweka F.P., ongoing failure of canopy replacement should be expected. We therefore recommend that forest managers employ professionals to cull deer to the lowest levels possible. While such efforts have traditionally been costly, improvements in ground and aerial hunting techniques such as use of thermal imaging tools have doubled the efficiency of intensive culling operations and made them more viable for conservation organisations with limited resources (Cox et al., 2023). Rather than technical feasibility and cost, the primary constraint over reducing deer numbers is social will. The political influence of sport hunters constrains the ability of managers to reduce deer populations and reverse regeneration failure. Intensive culling can also carry social, economic, ethical and ecological costs. For example, these costs can include conflict with sport hunters, reduced recreational activity, wasted food resources and disturbance of nontarget wildlife. Ideally, forest managers would be isolated from these social and economic pressures, but this is often not the political reality. As with most science, objective, evidence-based solutions are only as effective as society's willingness to adopt them.

AUTHOR CONTRIBUTIONS

Sean Husheer contributed to conceptualisation, data collection and analysis, funding acquisition, original draft and review and editing. Andrew Tanentzap contributed to data analysis and review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data can be accessed from the Zenodo Digital Repository https://doi.org/10.5281/zenodo.8411841 (Husheer, 2023).

ORCID

Andrew J. Tanentzap https://orcid.org/0000-0002-2883-1901

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1: Supporting Information.

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