



ARTICLE

Long-term exclusion of invasive ungulates alters tree recruitment and functional traits but not total forest carbon

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Abstract

Forests are major carbon (C) sinks, but their ability to sequester C and thus mitigate climate change, varies with the environment, disturbance regime, and biotic interactions. Herbivory by invasive, nonnative ungulates can have profound ecosystem effects, yet its consequences for forest C stocks remain poorly understood. We determined the impact of invasive ungulates on C pools, both above- and belowground (to 30 cm), and on forest structure and diversity using 26 paired long-term (>20 years) ungulate exclosures and adjacent unfenced control plots located in native temperate rainforests across New Zealand, spanning 36–41° S. Total ecosystem C was similar between ungulate exclosure (299.93 ± 25.94 Mg C ha⁻¹) and unfenced control (324.60 ± 38.39 Mg C ha⁻¹) plots. Most (60%) variation in total ecosystem C was explained by the biomass of the largest tree (mean diameter at breast height [dbh]: 88 cm) within each plot. Ungulate exclusion increased the abundance and diversity of saplings and small trees (dbh ≥ 2.5 , <10 cm) compared with unfenced controls, but these accounted for ~5% of total ecosystem C, demonstrating that a few, large trees dominate the total forest ecosystem C but are unaffected by invasive ungulates at a timescale of 20–50 years. However, changes in understory C pools, species composition, and functional diversity did occur following long-term ungulate exclusion. Our findings suggest that, although the removal of invasive herbivores may not affect total forest C at the decadal scale, major shifts in the diversity and composition of regenerating species will have longer term consequences for ecosystem processes and forest C.

KEYWORDS

biological invasion, carbon cycle, climate change mitigation, exclosure treatment, forest ecosystem processes, functional dispersion, large herbivore effects in forests, long-term permanent plot network, nonnative species' impacts, plant population responses

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INTRODUCTION

Natural forests, or forests comprised predominantly of native tree species with few signs of disturbance from human activities, account for 93% of global forest cover (~30% of the terrestrial biosphere) and can sequester up to 25% of annual anthropogenic greenhouse gas emissions in their vegetative biomass and soils (FAO and UNEP, 2020; IPCC, 2021; Pan et al., 2011). They are among the largest terrestrial carbon (C) sinks but vary widely in diversity, functioning, and structure, making it challenging to understand their ability to sequester C (Waring et al., 2020). Rates of C sequestration vary along gradients of climate and soil fertility (Guo et al., 2019) and this is exacerbated by the growing number of new or expanding disturbances to these systems from pests, pathogens, and invasive nonnative species globally causing widespread forest degradation and fragmentation (Fei et al., 2019; Lovett et al., 2016). Invasive species can have multiple direct and indirect effects on forest ecosystems, but their overall impact on forest C stocks or pools remains poorly understood (Seidl et al., 2018).

Invasive nonnative ungulates, and hyperabundant native ungulates, can exert strong direct and indirect effects on forest structure and ecosystem processes (Tanentzap & Coomes, 2012). Direct effects of browsing by ungulates, such as deer, feral pigs, and goats, include reduction and damage of understory biomass, decreased litter C return, and depletion of seedling regeneration (Ramirez et al., 2018, 2019; Wardle & Peltzer, 2017). Moreover, trampling by feral goats in sloping landscapes and rooting by feral pigs disturb soils and can exacerbate soil erosion (Chynoweth et al., 2013; Cole & Litton, 2014). Deposition of excreta and urine and trampling by larger herbivores, such as deer, can also directly influence local nutrient storage and plant growth (Schmitz & Leroux, 2020). Indirect effects of browsing arise through modifying plant community composition and, consequently, plant functional traits (Mason et al., 2010). An increase in the abundance of unpalatable species, characterized by having relatively low foliar nutrient concentrations and high concentrations of secondary defense compounds (e.g., fiber, lignin, tannins, resins), can occur as a result of browsing (Bardgett & Wardle, 2003; Schmitz et al., 2018). These changes in vegetation composition and function can alter ecosystem processes associated with nutrient cycling, for example through reduced nutrient returns to the soil and altered litter decomposition rates (Felton et al., 2018; Forsyth et al., 2005), and thus exert long-term impacts on forest C storage capacity (Vitousek, 1990). However, empirical evidence for the ecosystem effects of these globally important browsers is often lacking (Leroux et al., 2020; Tanentzap & Coomes, 2012).

The strongest evidence for the effects of ungulates on biogeochemical properties and processes, including C storage, is from experimental ungulate removals (Schmitz & Leroux, 2020). Several long-term (>25 years) ungulate exclusion studies in temperate forests have shown that aboveground C storage in fenced vs. unfenced sites ranged from barely detectable increases to those more than 20 Mg C ha⁻¹ (Tanentzap & Coomes, 2012). This range could reflect differences among enclosure sites in community composition and stand development stage (Mason et al., 2010), other biotic drivers (e.g., seed rain or availability of mycorrhizal fungi for seedling establishment; Wood et al., 2015) or differences in abiotic environmental factors (e.g., moisture and temperature) associated with forest productivity (Mason et al., 2010; Wright et al., 2012).

Effects of ungulates on C stocks should be strongest in forests where they are nonnative and naturally absent (e.g., New Caledonia, Hawai'i, Mauritius, and New Zealand; Weller et al., 2018). Carbon stocks in these forests are often large (Keith et al., 2009) and, if exposed to new disturbances, including novel herbivores, they could experience high losses. Island systems, such as New Zealand, often provide global precedents for long-term, large-scale management of ecosystems to biological invaders (Hulme, 2020; Peltzer et al., 2019; Simberloff, 2019). Because the introduction and establishment of invasive ungulates in New Zealand occurred largely over the last century, the impacts of invasive ungulates on New Zealand forests have been well documented, with ungulates causing local declines in highly palatable forest species in some types of forest shortly after introduction (Mark & Baylis, 1975), as well as ongoing shifts in both forest structure (Coomes, Allen, et al., 2003; Peltzer et al., 2014) and composition (Lusk et al., 2021). However, both ungulate abundance and impacts vary through time (Figure 1) and long-term data are needed to determine their effects on long-lived tree species and forest ecosystem properties, such as C sequestration (Wardle & Peltzer, 2017).

Here, we report C stocks above- and belowground between sites fenced to exclude ungulates for >20 years and adjacent unfenced sites in old-growth native temperate evergreen rainforests that contain plant species ranging in functional traits and palatability to invasive ungulates (Appendix S1: Figure S1). We ask: (Q1) Does the long-term exclusion of ungulates increase total C stocks, above- and belowground? Because ungulates are expected to exert their strongest effects on forest understories (Kuijper et al., 2010), (Q2) does long-term ungulate exclusion increase understory C pools, and to what extent does that increase total C stocks? And (Q3) will regenerating tree communities inside enclosures exhibit higher species and functional diversity that supports ecosystem C storage capacity? Finally, (Q4) do the effects of

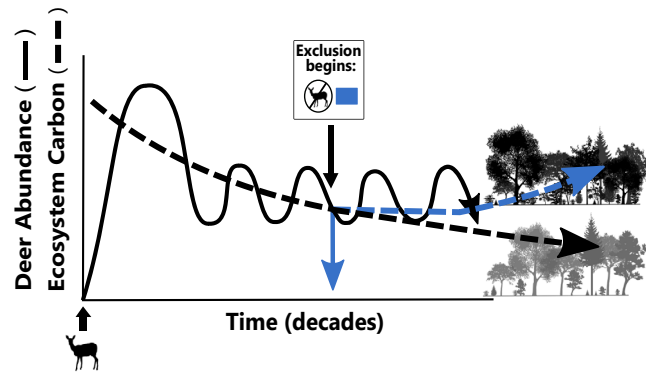


FIGURE 1 Conceptual figure of introduced deer establishment and abundance through time and potential effects on forest ecosystem C stocks. The solid black line represents deer abundance and population development after introduction (Leopold, 1943), with an immediate decrease in deer abundance following exclusion (solid gray line). The dashed line represents changes in ecosystem C stocks, with illustrative divergence in C stock changes under ungulate exclusion (blue dashed line) and ungulate browsing (black dashed line).

ungulate exclusion differ across New Zealand temperate forest sites as a result of forest composition and structure, other biotic factors, or abiotic environmental factors? Resolving these questions provides important insights into whether management interventions aimed at eradicating wild ungulate populations have the potential to increase C sequestration by old-growth temperate forests.

METHODS

Site selection and characteristics

We used an established network of fenced ungulate exclosures largely built by the former New Zealand Forest Service from the 1950s to the 1980s (Wardle et al., 2001). At each exclosure, fences (minimum 1.8 m height) excluded ungulates including European red deer (*Cervus elaphus*), fallow deer (*Dama dama*), sika deer (*Cervus nippon*), feral goats (*Capra hircus*), and feral pigs (*Sus scrofa*). Small-bodied arboreal mammals (rodents and brushtail possum; *Trichosurus vulpecula*) were not excluded. We selected exclosures from the wider plot network that: were located where invasive ungulate populations were established and are still present (Figure 1; Appendix S1: Figure S2); had a fence established and maintained for >20 years at the time of sampling (mean = 27 years); contained $\geq 25\%$ broadleaved evergreen tree species by basal area; and included high C-storing species (see tab. 7, Bellingham et al., 2014). In New Zealand, there are broadly two functionally distinct evergreen rainforest

types: species-poor Nothofagaceae-dominated communities; and species-rich communities of broadleaved evergreen angiosperm and conifer tree species (McGlone et al., 2016). This study focused only on broadleaved evergreen angiosperm-conifer forests because they: (1) cover approximately one-third of the country's remaining mature natural forest (Wiser et al., 2011), (2) contain mixtures of tree species that range widely in their palatability to ungulate herbivores (Bee et al., 2011), and (3) are identified by practitioners (through the New Zealand Department of Conservation's Wild Animal Control for Emissions Management Program; Allen & Carswell, 2008; see also Hackwell & Robinson, 2021) as a conservation priority for forest C management. Overall, forest type and site selection were driven primarily by managers, historically through the establishment of ungulate exclosures to monitor concerns about deer irruptions and damage to forests, and more recently by interest in whether there are C benefits from managing invasive ungulates.

Twenty-six pairs of exclosures, spanning latitudes 36° – 41° S and longitudes 172° – 177° E, met our selection criteria (Appendix S1: Figure S3). Across all sites, the mean annual temperature ranged from 6.4 to 14.7°C , mean annual precipitation ranged from 1189 to 2775 mm, and elevation ranged from 30 to 1200 m above sea level (asl). Unfenced control plots were located approximately 50 m from each exclosure plot, thus in a similar forest type, with a similar landscape position and soil type. Site locations are available online (uploaded here: <https://datastore.landcareresearch.co.nz/dataset/ungulate-removal-and-forest-carbon-stocks>; Richardson et al., 2023) and a detailed description of pair characteristics can be found in the supplement of Kardol et al. (2014). Fieldwork was conducted during the austral summer of 2009–2010.

Aboveground responses

A detailed description of methods used to estimate aboveground forest structure and composition, biomass, and C stocks are provided in Appendix S2: Section S1.1. We quantified forest structure and composition in $20\text{ m} \times 20\text{ m}$ plots (Appendix S2: Figure S1) established inside each exclosure and corresponding unfenced control plot using the methods of Hurst and Allen (2007). Within each exclosure, $20\text{ m} \times 20\text{ m}$ plots were placed at least 0.5 m away from fences to prevent ungulate browsing of plot vegetation through fence gaps, and to minimize disturbance on the sampling plot from fence construction and maintenance. We measured the tree heights (in meters) of all individuals. Aboveground biomass (AGB) for trees ≥ 2.5 cm diameter at breast height

(dbh) along with coarse woody debris (CWD) was estimated following Coomes et al. (2002). Saplings were counted and the biomass for each individual was designated as 100 g (Preece et al., 2015; Richardson et al., 2013). A fixed biomass per sapling was based on a priori knowledge that the contribution of saplings to forest ecosystem C would be relatively small (Holdaway et al., 2017) and data limitations on species-specific allometries for saplings. AGB for all woody vegetation and CWD was converted to C using a conversion factor of 0.50. Leaf litter and fine woody debris (FWD) were collected at 16 sampling points from four subplots, using either 0.1 m² quadrats (for FWD) or 10 cm diameter cores (for leaf litter), and pooled per plot. Oven-dried C values for each component were determined. Aboveground C stock (Mg C ha⁻¹) is the sum of the woody vegetation, CWD, FWD, and leaf litter C pools. Trees ≥ 2.5 cm dbh were classified into three size classes: (1) small trees: dbh ≥ 2.5 cm and < 10 cm, (2) medium trees: dbh ≥ 10 and < 30 cm, and (3) large trees: dbh ≥ 30 cm. We separated our trees into these commonly used size classes (Haywood et al., 2016; Richardson et al., 2009) to partition forest C stock responses to herbivory. Saplings reflect the present browse tier, small- and medium-sized trees tend to represent species cohorts that have recruited over the several decades of ungulate exclusion, and large trees generally reflect those individuals that pre-date ungulate exclusion and are likely to even pre-date ungulate introduction to New Zealand in the 19th century (Kardol et al., 2014).

Diversity for the entire tree community, each of our tree size classes, and saplings was estimated in three ways: (1) plot-level species richness; (2) Shannon diversity (*vegan* package; Oksanen et al., 2019); and (3) functional diversity. Functional diversity was based on trait data covering, the whole plant, stems, leaves, roots, and seeds (Laughlin, 2014; 20 traits in total; see Appendix S1: Table S1). Trait values and sources are available online (uploaded here: <https://datastore.landcareresearch.co.nz/dataset/ungulate-removal-and-forest-carbon-stocks>; Richardson et al., 2023). Any missing trait values for species were treated in one of three ways: (1) replaced using closely related species if no species-specific data were available (four species total), (2) replaced using the mean of all species if the species was identified as “unknown,” or (3) omitted from calculations if species exhibited low percent total basal area ($< 4\%$ for aboveground traits; Pakeman & Quested, 2007) across all sites (Appendix S1: Table S1). We calculated functional diversity (represented by functional dispersion [Fdisp]; Laliberté & Legendre, 2010) using traits with the strongest relationships to ecosystem C storage (see Appendix S2: Section S1.2).

Belowground responses

Root biomass was estimated as 25% standing vegetation (including dead trees) biomass (Holdaway et al., 2017) and was converted to C stocks using the same conversion factor as AGB (0.50). Total soil C represents organic soil and mineral soil down to 30 cm. In total, 16 soil cores for organic soil (10 cm diameter core) and mineral soil (6.5 cm diameter core, 10 cm depth intervals) were collected following the same sampling design for FWD and leaf litter (see Appendix S2: Section S1.1 and Figure S1). Subsamples from each layer were pooled per plot. Organic soil was homogenized, and C was calculated on oven-dried (to a constant mass) sample weights. Mineral soil was sieved to 2 mm to remove rocks and roots, oven dried, and C was determined on the total volume of the ≤ 2 mm fraction. Carbon was measured using a Leco CNS analyzer (Leco Laboratory Equipment Corp., St Joseph, MI, USA). Belowground C stocks (Mg C ha⁻¹) represent the sum of the total root C and total soil C pools.

Data analysis

We used linear mixed-effects models (*lme4* package; Bates et al., 2015) to determine the effect of decadal-scale ungulate exclusion on (Q1) forest C stocks (response variables: total ecosystem, above- and belowground C [all Mg C ha⁻¹]) and (Q2) individual C pools (see Appendix S1: Tables S2 and S3), as well as forest structural attributes (basal area [in square meter per hectare] and tree count [no. trees per hectare]) and (Q3) diversity measures (species richness, Shannon diversity, and functional diversity [Fdisp]). Each model included treatment (exclosure vs. control) as a fixed effect and exclusion pair (26 levels) as a random effect to account for variation between pairs. A null model with the random intercept of the exclusion pair was used to determine whether adding treatment improved model fit (Ellis & Leroux, 2017). All model residuals were visually inspected for normality and homoscedasticity of variance. Where necessary, response variables were log-transformed to satisfy assumptions of normality and achieve homoscedasticity of variance. We report the Akaike information criterion corrected for the small sample size (AIC_c; Burnham & Anderson, 2002) and differences between treatment means ($p < 0.05$) as evidence supporting an effect of ungulate exclusion on ecosystem C stocks and pools, forest structural attributes, and diversity measures. We also report marginal and conditional R^2 (Nakagawa & Schielzeth, 2012) for each model derived using the *piecewiseSEM* R package (Lefcheck, 2016) to illustrate variance explained by the fixed effect and variance explained by the entire model (i.e., both fixed and random effects), respectively.

We identified key environmental factors influencing forest C stock differences across our ungulate exclusion pairs (Q4) using a model selection approach (Rizzuto et al., 2019). We fit general linear models with the proportional difference or effect of ungulate exclusion on total ecosystem C, aboveground C, or belowground C stocks as the response variable and a suite of environmental factors as explanatory variables selected using a priori knowledge (see Appendix S1: Table S4). The exclusion effect on ecosystem C stocks was quantified as $([\text{exclusion C stock} - \text{control C stock}]/[\text{exclusion C stock}])$ following Wardle et al. (2001), where negative values indicate that a C stock is higher outside of the enclosure. We included ungulate and possum abundance (Bellingham et al., 2020), representing common biotic interactions within these forests and key known environmental factors affecting productivity including mean annual temperature, water deficit, basal area, functional diversity, and soil fertility (Coomes et al., 2005; Holdaway et al., 2017; Mason et al., 2010; Richardson et al., 2004; Whitehead et al., 2001). Data were derived from either fecal pellet counts (see Appendix S2: Section S1.3), interpolated climate layers (NZE_{EnvDS}; McCarthy et al., 2021b), or plot-level observations (from enclosure sites following Mason et al. (2010)) and are available online (uploaded here: <https://datastore.landcareresearch.co.nz/dataset/ungulate-removal-and-forest-carbon-stocks>; Richardson et al., 2023). To reduce the number of parameters in our general linear models while maintaining as much variability in our explanatory variables as possible, we created a soil fertility variable using principal components analysis (PCA; Barnes et al., 2017). Observed soil pH, C:N ratio, and available phosphorus (Bray II method; Bray & Kurtz, 1945) from the mineral soil (to 30 cm depth) were ordinated and scores from the first

principal component (PC1; accounting for 77% of total variation) were used to represent soil fertility in our models. We plotted scores from PC1 against each observed soil fertility variable to ascertain trends within the component (Appendix S1: Figure S4), illustrating that our sites with negative PC1 scores have more acidic soils, with lower available soil phosphorus and higher C:N ratios. None of our explanatory variables exhibited multicollinearity ($VIF < 4$; tested using *vif()*; *car* package; Fox & Weisberg, 2019), and all explanatory variables were standardized. Models were fit either as intercept-only models (i.e., null model), with each of our explanatory variables alone, or with additive combinations of our explanatory variables. Our full model set included 119 competing models. We selected the most parsimonious model based on the AIC_c (Burnham & Anderson, 2002) using $AIC_c()$ from the *AIC_cmodavg* R package (Mazerolle, 2020). We identified key environmental factors that influence differences in ecosystem C stocks under ungulate exclusion using ΔAIC_c , selecting top-ranked models that were within two AIC_c from the most parsimonious model, as well as removing models with uninformative parameters from the model set of each response variable following Leroux (2019).

All data analyses were completed using R v. 4.0.2 (R Core Team, 2020).

RESULTS

Forest C stocks

Total ecosystem C stocks did not differ significantly between enclosure and unfenced control plots ($p > 0.1$;

TABLE 1 Results from linear mixed-effects models to determine the effect of ungulate exclusion ($n = 26$) on total ecosystem, aboveground, and belowground C stocks (Mg C ha^{-1}).

Response	Treatment means \pm SE		Top-ranked models	<i>k</i>	<i>LL</i>	ΔAIC_c	ωAIC_c	R^2	
	Exclosure	Control						Marginal	Conditional
Total ecosystem C	299.93 \pm 25.94 ^a	324.60 \pm 38.39 ^a	Null	3	16.28	0.00	0.98	NA	0.74
			Treatment	4	13.72	7.46	0.02	<0.001	0.73
Aboveground C	167.55 \pm 17.98 ^a	187.51 \pm 28.48 ^a	Null	3	5.85	0.00	0.97	NA	0.67
			Treatment	4	3.55	6.94	0.03	<0.001	0.66
Belowground C	132.38 \pm 9.47 ^a	137.08 \pm 11.63 ^a	Treatment	4	-265.01	0.00	0.88	0.002	0.71
			Null	3	-268.19	4.00	0.12	NA	0.71

Note: Total ecosystem C is the sum of above- and belowground C stocks. Aboveground C represents the sum of C pools for all trees, litter, fine woody debris, and coarse woody debris. Belowground C is the sum of the total soil C pool (to 30 cm depth) and the total root C pool. Means (\pm SE) for each treatment (i.e., exclosure vs. control) followed by different lowercase letters indicate significant differences between treatments ($p < 0.05$). Models were fit as either null (response ~ 1) or Treatment (response ~ Exclosure/Control) with exclusion pair as the random variable. For each model, we present: *k*, no. parameters; *LL*, log-likelihood; ΔAIC_c , difference in the Akaike information criterion from most parsimonious model; ωAIC_c , weight of models, *Marginal* R^2 , variance explained by fixed effects; *Conditional* R^2 , variance explained by entire model (i.e., both fixed and random effects). NA indicates absence of fixed effect in null model.

Table 1). The exclusion pair explained most of the variation in the total ecosystem (marginal $R^2 < 0.001$; conditional $R^2 = 0.74$), aboveground (marginal $R^2 < 0.001$; conditional $R^2 = 0.67$) and belowground (marginal $R^2 = 0.002$; conditional $R^2 = 0.71$) C stocks. Some component C pools (saplings and their roots, small-sized trees and their roots, and CWD) differed significantly ($p < 0.05$) between exclusion and control plots (Figure 2; Appendix S1: Table S2 and Figure S5). Ungulate exclusion had an overall positive effect on sapling (0.46 ± 0.07) and small-sized tree C pools (0.20 ± 0.17) and a negative effect on the CWD C pool (-1.07 ± 0.34 ; Appendix S1: Figure S5). However, the sum of these five C pools across both exclusion and control plots ($n = 52$) represented only 6% of the total ecosystem C stock (Figure 2). In comparison, the largest tree size class (dbh ≥ 30 cm) and their roots contributed 44% of total ecosystem C across both the exclusion and control plots (Figure 2; Appendix S1: Table S2). All other above- and belowground C pools measured (Appendix S1: Table S3) did not differ between treatments, with the most variation in these C pools explained by exclusion pair (see marginal and conditional R^2 ; Appendix S1: Tables S2 and S3). Exclusion and unfenced control plots did not differ in total ecosystem biomass or biomass of the largest tree per plot

($p > 0.4$; Appendix S1: Table S5). Total ecosystem biomass at a plot level and biomass of the largest tree per plot (see Appendix S2: Section S1.4) had a significant relationship, with the largest tree accounting for 0.03%–3.4% of total ecosystem biomass, and 60% of the variance in total ecosystem biomass (Figure 3; $R^2 = 0.62$; $p < 0.001$).

Factors influencing ecosystem C stocks

Differences in the total ecosystem and aboveground C stocks (see Appendix S1: Figure S5) between paired exclusion and control sites were influenced by climate, forest structure, diversity, and animal abundance. Water deficit and basal area were identified as key environmental factors and appeared in all top-ranked models explaining differences in the total ecosystem and aboveground C stocks under ungulate exclusion (Table 2). Together, these two environmental factors accounted for 35% and 37% of the variation in ungulate effects on total ecosystem C and aboveground C, respectively (see R^2 in Table 2), and negatively influenced differences in these two C stocks. Alongside water deficit and basal area, mean annual temperature (MAT) and functional

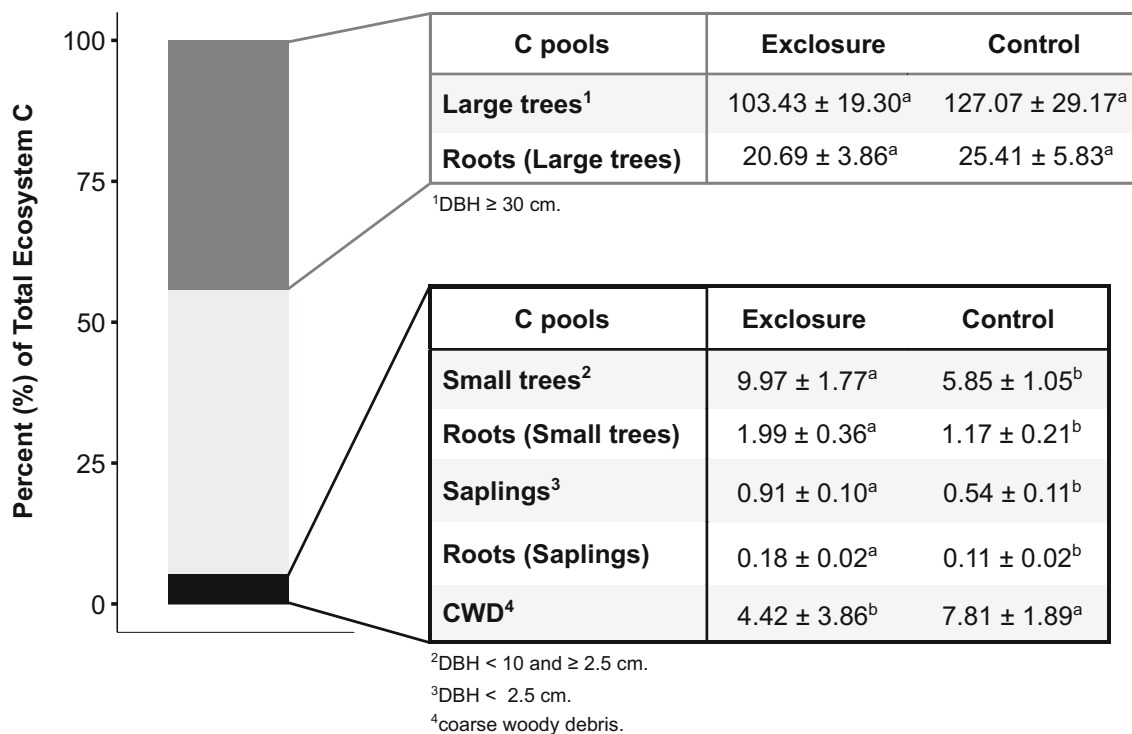


FIGURE 2 Percent of total ecosystem C ($n = 52$) comprised of C pools for large trees and their roots (dark gray portion of stacked bar), small trees and their roots, saplings and their roots, and coarse woody debris (CWD; black portion of stacked bar). Light gray portion of stacked bar represents all other above- and belowground C pools measured (see Appendix S1: Table S3). Inset tables contain means (\pm SE) between plots in which ungulates were excluded or not (control) for large tree C pools (top) and the smaller C pools (bottom). Different lowercase letters indicate significant differences between treatments ($p < 0.05$; for model results see Appendix S1: Table S2).

diversity also contributed to variation in ungulate effects on total ecosystem C (Appendix S1: Table S6), with functional diversity negatively influencing and MAT positively influencing differences in the total ecosystem C stocks under ungulate exclusion (Table 2). Top-ranked models for differences in aboveground C also included MAT (alongside water deficit and basal area), as well as possum abundance (Appendix S1: Table S7), with MAT positively influencing and possum abundance negatively influencing ungulate

effects on aboveground C (Table 2). The top-ranked model explaining ungulate effects on belowground C stocks was the intercept-only model (Table 2). Indicating that none of the environmental factors accounted for variation in belowground C between paired exclusion and control sites (Appendix S1: Table S8).

Forest structure and diversity

Although a large proportion of the variation in forest structural and diversity attributes was explained by exclusion pair (see marginal and conditional R^2 ; Appendix S1: Tables S10 and S11), we found that differences in forest structure and diversity between paired exclusion and control sites were consistently greater for understory and regenerating tree size classes, relative to larger tree communities (Figure 4). For example, the basal area of the smallest tree size class was 70% greater in exclusions (marginal $R^2 = 0.06$; $\Delta AIC_c = 0.00$; $p > 0.01$; Appendix S1: Table S9). Exclusures averaged 1800 more small-sized trees per hectare (marginal $R^2 = 0.07$; $\Delta AIC_c = 0.00$; $p > 0.01$) and 7400 more saplings per hectare relative to control plots (marginal $R^2 = 0.12$; $\Delta AIC_c = 0.00$; $p > 0.01$), with a significantly higher tree density for the entire tree community under ungulate exclusion (marginal $R^2 = 0.08$; $\Delta AIC_c = 0.00$; $p < 0.001$; Appendix S1: Table S11).

Tree and sapling species richness was 44% higher for small-sized trees (marginal $R^2 = 0.12$; $\Delta AIC_c = 0.00$; $p < 0.02$) and 68% higher for saplings (marginal $R^2 = 0.27$;

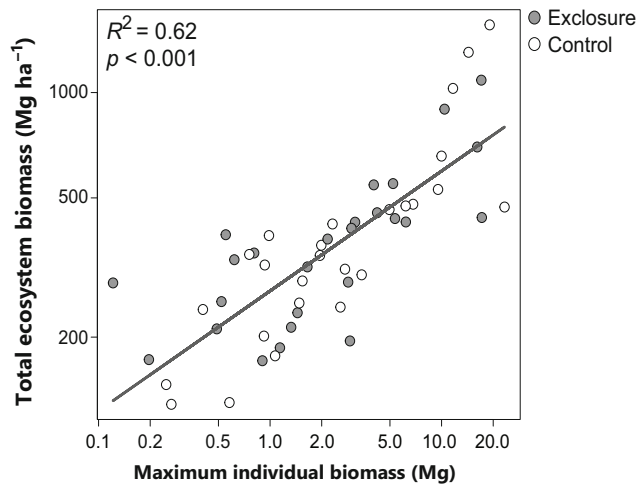


FIGURE 3 Relationship between total ecosystem biomass ($Mg\ ha^{-1}$) and the biomass (Mg) of the largest individual trees observed in each ungulate exclusion (gray) and unfenced control (white) plot ($n = 52$). Note the log scale on both axes.

TABLE 2 Top ranking linear models (with $\Delta AIC_c < 2$) exhibiting the most informative explanatory variables (Leroux, 2019) associated with ungulate exclusion effects on ecosystem C stocks.

Top-ranked models (coefficients \pm SE)	<i>k</i>	LL	ΔAIC_c	R^2
Δ Total ecosystem C				
Intercept (-0.03 ± 0.06) + Water deficit (-0.21 ± 0.07) + Basal area (-0.19 ± 0.07)	4	-4.37	0.00	0.35
Intercept (-0.03 ± 0.06) + MAT (0.14 ± 0.08) + Water deficit (-0.32 ± 0.09) + Basal area (-0.22 ± 0.07)	5	-2.86	0.08	0.42
Intercept (-0.03 ± 0.06) + MAT (0.17 ± 0.09) + Water deficit (-0.37 ± 0.10) + Basal area (-0.19 ± 0.07) + Functional diversity (-0.09 ± 0.08)	6	-1.96	1.71	0.46
Δ Aboveground C				
Intercept (-0.07 ± 0.08) + MAT (0.24 ± 0.08) + Water deficit (-0.50 ± 0.13) + Basal area (-0.37 ± 0.10)	5	-12.63	0.00	0.47
Intercept (-0.07 ± 0.08) + MAT (0.26 ± 0.12) + Water deficit (-0.48 ± 0.13) + Basal area (-0.29 ± 0.11) + Possum abundance (-0.14 ± 0.10)	6	-11.46	1.07	0.51
Intercept (-0.07 ± 0.08) + Water deficit (-0.31 ± 0.10) + Basal area (-0.32 ± 0.10)	4	-14.78	1.19	0.37
Δ Belowground C				
Intercept (-0.02 ± 0.04)	2	2.40	0.00	0.00

Note: The proportional difference or effect of ungulate exclusion on each C stock (i.e., Δ Total ecosystem, Δ Aboveground, and Δ Belowground) was calculated as $([\text{exclusion C stock} - \text{control C stock}]/[\text{exclusion C stock}])$ following Wardle et al. (2001). For each model, we present: coefficients for each explanatory variable \pm SE in parentheses, *k*, no. parameters; LL, log-likelihood; ΔAIC_c , difference in the Akaike information criterion from most parsimonious model; R^2 , variance explained by fixed effects; MAT, mean annual temperature.

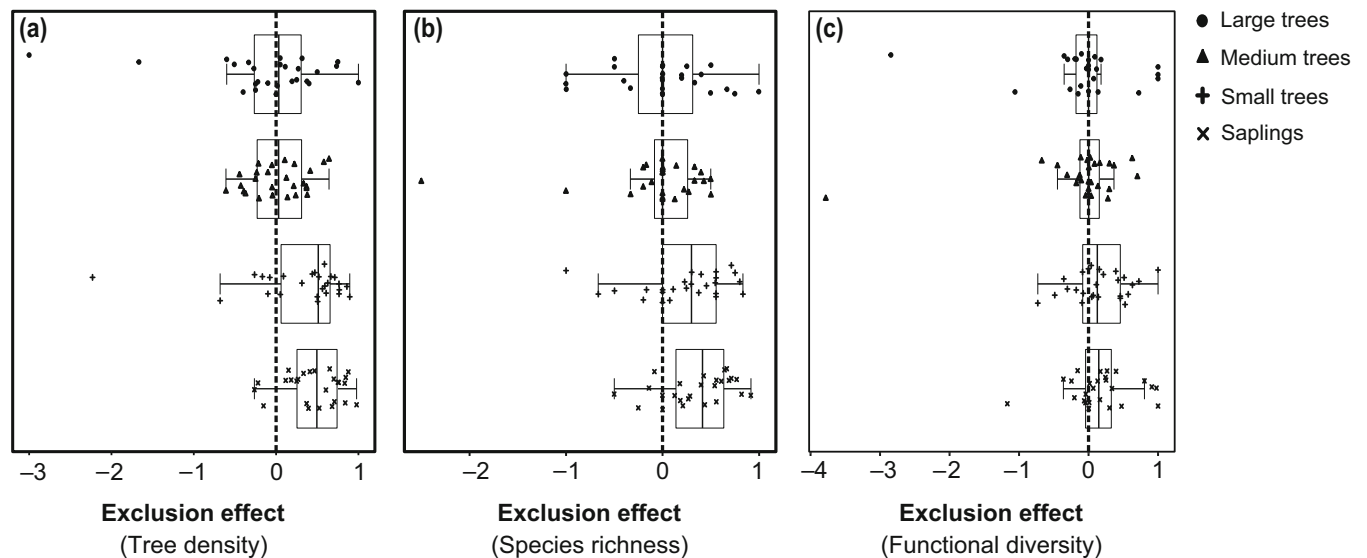


FIGURE 4 Effect of exclusion on (a) tree density, (b) species richness, and (c) functional diversity between paired ungulate enclosure and corresponding unfenced control plots ($n = 26$; except for large trees $n = 24$) among tree and sapling communities. The proportional difference or effect of exclusion on each variable is expressed as $([\text{variable inside enclosure} - \text{variable outside enclosure}] / [\text{variable inside enclosure}])$, where negative values indicate a variable is greater outside enclosure (Wardle et al., 2001). The vertical dashed line represents intercept at zero. Individual values for each pair are represented by different shapes. Large trees are ≥ 30 cm diameter breast height (dbh). Medium trees are < 30 and ≥ 10 cm dbh, and small trees are < 10 cm and ≥ 2.5 cm.

$\Delta\text{AIC}_c = 0.00$; $p < 0.02$) in enclosures (Appendix S1: Table S10), with significantly higher species richness across the entire tree community (marginal $R^2 = 0.09$; $\Delta\text{AIC}_c = 0.00$; $p < 0.001$; Appendix S1: Table S11). Shannon diversity in the enclosure plots was 23% and 37% higher for small-sized trees (marginal $R^2 = 0.06$; $\Delta\text{AIC}_c = 0.00$; $p < 0.02$) and sapling (marginal $R^2 = 0.17$; $\Delta\text{AIC}_c = 0.00$; $p < 0.02$) communities, respectively. Functional diversity (here represented by Fdisp) of the medium- and large-sized tree communities was similar (Appendix S1: Table S10) while functional diversity of the small-sized tree (marginal $R^2 = 0.12$; $\Delta\text{AIC}_c = 0.00$; $p < 0.02$) and sapling ($R^2 = 0.27$; $\Delta\text{AIC}_c = 0.00$; $p < 0.02$) communities was lower in control plots, relative to enclosures (Figure 4c).

For the entire tree community, there was a positive, significant relationship between Fdisp and both the log of aboveground C stocks (enclosure: $R^2 = 0.42$; $p < 0.05$; control: $R^2 = 0.23$; $p < 0.01$) and belowground C stocks (enclosure: $R^2 = 0.38$; $p < 0.01$; control: $R^2 = 0.19$; $p < 0.05$) across both treatments (Figure 5). However, the strength of these relationships diminished with decreasing tree size class (relationship between Fdisp and the log of aboveground C stocks: small-tree $R^2 = 0.0006$, $p > 0.05$; sapling $R^2 = 0.02$; $p > 0.05$; the relationship between Fdisp and belowground C stocks: small-tree $R^2 = 0.0006$, $p > 0.05$; sapling $R^2 = 0.07$, $p > 0.05$).

DISCUSSION

Long-term ungulate exclusion did not alter total ecosystem C but increased the abundance and diversity of browse-level vegetation. Most (60%) variation in total ecosystem C is explained by the biomass of a few large trees that were unaffected by ungulate exclusion. Browse-level vegetation responded to the exclusion by increasing understory C pools, forming communities with higher tree density and species richness, and shifting functional diversity toward traits related to ecosystem C storage. Thus, while there may be no significant short-term increases in C storage in response to ungulate exclusion, in the longer term altered forest dynamics may achieve this management goal.

Changes in C sequestration rates following herbivore control suggest that effect sizes are small, variable in direction, and likely to involve complex indirect mechanisms (Holdaway et al., 2012; Schmitz & Leroux, 2020). For example, we observed no differences in soil C pools or litter, but nearly two-fold more deadwood (CWD) in control plots compared with > 20 years of ungulate exclusion (Appendix S1: Table S4). However, it is unresolved whether these differences in CWD result from greater inputs (e.g., canopy decay, tree mortality), slower decay rates (e.g., related to microclimate, lower soil moisture, or lower decomposers), shifts in tissue density and chemistry (Rooney & Waller, 2003), or how these responses

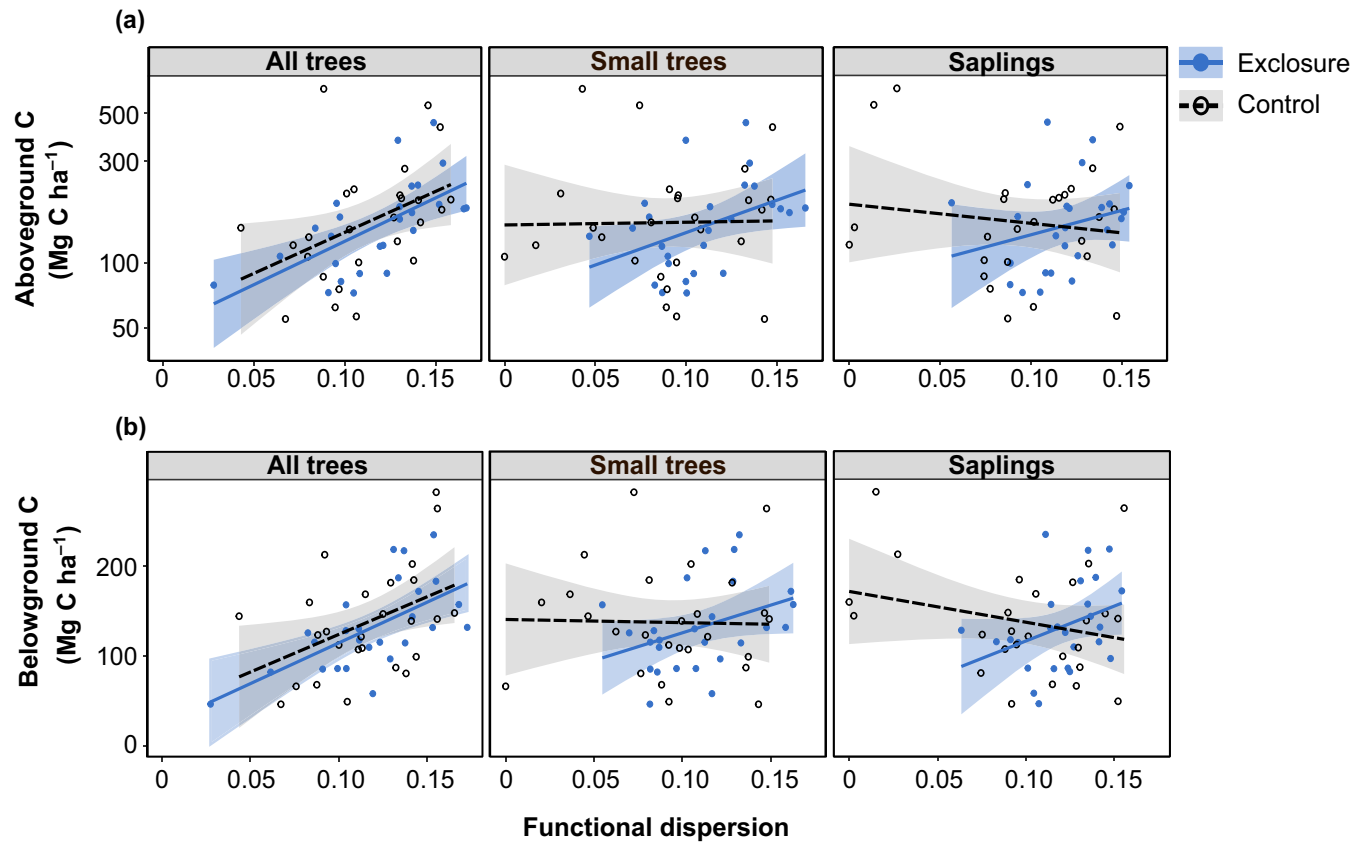


FIGURE 5 Summary of relationships between (a) the log of aboveground C stocks (Mg C ha^{-1}) or (b) belowground C stocks (Mg C ha^{-1}) and functional dispersion of woody vegetation observed in plots from which ungulates were excluded (blue closed points and solid line; $n = 26$) and unfenced controls (black open points and dashed line; $n = 26$) for the entire tree community (All trees), small-tree community (Small trees: $\text{dbh} < 10$ and ≥ 2.5 cm) and saplings (Saplings: $\text{dbh} < 2.5$ cm). Error bands correspond to treatment and represent 95% confidence intervals.

vary in both magnitude and direction among forest types (e.g., Litton et al., 2018; Schmitz & Leroux, 2020). Quantifying important mechanistic information (e.g., soil CO_2 emissions; see O’Bryan et al., 2021) on how invasive species impact C fluxes needs to be integrated with ecosystem C stock data to fully understand when or where benefits of ungulate control occur (Forbes et al., 2019).

Structural responses

Large trees formed almost half (44%) of the total ecosystem biomass and were relatively unresponsive to ungulate exclusion whereas, small trees and saplings responded strongly to exclusion but contributed only 7% to total aboveground live biomass in exclosures and 3.8% in control plots. Large trees are significant drivers of total forest ecosystem C stocks: Lutz et al. (2018) determined that the largest 1% of trees contained 50% of total aboveground live biomass across 48 forest plots globally. Similarly, in an unbiased sample across New Zealand’s forests, trees ≥ 60 cm dbh comprised just 0.77% of stems but contained

41% of total aboveground live biomass (Holdaway et al., 2017). Collectively these findings suggest that forest C stocks may be maintained despite browsing pressure, provided a few individuals can reach the canopy and achieve large diameters. The cumulative processes that lead to the growth and survival of large trees are complex (Cannon et al., 2022; Lindenmayer & Laurance, 2017) and in New Zealand forests, with many long-lived tree species and slow diameter growth rates ($1\text{--}2 \text{ mm year}^{-1}$; Russo et al., 2010), these are manifest over many decades to centuries, spanning a range of environmental conditions. As such, additional effort to increase our understanding of how browsing and other short- and long-term drivers modulate processes generating large trees in the future is warranted (Akashi & Nakashizuka, 1999; Cannon et al., 2022; Coomes, Duncan, et al., 2003).

Diversity and functional trait responses

Ungulate exclusion increased plant species richness and diversity of understory and regenerating tree species, along

with tree density and functional diversity (Figure 4), suggesting that ungulates reduced the diversity and function of species in the browse tier (Mason et al., 2010). These results emphasize that excluding ungulates can generate distinct understory communities at timescales of 20–50 years. Given the predictable shifts in diversity and functional traits related to palatability present in our understory that include regenerating tree species (e.g., increased foliar fiber content and lower foliar nutrient concentrations outside exclosures; Appendix S1: Figure S6), these changes should affect ecological processes over the longer term such as litter quality, nutrient cycling, and functional capacity for sequestering C (Leroux et al., 2020; Peltzer et al., 2010; Ramirez et al., 2021). Moreover, we expect that these processes should differ predictably among different forest types (Wardle et al., 2001) and a promising approach for predicting long-term changes in forest C sequestration could be to link plant functional traits and palatability to invasive herbivores, with the effects of those traits on ecosystem processes and tree demographics.

Dynamics, lags, and longer term implications of ungulates

The largest effects of exclosures on C stocks were observed in stands with a low basal area, consistent with previous findings that ungulate exclusion can exert its strongest effects in early successional stands (Mason et al., 2010). Plant species in these stands often have high leaf nitrogen concentrations, low fiber content, and lower leaf mass per unit area, a trait syndrome often reflecting high palatability to ungulates (Felton et al., 2018; Forsyth et al., 2005). Abundant ungulates can also retard succession (Richardson et al., 2014) and exert long-term effects on forest composition (Côté et al., 2004; Royo & Carson, 2022). Therefore, a caveat for our overall finding—a lack of an effect of excluding ungulates on ecosystem C stocks—is that the exclosures available for this study did not include early successional forests and stands affected by major disturbances, such as wind throw, volcanic activity, or landslides after heavy rainfall and earthquakes (Wyse et al., 2018), where larger effects of ungulate exclusion might occur. Thus, the maintenance of current exclosure experiments, as well as establishing new exclosures across successional gradients are necessary to evaluate the long-term effects of ungulates (Wardle & Bardgett, 2004).

Most long-term studies of the effects of abundant deer derive from ecosystems where plants and ungulates have coevolved (Côté et al., 2004), or deciduous temperate forests (Ramirez, 2021) that differ in seasonal light availability and plant growth rates from broadleaved evergreen forests (Bee et al., 2007). Thus, there is a particular

need for continuing, multidecadal evaluation of ungulates in forests on islands such as New Zealand, where the flora is naïve to ungulate herbivory and across different types of forests. The shifts in understory diversity and tree density in plots browsed by ungulates have parallels in other exclosure studies on islands (Anujan et al., 2022; Chollet et al., 2021), and the shift in the understory and regenerating species diversity caused by ungulate browsing may translate to a future shift in canopy structure and composition (e.g., Reed et al., 2022; Rogers et al., 2008). In New Zealand, there is evidence of widespread low levels of recruitment of understory trees, which has been attributed to ungulate browsing (Coomes, Allen, et al., 2003) but because most native tree species are slow-growing and long-lived (Kelly & Sullivan, 2010; Russo et al., 2010), we could expect that any shift in canopy composition will occur slowly.

Management implications

Managing forests for C sequestration is a widely viewed mechanism for mitigating the effects of climate change (e.g., Griscom et al., 2017). Despite ongoing interest in the state and change of C in existing forests globally, there are few options for manipulating these systems at large scales aside from the management of biological invasions (Seidl et al., 2018; Wardle & Peltzer, 2017). Our findings suggest that the management of invasive ungulates may not increase net total C within the timescales being considered by both managers or governments to meet international obligations for reducing or offsetting emissions (He Pou a Rangi - Climate Change Commission, 2021). This contrasts with claims that managing invasive herbivores could benefit forest C sequestration in the short term (e.g., Hackwell & Robinson, 2021). Our results and many previous studies suggest that management of invasive herbivores in forest ecosystems promotes understory plant diversity and a wider range of functional traits at the decadal time scale, but the longer term (>50 years) effects on C sequestration require further investigation (Ramirez et al., 2018; Russell et al., 2017). Taken together, these findings emphasize that the original focus of invasive ungulate management for biodiversity, is more strongly supported by current evidence than is the more recent goal of managing for C per se.

Our results also suggest that the combined management of invasive ungulates and other invasive herbivores should have greater impacts in less diverse early successional forest stands in warmer, wetter regions (Table 2). This is consistent with previous work emphasizing that the effects of ungulate management vary predictably along environmental gradients and, in the first instance,

should focus on highly productive regenerating forests rather than old-growth forests (Mason et al., 2010; Ramirez et al., 2018). Furthermore, interactions among forest productivity, herbivory, and disturbance are likely to generate a greater range of potential impacts of management with future climate change (Seidl et al., 2018). For example, in the future, New Zealand's dry forests will get drier, its wet forests will get wetter, and more intense storms and cyclones are likely (IPCC, 2021), thus potentially amplifying differences among sites in the impacts of invasive ungulates on forest C pools. The invasive browsing ungulates present across our sites share similar diet patterns (based on foliar fiber and nutrient contents; Forsyth et al., 2002); however, it is still unresolved how interactions between invasive ungulates, arboreal browsers (i.e., brushtail possums that feed on native tree species, fruits, invertebrates, and birds; Nugent et al., 2001), and feral pigs (i.e., their rooting can damage seedlings and modify soils; Parkes et al., 2015), all present across our sites to varying degrees, could be impacting forest ecosystem dynamics. Thus, fully understanding the consequences of climate change and biological invasions requires long-term data collected at scales that capture ecosystem-level processes (Kuijper et al., 2010). Taken together, our results and previous studies strongly emphasize that an increased understanding of when and where management is likely to have benefits for C, diversity, or other goals in forest ecosystems is crucial (Spake et al., 2020). Such an approach provides fundamental information needed to improve policy and management of forest ecosystems for C, diversity, and other objectives.

AUTHOR CONTRIBUTIONS

Fiona E. Carswell, Robert B. Allen, Duane A. Peltzer, Mark G. St. John and Peter J. Bellingham conceived and designed the study; Sean W. Husheer, Duane A. Peltzer, Mark G. St. John, Larry E. Burrows, Peter J. Bellingham and Sarah J. Richardson collected and/or contributed data; Mark G. St. John, Kara Allen and Sarah J. Richardson conducted data analysis; Kara Allen, Duane A. Peltzer, Peter J. Bellingham, and Sarah J. Richardson drafted the first version of the manuscript; all other authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT


The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All vegetation survey data are archived in the National Vegetation Science databank, which can be accessed online at: <https://nvs.landcareresearch.co.nz/>. Site names and locations (see "Plot-level names and locations"), including the "NVS_name" for retrieving site-specific vegetation data from the National Vegetation Science databank, along with litter and soil C data (see "Plot-level data on litter and soil C stocks"), plant traits data (see "Species-level mean trait values"), and environmental factors data (see "Plot-level environmental factors") can be accessed online at: <https://datastore.landcareresearch.co.nz/dataset/ungulate-removal-and-forest-carbon-stocks> (Richardson et al., 2023). The interpolated climate layers provided in the online dataset were obtained from the publicly available New Zealand Environmental Data Stack (<https://datastore.landcareresearch.co.nz/dataset/nzenvds>) published in McCarthy et al. (2021a). The index of ungulate and possum abundance was created using Biodiversity Monitoring and Reporting System data, which includes information licensed by the New Zealand Department of Conservation for re-use under a Creative Commons Attribution 4.0 International License and can be requested from <https://www.doc.govt.nz/our-work/monitoring-reporting/request-monitoring-data/>. To retrieve nationwide fecal pellet count data, on the online form, in the "Date-time" box enter "2011–2015", in the "Site(s) or areas of interest box" enter "national" and select "National Level Monitoring—Mammals" specifying "ungulates" and "possums" in the "Other" box provided.

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SUPPORTING INFORMATION

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

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