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Landcare Research

Review of the likely magnitude and manageability of deer impacts on carbon stores in indigenous forests

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Contents

Summary

Project and client

The New Zealand Game Animal Council (GAC) sought advice from Manaaki Whenua – Landcare Research on the evidence that game animals, particularly deer, have large effects on indigenous forest (native forest) forest carbon (C). Recent statements in the press and central government that reducing the numbers of deer and other introduced herbivores could be a cost-effective way of increasing forest C sequestration prompted the GAC to seek this advice.

Objectives

We aimed to provide:

An assessment of the probable short-, medium-, and long-term impacts of deer on native forest carbon stores at three broad levels of deer abundance (low, medium, and high).

A comparison of the likely nature of possum effects on carbon stores relative to the effects of deer.

A brief assessment of the reversibility and manageability of deer effects on carbon storage and emissions, focussed mainly on tall forest types.

Methods

We reviewed the published academic and grey literature for insights into the impacts of introduced ungulates on native forest vegetation dynamics and ecosystem carbon, primarily for common deer species (red deer – *Cervus elaphus*; fallow deer – Dama dama; sika deer – *Cervus nippon*; white-tailed deer – *Odocoileus virginianus*) along with feral domestic goats (*Capra aegagrus hircus*), Himalayan tahr (*Hemitragus jemlahicus*), chamois (*Rupicapra rupicapra*), and brushtail possums (*Trichosurus vulpecula).*

We then provide general concepts and frameworks for understanding the role of animals in the carbon cycle along with key points and recommendations.

Synthesis and discussion

The major points from our synthesis are listed below.

Game animals can have negative, neutral or positive effects on forest carbon (C) pools depending on animal population density, forest type and disturbance history. The effects of animals on forest dynamics and diversity also varies greatly with animal density and forest-types or sites.

A series of research projects called Wild Animal Control for Emissions Management (WACEM) completed over 2008–2015 provided a major synthesis of when and where wild animals could influence ecosystem C. The WACEM studies concluded that the greatest potential of C gains from animal management are in successional environments; this includes c. 1.5 million ha of naturally regenerating woody vegetation, and some recently disturbed sites within native forest. In contrast, few gains in C were considered likely from animal management in intact (i.e. undisturbed) indigenous forests.

The plot-based quantitative assessment used for national carbon estimates (i.e. the Land Use and Carbon Analysis System, or LUCAS) provides a robust source of information, primarily on public land, for changes in ecosystem C across all forest types. Analysis of the first remeasurement of this plot network shows declines in total C in some forest types (e.g. kamahi–podocarp forests), increases in other forest types, but no net increase or decrease in total C pools nationally. Some of the C declines in forests containing kāmahi (*Weinmannia racemosa*) may be attributable to ungulates in some locations, but other drivers are likely: these include differences in the measurement of deadwood pools between plot measurements, major disturbances in some regions, and increased tree mortality from other herbivores such as possums. However, no analyses of the effects of these different drivers on forest C has yet been completed.

Analyses of long-term ungulate exclosures (i.e. deer-fenced plots) that essentially reduce ungulate abundance to zero, revealed no overall changes in forest C in the absence of ungulates over several decades; this is because most C is in larger trees (>30 cm diameter at breast height) which are largely unaffected by ungulates on a decadal timescale. Similarly, other large C pools in deadwood and soils show small or undetectable responses to ungulate exclusion. In contrast, understorey plant diversity and the abundance of highly palatable plant species is usually higher where ungulates are excluded.

Attributing declines in forest C directly to wild animals is fraught because the evidence base and supporting data are seldom collected. Similarly, threshold and density effects between animal abundance and their impacts on C are largely unknown.

Variations in forest productivity and potential C sequestration occur among sites and forest types, making broad generalisations about the effectiveness of wild animal management for C gains overly simplistic. Site- or forest-specific information is required, and should be used to better understand where animal management will increase forest C through increased regeneration and replacement, or decreased mortality, of canopy tree species.

The strongest responses to changes in the abundance of ungulate browsers are in the composition, survival and growth of palatable plant species in the understorey, which comprises only a small percentage (<5%) of total ecosystem carbon. Species and functional diversity increases in the understorey with ungulate exclusion.

Conclusions and recommendations

Available evidence strongly supports a view that wild animal management benefits some species (and not others) depending on the mix of animal species present and the intensity of animal control, resulting in changes in forest composition that vary widely among forest-types and locations.

In some forests, deer can reduce C associated with palatable tree species. However, losses from palatable species can be replaced by unpalatable species, and these include many of the largest and longest-lived canopy species (which could potentially result in increased C over the longer term).

The evidence for changes in C for intact forests caused by deer or resulting from their management is poor. However, the available data suggest small to trivial responses at the decadal timescale (based on both the relatively small size of C pools affected, and the sampling effort used to detect C changes over time).

Overall, better evidence on when and where to control wild animals for C sequestration is needed. Potential C gains from such control are small and highly variable whereas biodiversity gains for highly palatable plant species in the browse tier are well supported; but both responses occur over decades. Management for C is better targeted in successional environments or post-disturbance sites, which are known to provide far greater opportunities for potential C sequestration.

We therefore recommend the GAC undertake these actions.

Seek assessment of the trends in forest C based on the most recent remeasurement period of the LUCAS plots.

Support additional interrogation of the LUCAS data so as to better understand where positive or negative changes in forest C can be attributed.

Support the maintenance and remeasurement of ungulate exclosures (and permanent plots) across different forest-types so they continue to provide strong long-term data for understanding the potential effects of reducing ungulate populations on both biodiversity and C.

Support the development of predictive forest canopy succession models capable of comparing the nature, magnitude and timescales for the unmanaged impacts of deer, possums, and of possums and deer combined.

Insist DOC, the Ministry for Primary Industries, and the Ministry for the Environment (the 'natural resources cluster') collect and maintain information on the distribution and trends in abundance of mammal species.

Seek clarification from DOC (or the natural resources sector including MPI and MfE) on how mammal management is being prioritised for both biodiversity goals and carbon sequestration.

Seek full C accounting of management activities and responses from DOC.

Increase training and expertise in animal ecology and management to fill some capacity gaps in New Zealand.

Develop a clear position for GAC on the maintenance of biodiversity and ecological integrity.

Undertake more strategic, long-term planning for management of game animals for C, biodiversity or other goals.

Introduction

Background

Interest in managing forests for carbon sequestration has accelerated over the past decade, driven generally by the global desire to mitigate climate change, and specifically to meet New Zealand's international commitments such as those made under the Kyoto Protocol and Paris Agreements, and the United Nations Framework Convention on Climate Change. The current state and potential changes in carbon (C) stored in New Zealand's extensive publicly owned indigenous forests (i.e., forest lands dominated by native tree species; summarised in Section 2) are currently of broad interest for maintaining terrestrial C sinks and potentially for offsetting emissions at a national scale. New Zealand's native forests are also occupied by non-native herbivores, most notably several species of deer and possums (King & Forsyth 2021). Deer (and deer-like ruminants such as goats, chamois and thar) are valued as game animals by some New Zealanders, an interest that is represented by the New Zealand Game Animal Council (GAC). Recent increases of deer abundance across regions have also raised interest in and awareness of the wild animals and their management (Moloney et al. 2021). However, browsing by deer and possums alters the composition of native forest, so others perceive these species as conservation pests. That view of deer is also held by some within New Zealand's government (Department of Conservation 2001). There is also concern that the changes in forest composition caused by non-native browsers could have negative effects on C sequestration and storage within native forests. This has prompted a number of investigations into this possibility, most notably the Wild Animal Control for Emissions Management (WACEM) programme instigated by the Department of Conservation (DOC). That programme is largely summarised in Carswell, Holdaway et al. 2015), which concluded that it would be extremely difficult to identify and quantify C sequestration in existing forests that could be attributed to wild animal control. Despite that, a recent report (Hackwell & Robinson 2021) produced for a conservation interest group (Forest & Bird) concludes that control of mammalian herbivores is one of the most significant and cost-effective options for protecting and enhancing forest C stores.

Given these contradictory conclusions, the GAC commissioned this assessment of the nature, magnitude, and manageability of deer impacts on carbon stores in New Zealand's indigenous forests, with a primary focus on deer. For convenience, the term 'deer' hereafter includes deer-like ruminant browsers such as chamois, goats, and thar (but not pigs). We distinguished between the likely effects from ungulates and possums on forest C because their impacts in forests and their management are different.

Objectives

We provided:

An assessment of the likely short-, medium-, and long-term impacts of deer on native forest carbon stores at three broad levels of deer abundance (low, medium, and high).

A comparison of the likely nature of possum effects on carbon stores relative to the effects of deer.

A brief assessment of the reversibility and manageability of deer effects on carbon storage and emissions, focussed mainly on tall forest types.

Report structure

We review the published and unpublished scientific literature related to these objectives to summarise the current state of knowledge about these issues. We then generate key points and recommendations for understanding where and when deer control could potentially have beneficial effects on increasing forest C stocks.

In Section 2, we briefly describe indigenous forest C stocks. This includes an assessment of the robustness of the assumptions implicit in linking deer control to increased forest C sequestration.

In Section 3 we then provide a general background or framework for understanding herbivore impacts in general on forest C, and present some examples of the effects and effectiveness of wild animal management both generally in relation to conservation outcomes, and more specifically in relation to forest C. This includes a summary of the main mechanisms by which deer (and possums) potentially affect forest C.

Section 4 provides a brief summary of the large number of investigations and reviews of the impacts of introduced browsers on plant species composition in indigenous forest systems. This is not an exhaustive synthesis or review and does not review or evaluate the details of C calculations, economics, or policy. Rather, we assess the underpinning scientific knowledge into the probable effects of non-native browsers on indigenous forest C. It includes some assessment of the likely differences in potential effects of deer and possums, and, more broadly, the nature and likely importance (relative to deer and possum impact) of other major drivers of forest ecosystem dynamics that also affect forest C sequestration rates.

The focus of Section 5 is on whether reducing the abundance (locally or nationwide) of non-native browsers (primarily considering deer) might result in short- or longer-term changes in C sequestration. This includes an assessment of the likely reversibility of current and historical effects under three broad classes of deer management (no control, some control, or complete or near-complete elimination).

In Section 6, we provide a summary of the main findings derived from this and previous reviews, suggest where the greatest potential for C gains through deer control may lie, and hypothesise about what level of deer control would be required to achieve those gains.

Finally, in Section 7, we make recommendations for applying this evidence to ongoing debate and decisions surrounding the management of deer and other browsers for C sequestration purposes in indigenous forests.

Appendix B provides a glossary of common names and binomials for species.

Indigenous forest carbon stocks

Background

Forests are major carbon (C) sinks, but their ability to sequester C and help mitigate climate change varies with environment, disturbance regime, and biotic interactions. Indigenous forests in New Zealand are nationally important for climate regulation and C sequestration, occur on about 30% of our land area, contain major habitats and biodiversity values, and provide numerous other services not detailed here (see Wardle 1984; Allen et al. 2013; Wyse et al. 2018).

National assessments of forest carbon

The national system for measuring and monitoring changes in indigenous forest C stocks is the Land Use and Carbon Analysis System (LUCAS). LUCAS is a national network of permanent forest plots that uses standard methods developed under the National Vegetation Survey (NVS) to measure C in vegetation, litter, deadwood and soil pools (Allen 1993; Coomes et al. 2002). A network of 1,195 plots on a randomly placed 8 × 8 km grid (Figure 1) provide robust and representative estimators of biomass and carbon on 7.74 million ha of lands mapped as pre-1990 forest (Ministry for the Environment 2020). Most plots were established over 2002–2007, but about 18% were previously established for other purposes.

Although subject to the caveats[1] listed below, the two quantitative national estimates of forest C pools both suggest there have been no major changes (i.e. net increases or losses of total C) over the past two decades for indigenous forests.

Holdaway et al. (2017) analysed C stock changes from 874 plots. They estimated an average increase of 0.67 tC $ha^{-1} yr^{-1}$ for forest biomass including live above- and below ground plant biomass, litter, and deadwood (C is about 50% of biomass); this

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[1] Caveats

- There are many decisions, assumptions and estimates involved in determining C pools and their change through time that are not covered here (details in Coomes et al. 2002; Holdaway et al. 2014, 2017; Paul et al 2021). Briefly, the largest sources of error associated with calculating the C budgets include measure error (e.g., mismeasurement of trees or coarse woody debris), and model uncertainty is considered to be <1% of C stocks, suggesting that that national-scale plot-based estimates of C stocks and change are robust to measurement error and model uncertainty.
- Although deadwood comprises about a quarter of C in forests, its measurement is highly variable, and decay values for deadwood are only available for relatively few species and sites. These problems can lead to underestimating stocks and changes of C in deadwood pools. Instead of relying on field data, modelled estimates of deadwood C are sometimes used (Richardson et al. 2009; Kimberley 2019).
- None of the analyses include estimates of soil carbon. However, this is likely to be a major and persistent pool of C, and much slower to respond to management interventions than live biomass pools. Soil carbon estimates of up to 268 tC ha^{-1} have been reported in the top 1 m of soil in New Zealand forests (Tate et al. 1995), indicating that this pool can be of similar magnitude to that for forest plant biomass.
- No litter measurements (dead leaves, twigs) were made in the 2009–2014 measurement period.

was not statistically different from zero. Most (84%) of these plots were in old growth forests (i.e., mature, relatively tall forest) which increased in total C by 0.28 tC ha^{-1} yr^{-1} whereas secondary forests (i.e., successional forests regenerating post-disturbance increased by 2.78 tC ha^{-1} yr^{-1}.

Similarly, Paul et al. (2021) analysed data from the national grid of LUCAS plots. They compared first and second measurements conducted in the 2002–2007 and 2009–2014 periods respectively, with an average of 7.7 years between measurements, and showed:

no overall change in total C stocks (227.0 ± 14.4 tC ha^{-1} vs 227.2 ± 14.5 tC ha^{-1} for the first and second measurements, respectively

most (73%) C was in live plant biomass and the remainder in deadwood and litter. The total carbon stock estimates for tall forests of 252 tC ha^{-1} were similar for both measurements, and more than four times higher than the estimates of 53.6 and 58.1 tC ha^{-1} in regenerating forest for the two periods.

For most individual forest types (or forest vegetation alliances that are quantitatively defined, for example by Wiser et al. 2011), C stock changes between the two measurement periods did not differ statistically from zero , i.e. there were no detectable gains or losses of C (see Appendix A). The two exceptions to this were: (i) a decline in kāmahi-podocarp forest (-8.0 ± 6.1 tC ha^{-1}, n = 86 plots; see Appendix A); (ii) an increase in C for kānuka shrublands (+8.3 ± 5.6 tC ha^{-1}, n = 24 plots).

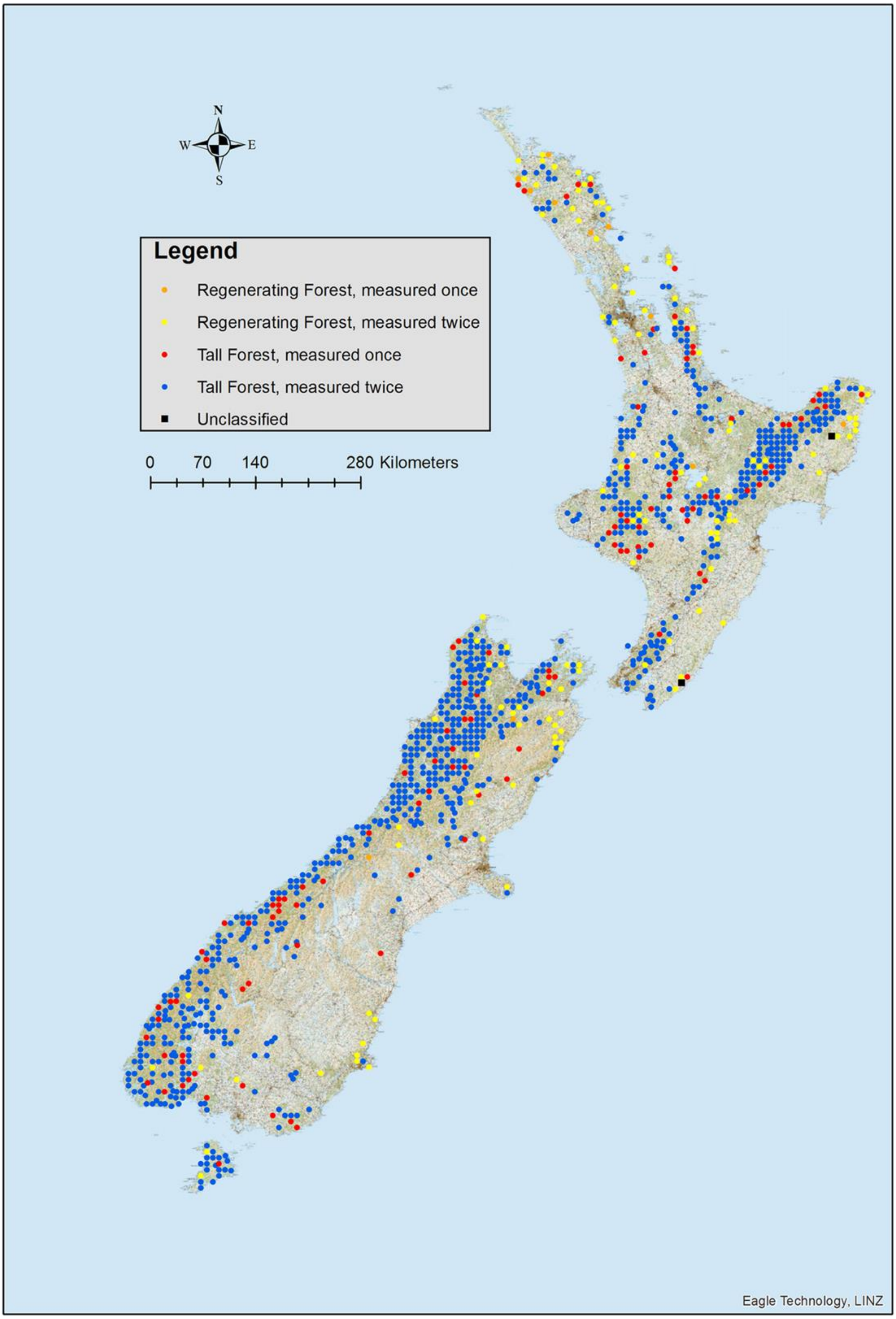


Figure 1. Distribution of indigenous forest plots in NZ used to generate national estimates of carbon (Source: reproduced from Paul et al. 2021 under Creative Commons CC BY license).

Each of the estimates above suggested no major increases or decreases in indigenous forest C nationally, but used slightly different datasets or numbers of plots to generate these estimates. This also reflects declines over time in data collection efforts that reduces the robustness of quality of the underlying information on forest C (Allen et al. 2023).

Assumptions linking animal management to forest C storage

Ongoing biodiversity concerns over the state and condition of our indigenous forests are well documented. Most recently, interest in the possibility that management interventions could increase the ability of indigenous forests to sequester (store) C has been driven by both major landscape-scale conservation efforts (e.g. Predator Free NZ 2050) and interest in whether such activities could protect or increase C stocks and be claimed for climate mitigation (e.g. Carswell, Holdaway et al. 2015; Hackwell et al. 2021). The specific focus of this report is on the question originally raised by DOC (WACEM) and, more recently, by Hackwell and Robinson (2021), of whether management (i.e. control) of non-native mammals generally, and browsing herbivores in particular, could increase C sequestration in indigenous forests.

The question of whether herbivores are currently driving declines of indigenous forest C stocks (also referred to just as 'C') nationally, and whether herbivore control or management could stop these declines or even increase forest C has been asked many times (e.g. Coomes et al. 2003; Holdaway et al. 2012; Carswell, Holdaway et al 2015; Hackwell & Robinson 2021). It involves several assumptions.

Firstly, any call for broad-scale national control of mammalian herbivores requires (as justification) evidence that *C is declining overall in indigenous forests.* However, as noted in the previous section, the available empirical estimates indicate there are no net gains or losses at the national scale for overall C stocks contained in indigenous forest biomass over the period 2002–2014. Pre-2002 changes in forest C are not available nationally, so historical trends and responses to initial mammal introduction on C are not quantified.

Alternatively, any call for more locally targeted control of mammalian herbivores requires that *declines are occurring in at least some specific forest types or locations.* Nationally, some forest types containing kāmahi had lower estimates of C stock in 2009–2014 compared with 2002–2007, with the largest change reported for kāmahi-podocarp forest (316.4 tC ha^{-1} vs 301.7 tC ha^{-1}) (Paul et al. 2021; see summary tables 5 and 6 from their publication in Appendix A). The change is small relative to the large statistical uncertainty around these estimates (95% confidence limits are >40 tC ha^{-1}). However, we note that if net forest C nationally is not changing (i.e. detectably different from zero), then declines in kāmahi forests must be offset by increases in other forest types that comprise >80% of indigenous forest, most of which contain both deer and possums. Findings from WACEM also suggested that the greatest potential gains in forest C will be from post-disturbance successional forests, and these regenerating forests are most likely to respond to wild animal management.

Secondly, it assumes *the observed C declines are being driven solely or largely by introduced mammals***.** However, the global scientific literature indicates that browsing by herbivores can result in either increases or decreases in forest C depending on site, forest type, species density and other major drivers of forest dynamics such as disturbance (e.g. fire, windstorms, earthquakes, vulcanism; Wells et al. 2001; Wyse et al. 2018). The changes caused by these other major drivers of forest ecosystem change can be several orders of magnitude greater than the effect of herbivores (Tanentzap & Coomes 2012). A subsidiary assumption relevant for this report is that *deer (rather than possums, rats, or pigs) are the major causes of declines in forest C declines.*

Thirdly, if deer (and/or possums) do cause declines in forest C, it is assumed that *control (i.e. culling or reduction in populations) of mammalian herbivores will cost-effectively increase forest C.* However, the few studies to date that have directly addressed this issue, show huge variability in the effects of herbivores on forest C. As a consequence, herbivore control rarely shows any detectable increases in total C in the short term (i.e. <20 years), and these effects are often hard to disentangle from other forest dynamics (e.g. succession, disturbance) (Tanentzap & Coomes 2012). A key aspect of this assumption is that benefits will outweigh the costs (in present value terms) even though the benefits may take decades or centuries to accrue. We are not aware of any study that has quantified the C costs of herbivore control against the purported C benefits.

A final implied or explicit assumption is that *sequestering C through deer and possum control would also contribute to achievement of conservation goals such as maintaining biodiversity***.** At its simplest, this assumes that freeing native forests from mammalian herbivores (i.e. achieving maximum protection of biodiversity) will result in increased C stores and biodiversity. This assumption has not yet been tested, but previous analyses suggest that diversity or compositional changes from herbivory may not be strongly linked to long-term forest productivity or C stocks (Coomes et al. 2005; Forysth et al. 2015). Although beyond the scope of this report, greater consideration of where and when managing for C, biodiversity, or other objectives is required over the longer term to meet, for example, aspirations of Te Mana o te Taiao (2021) or international commitments to protect and restore biodiversity (e.g. Convention on Biological Diversity).

These assumptions collectively underpin any calculations of the potential C benefits of reducing introduced herbivores numbers**.** Given the documented high variability and uncertainties of introduced herbivore density and their actual and potential effects on forest C among sites, future management decisions based on these assumptions will need to consider:

variability among sites, in order to prioritise and target management efforts among locations

how to deal with and acknowledge the high-level uncertainty arising from the complex and dynamic natures of the systems being managed.

The major unresolved question addressed by this report is: When and where do deer (and other herbivores) have effects on indigenous forest C that could be reversed cost-effectively and sustainably through the elimination or control of these species?

Framework for understanding animal impacts on forest carbon

Animal populations have both direct and indirect impacts on the ecosystems they inhabit. Direct impacts through consumption (i.e. herbivory, which for deer in forest ecosystems is largely by browsing of foliage) are well studied and are largely predictable from knowledge of the animal species and vegetation properties (e.g. palatability, browse resistance, and browse tolerance of plant species). In contrast, indirect effects of animals on ecological and ecosystem processes such as nutrient cycling are more complex but are major drivers of ecosystem properties including primary productivity and carbon balance.

A common approach to link direct and indirect effects is through trophic interactions and considering how functional traits related to herbivory (e.g. plant foliar nutrient contents) are also linked to ecosystem processes like decomposition and nutrient cycling (Bardgett & Wardle 2003; Peltzer et al. 2010) (Figure 2). Key international studies emphasise (i) that the lack of understanding of animal impacts on the carbon cycle is a global issue; (ii) that remote sensing and modelling do not capture important animal impacts on landscape carbon; (iii) that both positive and negative changes in C can occur depending on interactions among species and ecosystems (Tanentzap & Coomes 2012; Schmitz et al. 2018) (Figure 3).

A major global review (sparked by work from New Zealand) by Tanentzap and Coomes (2012) examined whether complete exclusion of large herbivores >10kg had changed terrestrial C stocks in 108 studies spanning 52 vegetation types. Their overall conclusion was that herbivore exclusion could increase terrestrial above- and below-ground carbon stocks across vegetation types but that the changes in C are small relative to stock size and require sufficient periods of time for systems to respond to herbivory (i.e. many decades). Additional points from their review that suggest small and highly variable responses to herbivore exclusion included:.

Reductions in above-ground C stocks are small in forests.

C stocks increase in many circumstances because of the influences of herbivores on litter decomposition and nitrogen mineralisation.

Below-ground responses are difficult to predict because they vary with the characteristics of both the vegetation and herbivores, and with different abiotic factors. However, there may be little overall effect on soil carbon cycling (Pastor et al. 1993).

Other ecological processes usually covary with the effects of herbivores on C stocks, and so herbivore removal/reduction might not lead to predicted or expected increases in carbon stocks.

Overall, removing (usually excluding) herbivores from the vegetation types covered in the by Tanentzap and Coomes (2012) review estimated changes in above-round C stocks ranging from increases of 1.96 tC ha^{-1} yr^{-1} to declines of 0.19 tC ha^{-1} yr^{-1}, and changes in soils ranging from increases of 3.81 tC ha^{-1} yr^{-1} to declines of 1.46 tC ha^{-1} yr^{-1}, depending on vegetation type. These changes were usually relatively small compared to the annual productivity of the various vegetation types.

Another (non-deer) example undermining the assumption that removing introduced mammals should usually increase C-stocks is provided by the eradication of rats on a number of New Zealand islands; rat control increased burrowing seabird abundance but decreased ecosystem C stocks because burrowing seabirds caused C losses through greater soil and plant disturbance (Wardle et al. 2007) (Figure 4).

In summary, animals create feedbacks with the environment, particularly through effects on nutrient cycling (biogeochemistry), that in turn regulate ecosystem productivity and carbon. The vast literature on this topic shows that the effects of animals vary among sites through feedback loops with vegetation – and that their effects on site fertility and vegetation can either increase or decrease ecosystem C (Figure 2). Although these feedbacks are well known internationally (e.g. Bardgett & Wardle 2003; Schmitz et al. 2018; Schmitz & Leroux 2020), they have seldom been considered in New Zealand. However, this information is essential for understanding how the effects of animals on ecosystem processes including C sequestration vary among sites; it requires data on animal abundance, soils and vegetation. Table 1 provides an overall framework for understanding the main mechanisms by which deer (and possums) affect the C balance in New Zealand forests.

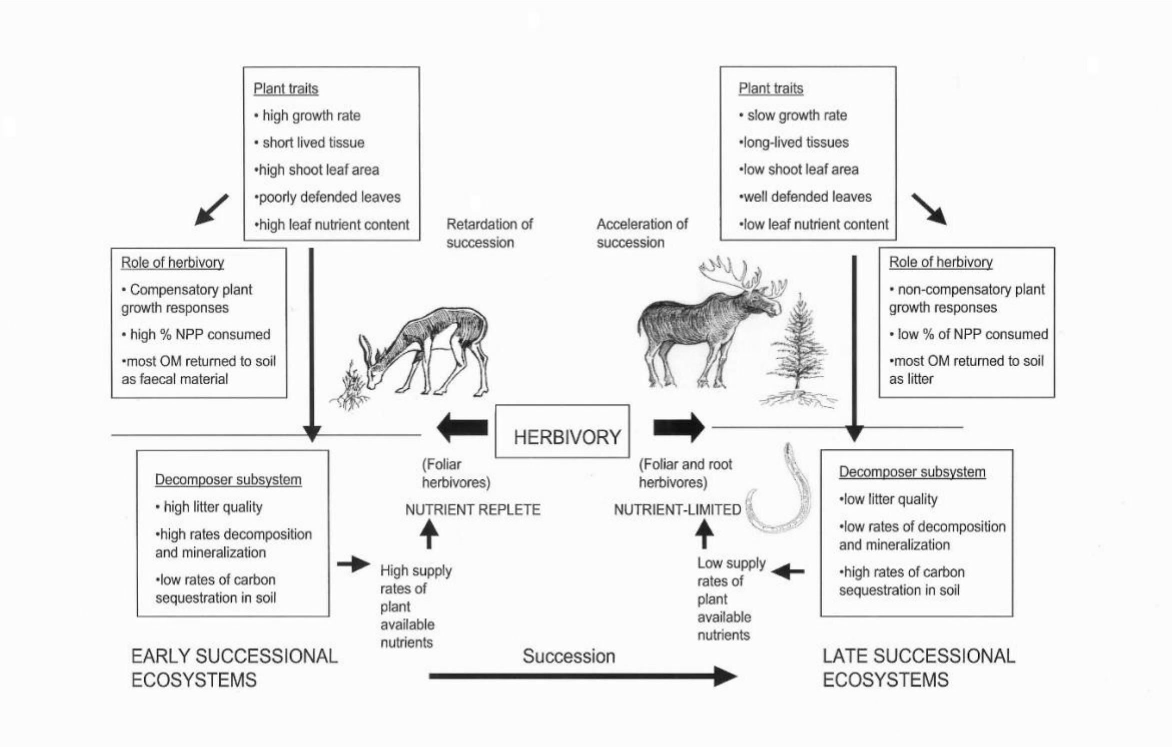


Figure 2. Wild herbivores can either increase or decrease ecosystem C through feedbacks with vegetation and nutrients that differ among sites or different forest-types. (Source: Bardgett & Wardle (2003) Figure 1. ©2003 by the Ecological Society of America).

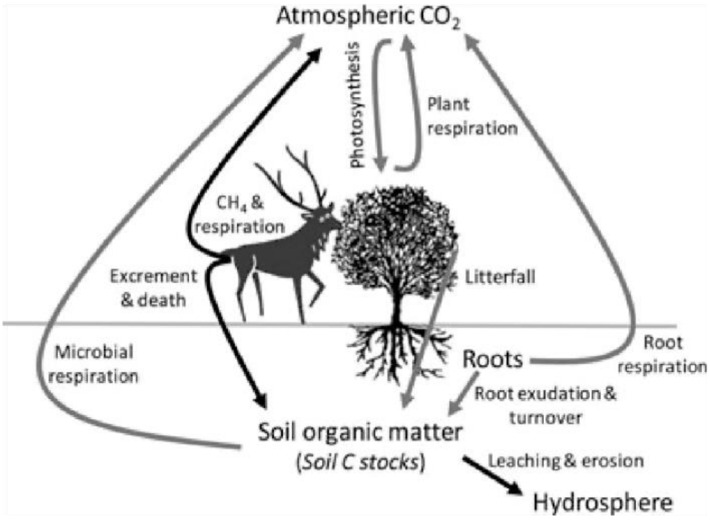


Figure 3. Effects of herbivores on carbon cycling in terrestrial ecosystems. Lines denote fluxes that are predicted to either increase (black lines) or decrease (grey lines) in response to herbivory.. (Source: Tanentzap & Coomes 2012 Figure 1 .©2011Cambridge Philosophical Society).

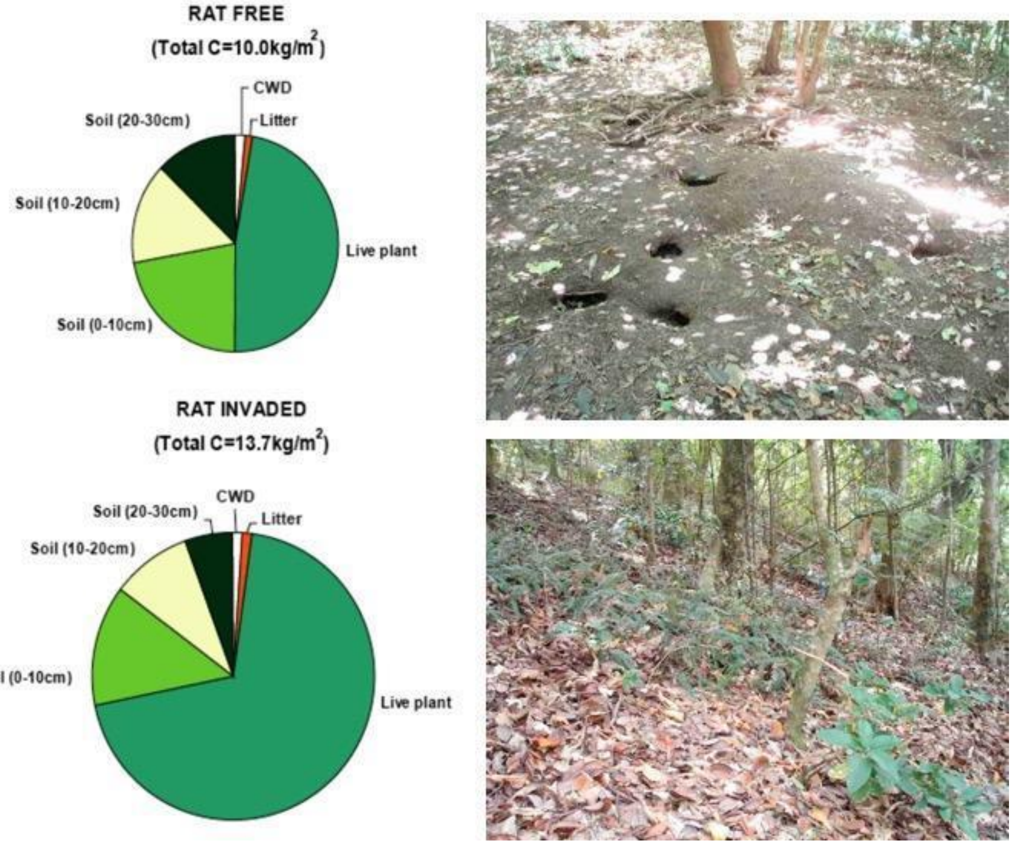


Figure 4. An example of animal management decreasing C stocks. Eradication of rats on islands lowers ecosystem C (pie charts) because rat predation reduces the soil and plant disturbances caused by burrowing seabirds (top right photo: vegetation without rats; bottom right: rats present). (CWD – coarse woody debris). (Source: Wardle et al. 2007 Figure 1 ©2007 The Royal Society).

Table 1. Summary of the main mechanisms of wild animal effects on forest C and associated ecosystem processes (see also Peltzer et al. 2014 and Wyse et al. 2018 for a summary of drivers of tree population processes).

Factor or interaction	Effects	Effects on carbon budget	Other effects	Illustrative references
Browsing	Direct consumption (reduction) of foliar, flower, and fruit biomass; Accelerated decomposition of faecal output	Minor to moderate compared to other processes	Selective decrease in palatable species biomass Lower recruitment/increased mortality of selected species Alteration of plant community composition	Tanentzap et al. (2009); Holdaway et al. (2016); Allen et al. (2023);
Trampling	Soil compaction	Unknown Probably minimal for possums and minor for deer at most in-forest sites	Declines in large-bodied invertebrates can occur	Wardle et al. (2001); Kardol et al. (2014).
Nutrient cycling	Can speed or slow biogeochemical processes and nutrient availability	Depends on site fertility	Feedbacks among animals, nutrients and C are well known overseas but not in NZ Alteration of leaf litter quality and decomposition	Wardle et al. (2001); Tanentzap and Coomes (2021); Kardol et al. (2014).
Direct emissions	Contribution of CO_2 and/or methane	Small compared to other processes	Avoidance of methane production by ruminant animals is a consideration for sustained control	Holdaway et al. (2012).

1 Impacts of deer on forest carbon stocks

WACEM review

Public conservation land (PCL) represents the largest land area in New Zealand under a single manager (DOC). This makes DOC's management of carbon critical for New Zealand and prompted DOC to commission a series of investigations under their Wild Animal Control for Emissions Management (WACEM) programme.

Key investigations and their objectives are shown below.

DOC 4023: To provide a synthesis of available information on C stocks in indigenous forests, shrublands and grasslands on PCL.

DOC 4024: To synthesise available information and knowledge about the ecology of indigenous vegetation cover and the effects of introduced mammalian herbivores.

DOC 4025: To design a programme of research fieldwork that would quantify the effects of wild animal control on total carbon stocks in indigenous vegetation.

Most findings are summarised in an overall synthesis by Carswell, Holdaway et al. (2015). Their main overall conclusion was:

'Wild animal impacts play a role in all three types of (C) gain (mostly reforestation and shrubland succession), but here we demonstrate that, for existing forests, it will be very *challenging to quantify sequestration in existing forests that (a) can be attributed to wild animal control and (b) is additional to the sink that already exists.* It is our view that the presence of a forest sink in existing forests is a strong endorsement of business-as-usual management of conservation land in forest and that this management should be maintained for the benefit of all New Zealanders.'

The following bullets outline the key recommendations and findings from the WACEM programme. The italics are our emphasis.

The fastest, and most cost-effective, responses to actions seeking to increase C sequestration on conservation land would be in unforested sites close to existing indigenous forest seed sources having rapid natural regeneration of forest species: this is most likely to occur in locations that are relatively warm (mean annual temperature > 9°C) and wet (> 1000 mm per year), can be retired from domestic animal grazing, and in which wild animal incursion can be restricted. About 600 000 ha of conservation land that was not in forest in 1990 could potentially support higher C stocks in indigenous vegetation (Mason, Bellingham et al. 2013; Carswell, Mason et al. 2015), as well as an unknown additional area of private and Māori land (not evaluated as part of WACEM). Lands with a mean annual temperature below 9°C have only a low probability naturally regenerating into forest (Mason, Wiser et al. 2013).

Any future effort to increase C sequestration through targeted wild animal control should focus on successional communities; removing wild animals from broadleaved-hardwood successions where palatable canopy tree species should become established. *The biggest areas of potential gain for both carbon and biodiversity per hectare now lie outside conservation land* (Carswell, Mason et al. 2015). The effects of ungulates or other species on forest succession (such as vegetation recovery following major disturbances such as fire, cyclones and landslides) is an area that requires additional investigation (Wyse et al. 2018).

Ascribing change in either C stocks or sequestration rate to any form of management, especially wild animal control, requires greater sampling effort (e.g. numbers of plots) than is currently used for most forest types. This is because high variability within and among sites can only detect relatively large effect sizes of >0.5 t C ha^{-1} yr^{-1} (Holdaway et al. 2012).

No effect of wild ungulates on total above-ground C levels has been recorded in several studies in broadleaved-hardwood forests. These include: (i) a network of fenced plots (with unfenced controls) in broadleaved-hardwood forests where deer and other ungulates have been excluded; (ii) repeated sampling (over 30 years) of a broadleaved-hardwood forest and in successional kānuka forest in Te Urewera known to have high deer densities;; (iii) assessment of tree mortality that may represent the effects of high densities of browsing mammals (probably possums in this instance) in a mature broadleaved-hardwood forest (Mason, Wiser et al. 2013; Richardson et al. 2014).

There is evidence that browsing animals are changing the species composition in the understorey of broadleaved-hardwood forests, and lowering seedling and sapling density, diversity and some C pools (see next section). This may have implications for longer-term successional trajectories (Richardson et al. 2014). Similarly, ungulate exclusion increases the recruitment of palatable species where forests have been subject to recent disturbance (Mason et al. 2010; see also Mason et al. 2011). These results suggest that *intensive control of ungulates (i.e. to near zero population density) could lead to an enhanced rate of succession of ungulate-preferred species in these forests at the multi-decadal timescale***.** In some cases, even small effects of herbivory on unpalatable species can slow growth or damage seedlings, but the potential effects of this on longer-term tree recruitment and forest dynamics are rarely investigated (Bellingham et al. 2016).

The WACEM programme made several specific recommendations for future work likely to be of most benefit in quantifying the effects of wild animal control for increasing carbon sequestration.

The extensive network of nationwide exclosure plots should be maintained (i.e. undertake regular inspection and rapid repair where necessary to prevent animal incursions) in order to permit measurement of multi-decadal changes in forest composition and structure and associated carbon.

Additional exclosures paired with control plots should be placed, and maintained, within successional communities where the deer-free trajectory is expected to be towards increasing deer palatable species (e.g. the Waikare catchment in Te Urewera).

Long-term monitoring of sites retired from grazing should be continued and new sites included through setting up permanent sample plots. Care should be taken to include measurement of the variables most likely to help (or hinder) woody succession.

The set of WACEM reports, and their conclusions and recommendations, are obviously relevant to the core focus of this report. However, they do not cover all the topics and issues that must be addressed before informed decisions about whether (and, if so, where, when, and how much) deer control is needed to increase carbon storage or decrease emissions. Some of those gaps have been identified as part of the WACEM synthesis (see Table 2, adapted from Carswell, Holdaway et al. 2015). However, other gaps include: understanding the relationships between herbivore density and their impacts on forest succession and related processes; understanding the likely time frames for forest C gains following herbivore control; and understanding the amount, duration, and cost of herbivore control required to deliver worthwhile C storage benefits.

Table 2. Summary of knowledge needed to determine whether C sequestration can be managed or enhanced in natural ecosystems. Green squares indicate topics addressed across the WACEM research programmes (adapted from Carswell, Holdaway et al. 2015).

	Management activity				
Potential management action	**Establish baselines**	**Encourage woody successions**	**Effective herbivore control**	**Manipulate other invasive species**	**Establish high-carbon-storage ecosystems**
What is the potential for C gains?	🟩 What are the potential C stocks?	🟩 What rates of C sequestration are possible?	🟩 What C gains are possible at selected sites?	Can invaders be categorised in terms of potential C stock impacts?	Can species combinations be designed to enhance C stocks and over what time period?
How are effective management actions to be implemented?	🟩 Which systems are resistant or resilient in terms of C?	🟩 Can seeding overcome dispersal limitation, or is expensive and C-intensive planting required?	Can forest C be maintained through pulsed recruitment?	When can non-native plants be used to enhance C storage? (and what are the risks for succession or disturbances like fire)?	Can critical components for high C systems be restored?
What other consequences are desirable?	What is the monetary benefit of achieving potential?	What are the consequences for water yields?	🟩 When are C and biodiversity gains congruent?	Does control of an invasive species reduce total exotic biomass?	Do high storage systems meet biodiversity goals?
How should benefits be quantified?	Will potential change with time?	🟩 How can additionality be determined?	🟩 Is it realistic to measure soil soil C changes?	Can invasive impacts on C stocks always be partitioned?	Can C benefits be modelled over relevant timescales?

Effects of deer exclusion on carbon stocks

Exclosures (fences) are used internationally to assess the impacts of terrestrial grazers and browsers on vegetation, plant diversity, and C pools; they have long been used in New Zealand to assess deer impacts (e.g., Allen et al. 1984). Ideally, exclosures ensure that deer numbers are maintained at zero density for at least several decades. Together with paired controls (i.e. deer-affected plots nearby), exclosures are often expected to show the greatest potential response to deer management (Tanentzap & Coomes 2012), assuming deer densities outside the exclosure are near maximum levels. Note that exclosures are fenced plots designed to eliminate all ungulate species, but do not exclude other species such as possums, mice and rats.

A national network of ungulate exclosures has been established throughout New Zealand in many forest types, some of which have been maintained for several decades. In a recent study (Allen et al. 2023) the effects of ungulates (primarily deer) in mixed conifer–hardwood forests were examined to determine differences in all major pools of carbon in vegetation and in soils to a depth of 30 cm. They examined 26 pairs of unmanipulated control plots and nearby c. 400 m^2 deer exclosure plots that were maintained for >20 years. The working hypothesis for that study is shown schematically in Figure 5.

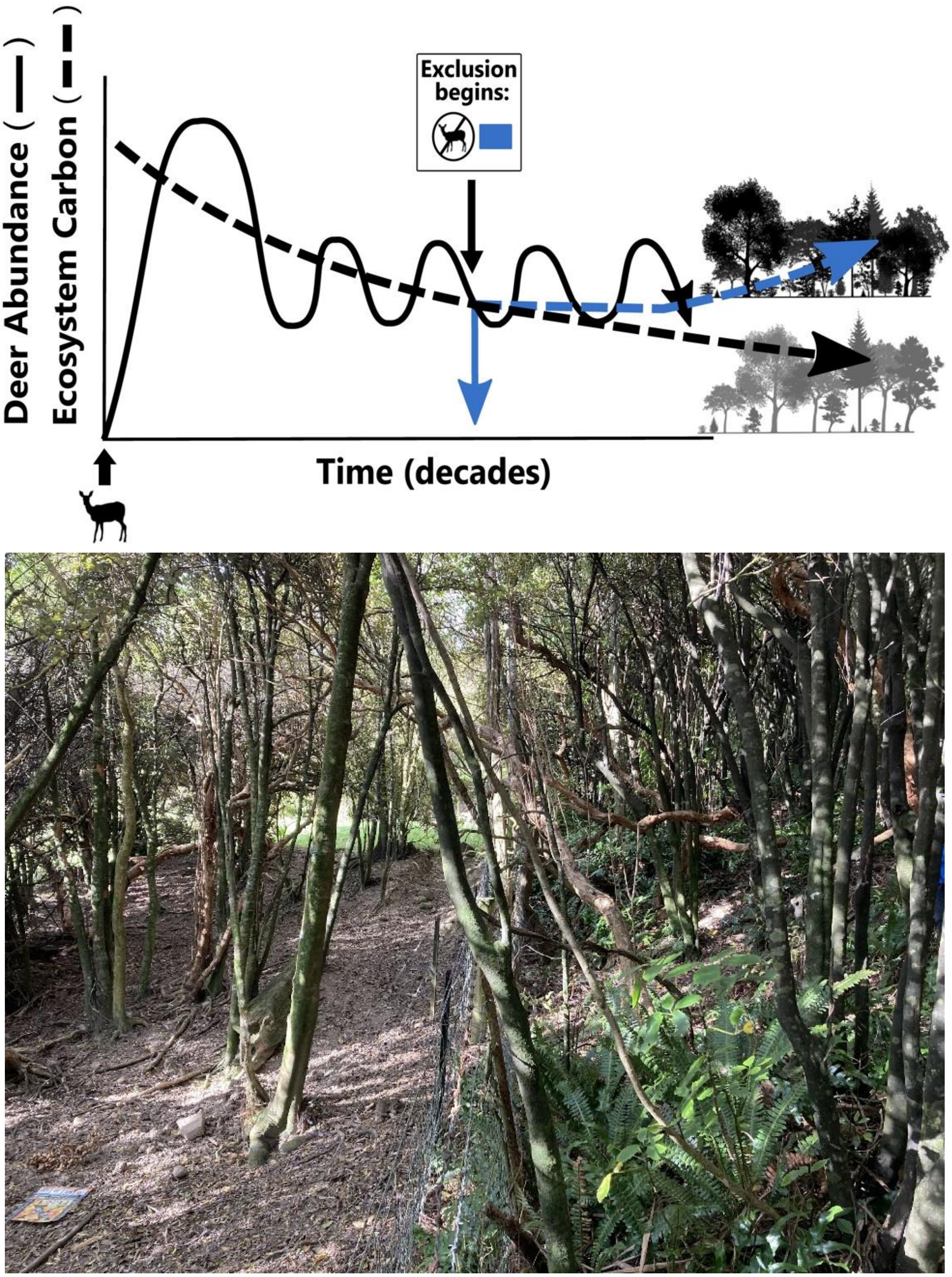


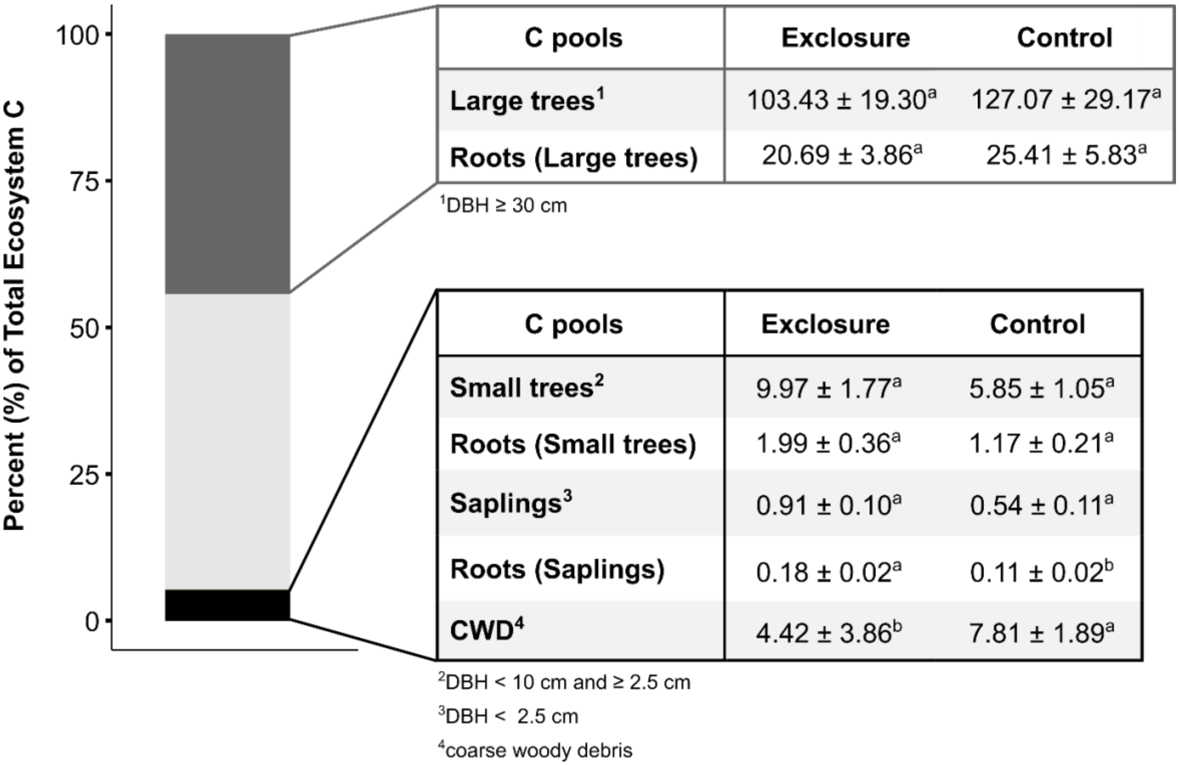
Figure 5. (Top): Conceptual figure of introduced deer establishment and abundance through time and potential effects on forest ecosystem C stocks. The solid black line represents deer abundance and population development after introduction, with an immediate decrease in deer abundance following exclusion (solid blue arrow). The dashed black line represents potential changes in total ecosystem C stocks, with illustrative divergence in C stock changes under ungulate exclusion (blue dashed line) and ungulate browsing (black dashed line). (Source: Adapted from Allen et al. (2023) Figure 1). Bottom panel: Photo illustrating the often marked differences in browse-tier vegetation between the insides and outsides of exclosures in areas with high ungulate densities (exclosure edge in 2013, Orongorongo Valley; photo from D. Peltzer).

The main findings in relation to C stocks are summarised below.

Most C was contained in large (>30cm dbh, diameter at breast height) trees that were unaffected by ungulate exclusion (Figure 6). The C stock on plots was closely related to the size of the largest tree on the plot (Figure 7). This suggests that the main driver of total ecosystem C is a few large trees, and that increased mortality of these individuals (e.g., through disturbance or folivory) is likely to have the greatest consequences for C.

There was no difference in the total stocks or tree pools of C between ungulate exclosures and paired control plots (Figure 6).

Some significant understorey (i.e. browse tier) responses were observed including higher seedling numbers (not shown), C stocks of sapling roots, and higher understorey species diversity inside exclosures (Figure 6). Although understorey vegetation contributes little to total C stocks, it is important for future recruitment and the potential resilience of forests to disturbances.



C pools	Exclosure	Control
Large trees[1]	103.43 ± 19.30[a]	127.07 ± 29.17[a]
Roots (Large trees)	20.69 ± 3.86[a]	25.41 ± 5.83[a]

[1] DBH ≥ 30 cm

C pools	Exclosure	Control
Small trees[2]	9.97 ± 1.77[a]	5.85 ± 1.05[a]
Roots (Small trees)	1.99 ± 0.36[a]	1.17 ± 0.21[a]
Saplings[3]	0.91 ± 0.10[a]	0.54 ± 0.11[a]
Roots (Saplings)	0.18 ± 0.02[a]	0.11 ± 0.02[b]
CWD[4]	4.42 ± 3.86[b]	7.81 ± 1.89[a]

[2] DBH < 10 cm and ≥ 2.5 cm

[3] DBH < 2.5 cm

[4] coarse woody debris

Figure 6. Percentage of total ecosystem C (*n* = 52 plots) comprised of C pools for large trees and their roots (dark grey portion of stacked bar), small trees and their roots, saplings and their roots, and coarse woody debris (CWD; black portion of stacked bar). The light grey portion of the stacked bar represents all other above- and below-ground C pools measured. Inset tables contain means (± SEM) between plots in which ungulates were excluded or not (control) for large tree C pools (top) and the smaller tree C pools (bottom). Different lower-case letters indicate significant differences between treatments (*P* < 0.05). (Source: Adapted from Allen et al. (2023) Figure 2).

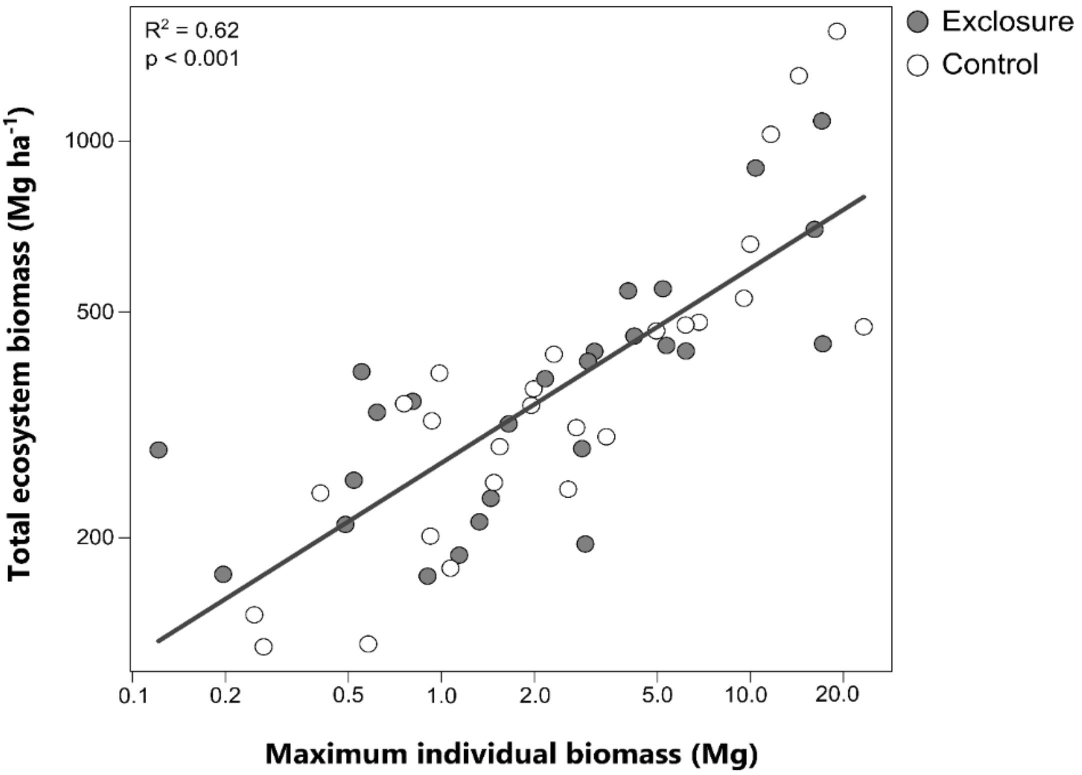


Figure 7. The relationship between the largest trees observed on plots (*x*-axis) and total vegetation biomass (C) (*y*-axis) across 52 paired exclosures (filled symbols) and control plots (open symbols). (Source: Adapted from Allen et al. (2023) Figure 3).

Two other studies (in addition to Allen et al. 2023) found no evidence that reduced regeneration of sapling and small trees translates into major reduction in C stocks. Wardle et al. (2001) reported small effects of herbivores on soil C stocks across paired exclosure plots across temperate forests, ranging from a reduction of 0.01 tC ha^{-1} to an increase of <0.01 tC ha^{-1} over 14–34 years. Carbon stocks in standing litter were reduced on average by 0.08 tC ha^{-1} over this period. A broader synthesis of exclusion effects on understorey by Wright (2012) showed the effects of long-term ungulate exclusion (of 4–43 years) ranged between a reduction in sapling density of 5.2 saplings per m^2 and an increase of 0.9 saplings per m^2. This was equivalent to a difference of 0.01 tC ha^{-1} m^{-1}, (assuming a mean above-ground sapling biomass of 100 g).

Deer feeding preferences and impacts on vegetation

The deer exclusion studies cited above, and numerous other studies implicate deer feeding preferences (often referred to as palatability) as one of the important drivers of change in New Zealand forests. Herbivores such as deer invariably have strong feeding preferences, and in general their browsing tends to reduce the abundance and biomass of the most-preferred species with subsequent compensatory increases in the least preferred or avoided species (Augustine & McNaughton 1998; Wardle et al. 2001). These changes can not only affect forest composition and structure but alter litter decomposition rates and nutrient cycling, all of which can potentially affect carbon storage (Wardle et al. 2001). An understanding deer feeding preferences and forage utilisation is therefore needed to understand their potential impacts on forest C.

In New Zealand, at least some native plant species are very rarely or never eaten by deer, most notably the shade-tolerant, small tree known as pepperwood or horopito (*Pseudowintera colorata*) but also most of the shade-intolerant podocarps. More broadly, most native plant species are *not* 'preferred' (i.e. proportion in diet < proportion of total forage availability) by introduced ruminants, with 61% of 44 tree species, 77% of 31 shrub species and 85% of 53 native grass and fern species classed as 'not preferred' or 'avoided' (values derived from the appendix in Forsyth et al. 2005). The relevance of this for C stocks is twofold: first, some plant species are not eaten by ungulates and persist – contributing to C stocks; second, some avoided or unpalatable species may further filter or reduce the recruitment of other species, e.g. through promotion of grass swards (Coomes et al. 2003; see also Royo & Carson 2006 for a global review). Feeding preferences also vary with neighbourhood and season (Bee et al. 2009, 2010) and with deer density (Nugent, Fraser & Sweetapple 2001). The effects of density are discussed in Section 5.1 below.

Although the Allen et al. (2023) study above (Figure 6) showed no change in total C after at least 20 years of deer exclusion, there were differences inside and outside the exclosures in the composition and diversity of saplings and small trees (Figure 8), with more saplings and small trees of more species inside exclosures than outside.

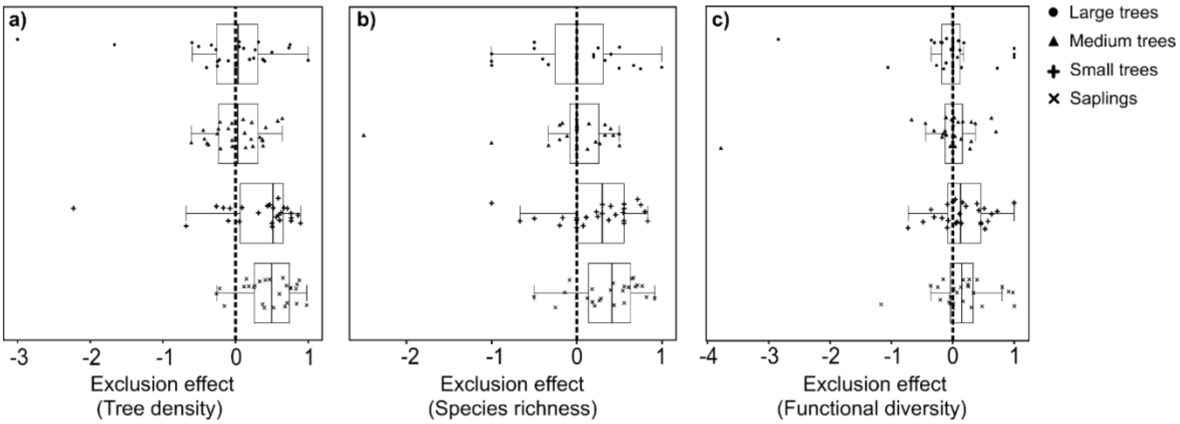


Figure 8. Effects of ungulate exclusion for different tree size classes on: a) stem density (abundance); b) plant species richness (diversity); c) functional diversity. The effect of exclusion on each variable is expressed as [(variable inside exclosure – variable outside exclosure)/(variable inside exclosure)], where negative values indicate a variable is greater outside the exclosure. Large trees are ≥30 cm diameter breast height (DBH). Medium trees are <30 cm and ≥10 cm DBH, and small trees are <10 cm and ≥2.5 cm. (Source: Adapted from Allen et al. 2023 Figure 4)

Those compositional changes echo previous studies showing seedling and/or sapling abundance or growth responded strongly to ungulate exclusion in different forest types and across a wide range of ungulate abundance or management regimes. Some examples are given below (see also Appendix B for glossary of species names).

Husheer (2007) measured 32 permanent forest plots and 9 exclosures in the Pureora Forest Park (PFP) and reported lower regeneration of several deer-preferred hardwood tree species (*Elaeocarpus dentatus*, *Griselinia littoralis*, *Melicytus ramiflorus*, *Schefflera digitata* and *Weinmannia racemosa*), and observed that these species were abundant as saplings or small trees only in the absence of deer. For context, red deer densities in PFP had probably ranged from 6–12 deer per km^2 over the preceding three decades (Nugent et al. 1997; Sweetapple & Fraser 1997), and parts of PFP had received intensive aerial possum control, and ground based-culling of goats to very low levels (<1 animal per km^2). Similar results from a comparable study design were also reported for the Aorangi forest (Husheer et al. 2005); see also (Husheer & Frampton 2005).

Husheer and Robertson (2005) compared the effects of ungulate exclusion and three levels of deer control (low – status quo, medium – recreational and commercial hunting, and high – aerial culling) over 1998–2001 in the Kaweka and Kaimanawa Ranges on seedling regeneration of a main canopy species there (mountain beech (*Nothofagus solandri var. cliffortioides*). Mountain beech appears to be the most palatable of the beech species. High levels of control reduced deer (mostly sika) abundance by about two-thirds (67%, or from >16 deer per km^2 to <6 deer per km^2 after 3 years) compared to the other management regimes and doubled seedling height growth of beech. The implication is that reducing deer densities to moderately low densities was probably sufficient to allow canopy replacement.

In a separate study, Husheer et al. (2006) used experimental manipulations of transplanted and naturally-occurring mountain beech seedlings in the Kaimanawa Ecological Region to consider deer effects on mountain beech regeneration. Exclusion increased the growth of transplanted seedlings (5–135cm tall plants) by about 100% and survivorship to sapling size (>135 cm height) by 10%, but did not affect annual mortality of naturally-occurring seedlings. Turf removal had much larger effects on increasing the survival and growth of transplanted seedlings into the same sites. The overall conclusion of this study was that deer have both direct effects on mountain beech regeneration and indirect effects by promoting browse-tolerant turfs, presumably induced by grazing.

A series of investigations by Coomes et al. (2002) was used to establish the LUCAS plot-based methods used to quantify C nationally. Along with summaries from investigations of plant species selection (e.g. Wright et al. 2012) and assessment of deer feeding preferences from diet and browsing studies (Forsyth et al. 2002, 2005; Nugent & Forsyth 2021), these studies provide additional insights into the potential effects of animals on C and nutrient cycling that can be generalised across forest-types.

Coomes et al. (2003) used permanent NVS plots and exclosures to quantify the effects of competition and disturbance for tree size class distributions. Part of this work suggests there was an 18% reduction in stem density in the 3–5 cm size class, possibly caused by reduced recruitment of species browsed by deer. However large-scale changes in stem densities are observed across forests more generally, and driven by several factors including climate change, fragmentation, disease, and large-scale disturbance events such as wind and earthquakes.

A series of studies by Bee et al. (2007, 2009, 2011) assessed plant species palatability and the effects of defoliation on native tree species under field conditions. These studies showed that species selection depends both on palatability and what other species are growing nearby (i.e. some species not usually eaten can be selected when in 'bad' neighbourhoods dominated by least preferred species.) Manual clipping of saplings found increased mortality over 2 years occurred at 100% removal of leaves, but did not differ among saplings that were 0%–80% clipped.

A major research programme at Waitutu Forest (Southland) to paramaterise the spatially-explicit forest dynamics model SORTIE-NZ provided new data and predictions to help understand how soil fertility, disturbance and animals can affect long-term (century-scale) forest productivity and composition (Forsyth et al. 2015). It revealed multiple effects, summarised in the points below.

Major disturbance from earthquakes or windthrow was needed to reproduce long-term forest dynamics and composition.

Ferns can operate as a major filter on tree recruitment, especially driving differences between broadleaf and conifer canopy species. This relates to greater ability of shade-tolerant broadleaf species than mostly shade-intolerant podocarps to regenerate in the presence of a dense layer of ground cover comprised of unpalatable fern species such as the crown fern (*Blechnum discolor*).

Deer, pigs and rodents each affect regeneration of woody plant species differently, with the greatest effects occurring on fertile alluvial areas compared to less fertile sites in the same forest class.

In the century-scale models, rodent- and deer-induced reductions in seedling abundances did not always translate into reduced sapling and adult tree abundances. When deer changed the abundance of a canopy dominant, other species were affected by altered interspecific competition; the presence of deer was also predicted to increase the dominance of conifers in both of the habitats modelled.

A series of investigations into using tree size class distributions for national reporting of forest condition also indicates linkages between introduced animal effects and forest condition:

Mason, Bellingham et al. (2013) evaluated the effects of ungulate exclusion on plant abundance and functional traits. Results suggested there were some increases in plant species abundances and traits (e.g. leaf nutrient contents, tissue density) associated with palatability to ungulates, but that these shifts were far larger in successional or disturbed forest than in with tall/mature forest.

Peltzer et al. (2014) quantified the size class distributions of tree species nationally and compared species that differed in their palatability to deer or possums. No evidence for regeneration failure within the LUCAS plot network was observed across different species, including those palatable to deer (Figure 9).

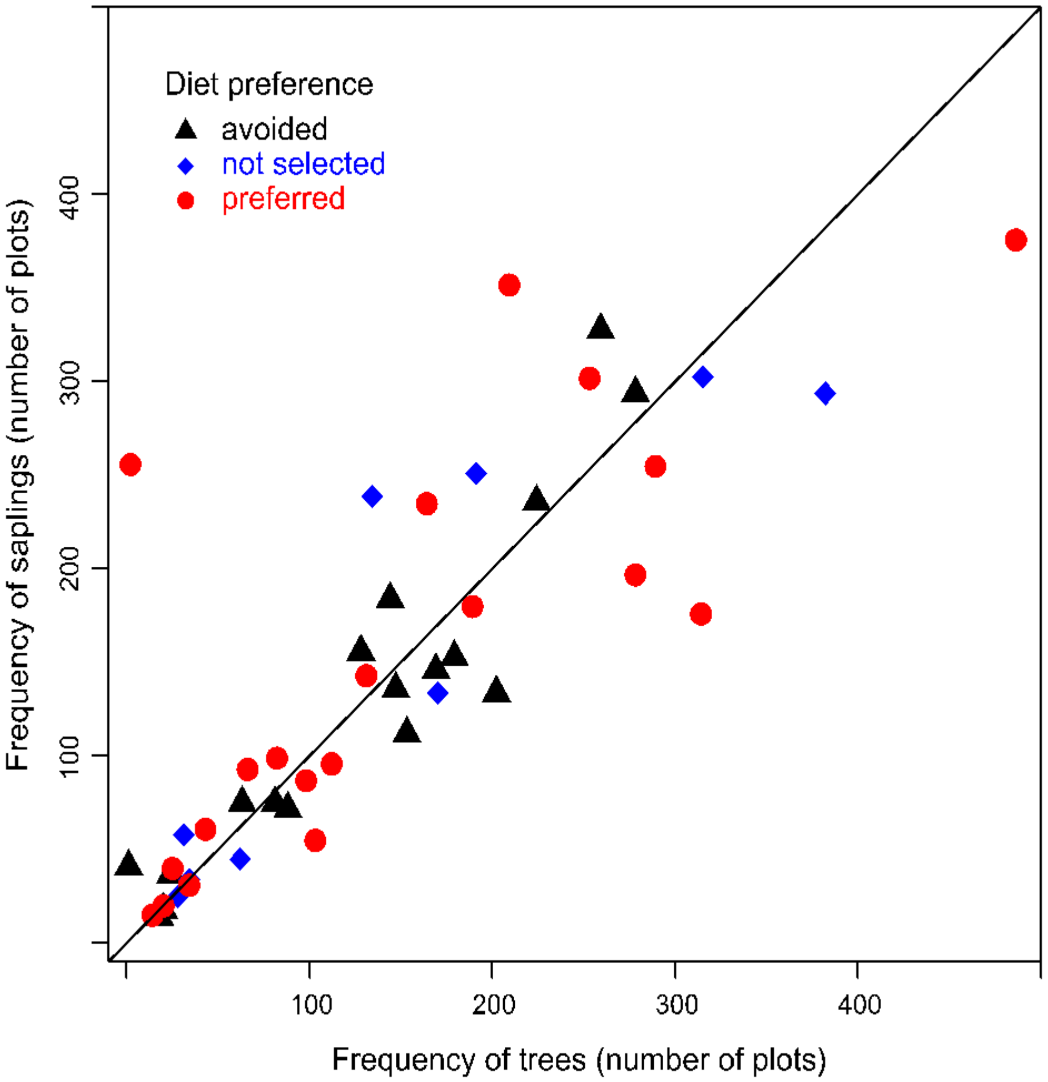


Figure 9. Relationship between sapling and tree presence (frequency) across all LUCAS plots. Measurements evaluate if there is large-scale suppression of regeneration for species that are avoided, not selected, or preferred (palatable) to deer. Diet selection categories follow Forsyth et al. 2002). Each point is a species, and the black diagonal line is the 1:1 relationship. (Source: Adapted from Peltzer et al. 2014 Figure 4).

In a broadleaved/podocarp forest at Waihaha, in the Pureora Forest Park, Nugent et al. (1997) estimated stem density for all individual plants of every woody species in three height classes. They also quantified forage production, utilisation, and diet, and derived a deer preference (PI) index (with PI>0 indicating a greater percentage of the species in the diet than in the deer accessible foliage and vice versa for PI<0). Overall, there were nearly 200,000 short (<51 cm) seedlings, c. 15,000 tall seedlings (50-200cm tall), and c. 5,000 saplings and trees per ha. With one exception (pōkākā), all of the deer-preferred species (PI>0) had fewer or the same number of tall seedlings than saplings and trees combined. However, without exception, species not preferred by deer (PI<0) had 1.8–19.0 times more saplings and trees than tall seedlings. The low number of tall seedlings for the most highly preferred species did not reflect seed source limitations as there were typically many thousands of small seedlings for these species. Broadleaf (*Griselinia littoralis*), the most important deer food source at Waihaha, had 30,050 small seedlings (almost all <5cm tall) compared to just 10 tall seedlings, while kāmahi (the second most important possum food) had 7,410 small and 20 tall seedlings. In contrast, there were 8,900 short and 910 tall seedlings for the four main podocarp species there (tōtara, miro, rimu and mataī).

In summary, deer cause major changes in plant species regeneration, abundance and diversity, leading to changes in understorey composition. However, the long-term consequences for overall forest composition and structure, and therefore for forest C sequestration is complex and difficult to predict (Figure 10; and see detailed discussions in Tanentzap & Coomes 2012; Allen et al. 2023).

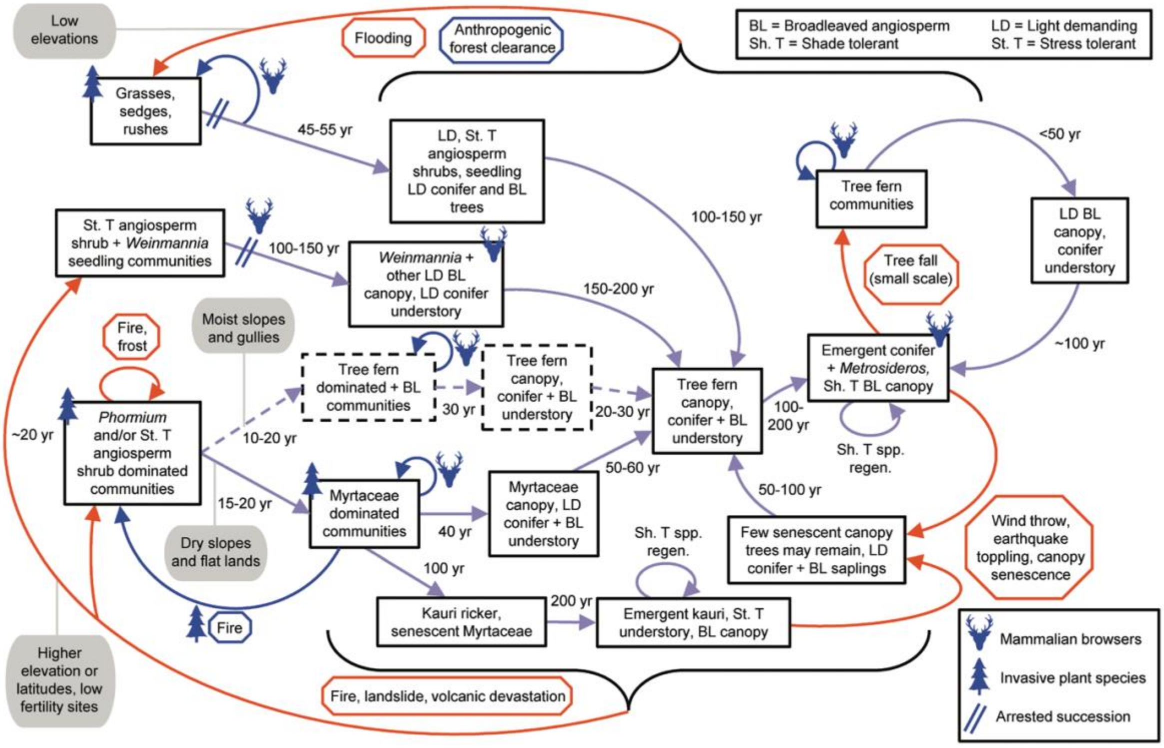


Figure 10. Conceptual model detailing the generalised dynamics of New Zealand conifer-angiosperm forests. Orange arrows indicate transitions between states caused by disturbances (named in octagons); purple arrows indicate transitions due to the passage of time in the absence of disturbance. Blue symbols indicate community states that may often have well-documented structural changes as a result of the modern influences of introduced mammalian browsers and invasive plant species. Blue symbols also signify human induced disturbances, increased disturbance as a result of introduced mammalian browsers and invasive plants, and where the effects of mammalian browsers may lead to arrested successions. Dashed lines indicate a poorly studied pathway (which we therefore have less confidence in), but which is included here as is it may nevertheless be important in some NZ forests. Time estimates are means of the values recorded in the literature. Species composition of states varies geographically. (Source: Wyse et al. 2018 Figure 6. © New Zealand Ecological Society).

Nonetheless, it is also clear that the long-term changes in canopy composition resulting from deer-induced changes will often be slow, occurring at a multi-decadal or century scale and possibly even at the millennial scale. It is possible, for example, that deer may be removing understorey plants earlier (i.e. as seedlings) in much the same way as would occur later under resource competition between saplings and small trees (see Coomes et al. 2003; Kunstler et al. 2013). If so, frequently observed differences in sapling densities may represent relatively ephemeral and small reductions in carbon stocks, with some of the least deer-preferred species possibly replacing the most preferred species with little eventual effect on above-ground carbon stocks (Coomes et al. 2003; Peltzer et al. 2014).

Effects of other introduced animals

A number of other introduced animals are also present in, and can potentially affect, indigenous forest structure and composition (and therefore forest carbon stocks). This includes possums as herbivores, but also pigs and rodents as seed- or seedling-eating omnivores, and even predators such as cats and stoats that can potentially affect the vegetation (by, for example, affecting rodent abundance). Possums are widespread and occur in most indigenous forests (Cowan 2021). For forest C, the major consideration is simply whether possums' arboreal browsing of canopy foliage directly increases mortality of large trees. From first principles, this would have a far larger direct effect on major pools of forest C because these are driven by large trees (Figure 6), but also indirectly through effects on deadwood production, decomposition, and nutrient cycling (see discussions above and Figure 10). Unfortunately, the Waitutu study mentioned above (Forsyth et al. 2015) did not include possums (simply because possums were under sustained control in that area).

There are no studies we are aware of that have specifically assessed the joint effect of simultaneous control of both deer and possums on forest C, or even of the effect of possum control alone. This is despite a substantial research effort into possum control and eradication in recent years as part of the Predator Free NZ programme (Leathwick & Byrom 2023).

However, there are some studies that evaluate the consequences of possum abundance or control for forest C; most focus on defoliation and potential changes in tree mortality, but the overall effects reported vary widely among studies. Mason, Bellingham et al. (2013) used a combination of long-term plot data and estimated decay rates of deadwood to determine changes in forest C that include consideration of deadwood decay using a large- scale dieback of many canopy tree species in the Hokitika River catchment putatively caused by possum browsing (e.g. Batcheler 1983; Rose et al. 1992). Although the dieback resulted in a significant loss of C, this was substantially ameliorated in the short term where southern rātā (*Metrosideros umbellata*) was previously abundant in the canopy because most of the C persisted in the dead spars which are decay-resistant and persist over many decades.

Batcheler (1983) considered that large-scale dieback events such as the collapse of forest canopies over large parts of the Ruahine Range in the mid-1990s was probably triggered by the combination of a unsustainably extremely high possum browsing pressure when they were at the peak of the initial invasive irruption (as depicted for deer in Figure 5) and a high proportion over-mature near senescent trees in the canopy. A key point is that such major impacts are likely to be less common in future at least in areas where possums have now been present for many decades..

Other studies have shown outcomes that were the reverse of what was expected. For example, long-term possum exclosures in the Kokatahi catchment on the West Coast of the South Island (Figure 11) were used to test the prediction that removal of possums that reduce palatable woody species having high quality litter will slow succession. Instead, possums removed competitive species like grasses that slow recruitment of woody species, so succession to woody species was more rapid when possums were present (Bellingham et al. 2016).

Figure 11. Long-term possum exclosures in the Kokatahi catchment. (Photo: P. Bellingham.)

However, quantitative assessments linking possum browse to tree mortality indicate that mortality from possum browse does occur and can be predicted as a function of foliar cover and possum forage intake (Holland et al. 2013; see also Gormley et al. 2012). What this emphasises is that, like other animals, the total impacts of possums on forest C are complex. The limited evidence suggests that non-palatable species tend to exhibit compensatory growth when competition from palatable species is reduced (Wardle et al. 2001; Forsyth et al. 2010; see also discussion in Section 5.2).

Other drivers of carbon sequestration

There are many other drivers of forest dynamics that could alter forest C, either largely independently or in conjunction with deer and possums. One example of the former is forest collapse due to landslides caused by earthquakes, as graphically illustrated in Figure 12. Previous work emphases that the potential for C sequestration is greater following disturbance and in succession forests, and this may offer an opportunity to manage animals for C, but this possibility has not been tested to date (see Holdaway et al. 2012; Carswell, Mason et al. 2015). Similarly, a major review of forest dynamics in New Zealand (Wyse et al. 2018) suggests that forest disturbances are common and are likely to interact in novel ways with different non-native species, climate change, and plant pathogens and that this will alter forest dynamics and composition ultimately C (Figure 10; see also Wells et al. 2001; Smale et al. 2016). Our current understanding of succession and forest processes provides a baseline against which to understand these future changes. However, many issues raised explicitly in WACEM remain to be resolved (Table 2) and include the following questions.

Is pulsed tree recruitment because of animal management or driven by variation among years (e.g. mast seeding)? Similarly, is forest tree species composition and C sequestration potential maintained despite this variability?

Do sites or forest types having the greatest potential for C sequestration also meet biodiversity goals?

Can the effects of different animal species be partitioned or disentangled, and additionally, how do these effects respond to management of one or multiple species?

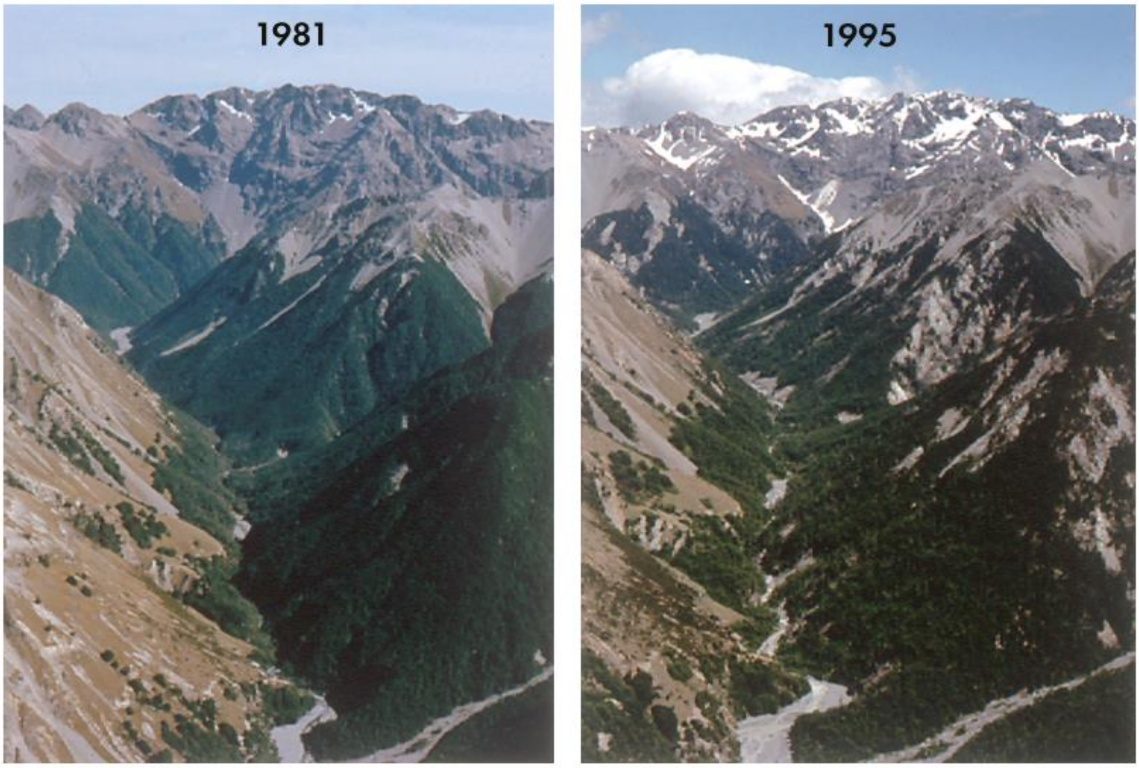


Figure 12. Earthquake disturbance in the Harper-Avoca catchment reveals the spatial extent and timing of disturbance events on forest structure, population processes and biomass (Source: Photographs by John Barran, New Zealand Forest Research Institute Ltd; see also Allen et al. 1999, 2020).

2 Factors affecting management of deer and their impacts on forest carbon stocks

Density-impact relationships

The exclosure studies cited above (Section 4.2) indicate that complete removal of deer (but not possums) results in changes in understorey composition within a few decades (e.g. Figure 8), but with little if any decadal impact on the number of large trees, and thus no significant change in the C stores on the plots over that timescale (Figure 5).

In deer-control terms, complete exclusion equates to eradication. However, deer eradication from all or most public conservation land is probably not currently possible because: (i) deer can be legally farmed on neighbouring private land, and ongoing escapes from farmland (and/or deliberate illegal translocations and releases) appear unavoidable (Fraser et al. 2000); (ii) there would not be the social licence to undertake eradication. Unless these factors change, reducing the effects of deer will require some form of ongoing control. In contrast, possums are already targeted for eradication by 2050 as part of the Predator Free 2050 initiative led by DOC.

The cost-effectiveness of control depends in part on how far below current levels deer density needs to be reduced to achieve any given desired effect. That requires an understanding of density-impact relationships, which, unfortunately, do not currently exist specifically for forest C. However, some inferences can be drawn from knowledge of relationships between herbivore density (relative to carrying capacity) and their impact on the regeneration and survival of various species. Carrying capacity (K) is the maximum number of deer an area can sustainably support in the absence of predation, hunting or control. At K, deer are close to starvation, with high mortality and low reproductive rates. This results in a recruitment rate of zero.

Deer most prefer a small group of angiosperm tree species (and a few fern species) as food and tend to consume all of the available foliage of those preferred species within the browse tier at all but the lowest densities. At K, deer are forced by starvation to increase consumption of less palatable species, or move to new sites. However, some species (including most of the canopy-forming beech and podocarp species) are seldom or not consumed at any density, and, importantly, can benefit from reduced competition for light, nutrients, and space (Coomes et al. 2003; Forsyth et al. 2015; see also Tanentzap et al. 2011).

Where deer have long been present in tall forest, they rely heavily on fallen (wind-broken or cast) leaves of the few highly preferred tree species (most notably broadleaf) as their major food source in both beech and conifer-broadleaved forest (Nugent & Forsyth 2021). This creates a non-linear deer-impact curve. At K, regeneration of even the most marginally palatable species can be impeded. Reducing deer density increases the per-capita availability of preferred foods, enabling deer to reduce consumption of the least preferred species, permitting increased regeneration. The Kaweka study mentioned in Sec 4.3 (Husheer & Robertson 2005) is an example of this. In contrast, ground-level regeneration of the most preferred tree species is unlikely to occur at any but the lowest densities, because their newly germinated seedlings appear to be preferred to senescent fallen foliage. Nugent et al. (2001) recorded an average broadleaf seedling height of just 3–5cm at 25 sites in the eastern Hauhungaroa Range, regardless of deer density (range 2-10 deer per km^2). The strong implication is that a relatively modest amount of control is required to allow the least palatable species to regenerate, but major reductions in deer density are required for regeneration of highly preferred species. This is largely because incremental reductions at the mid-range of deer densities simply result in deer being less reliant on senescent foliage that has fallen from the canopy for food (Figure 13).

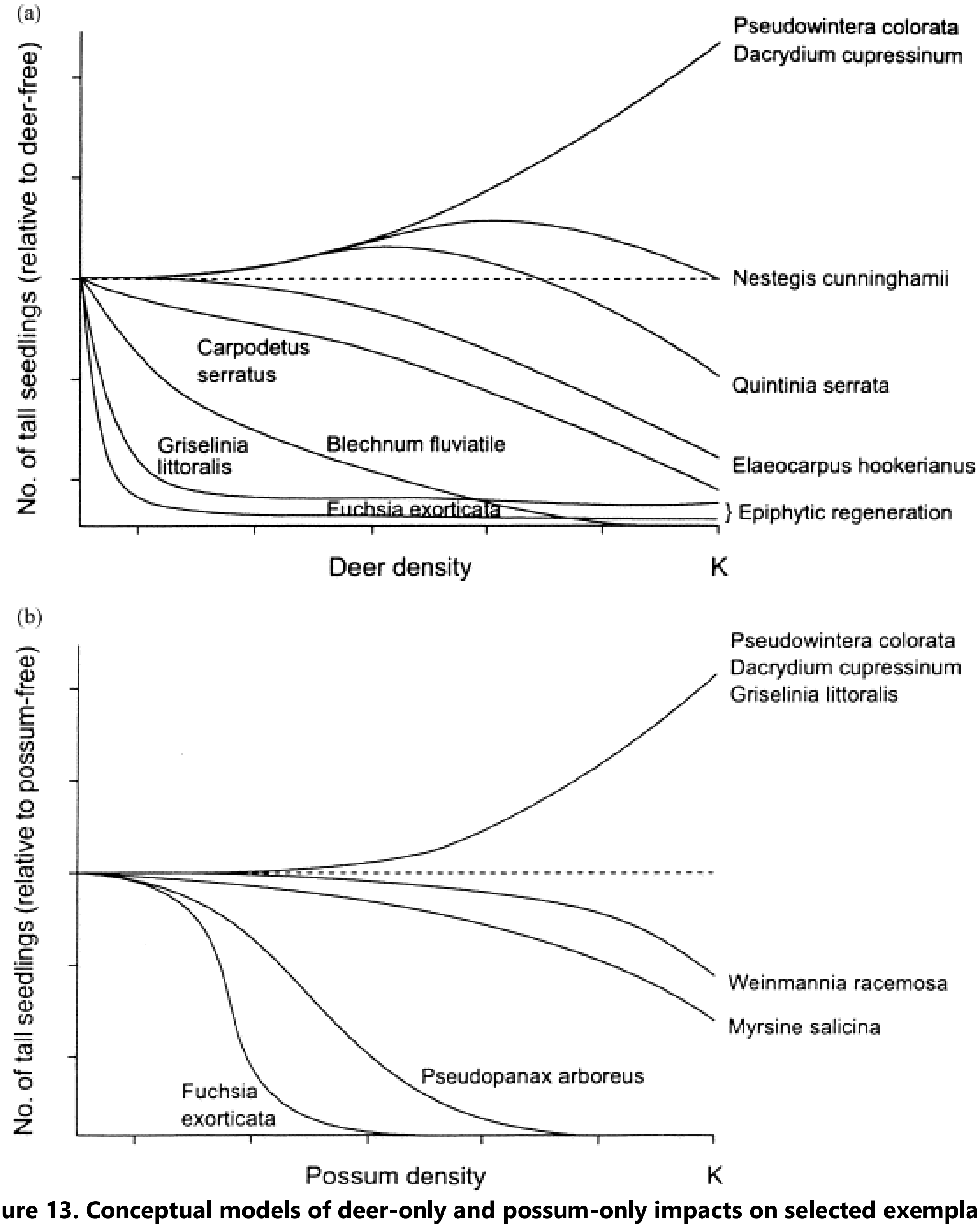


Figure 13. Conceptual models of deer-only and possum-only impacts on selected exemplar species at Waihaha, Pureora Forest Park. (a) For deer, the model is consistent with data for the recorded range of densities in the Waihaha catchment (i.e. approximately 2–10 deer per km^2), but hypothetical above that. (b) For possums, the model is largely hypothetical. For both species, the *x*-axis represents the full range of possible densities from zero to carrying capacity (*K*), which is thought to be >20 individuals per km^2 for deer and >400 individuals per km^2 for possums. (Source: Reproduced with permission from Nugent et al. 2001, Figure 4).

Possums are arboreal, so, unlike deer, can directly affect tree mortality as well as regeneration. They can locally eliminate some species within a few years of invading an area (e.g. tree fuchsia, *Fuchsia excorticata*, and tītoki, *Alectryon excelsus*, in the Orongorongo Valley; see figure 2.2 in Cowan 2021). However, possums are somewhat reluctant folivores, typically preferring to eat flowers, fruit, fungi and invertebrates when available. Whether this results in lower propagule production or long-term declines in recruitment is unresolved. That preference for non-foliar foods is illustrated by an immediate switch in possum diet after intensive possum control (to near-zero possum density) from a heavy reliance on canopy tree foliage to a diet of flowers, fruit, and the foliage of rare early-successional species (Sweetapple et al. 2013).

Overall, possums most prefer the foliage of fast-growing species such as pōhuehue, tree fuchsia, and wineberry. Other seral species, small trees, and shrubs such as māhoe, five-finger, tītoki and various *Coprosma* species tend to be somewhat less preferred. These intergrade in preference with slower-growing canopy and subcanopy species such as kāmahi, rātā species, toro, and tawa. Like deer, possums seldom eat the foliage of the major canopy species such as the beech spp. and the podocarps (with the important exceptions of Hall’s totara and pāhautea). Despite some overlap in foliar feeding preferences, the diets of deer and possum can differ markedly (Figure 14)

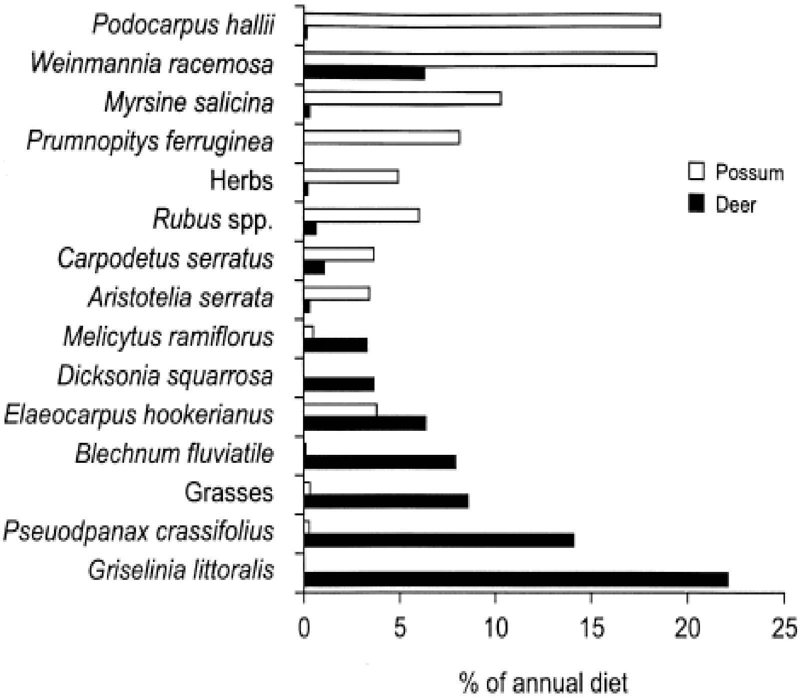


Figure 14. Diets of possums and deer in the eastern Hauhungaroa Range in the early 1990s, when possum densities were high (c. 300 individuals per km^2) and deer densities (c. 6 individuals per km^2) were likely to be at about half the carrying capacity. (Source: Reproduced with permission from Nugent et al. 2001 Figure 1.)

Possums’ ability to affect tall tree mortality directly, coupled with their strong preference for scarce non-foliar foods result in markedly different density-impact relationships for possums than for deer. Reducing possum density even moderately seems likely to markedly reduce their impacts on large tree mortality. A 10-year study in three regions of the impact of a single possum control operation on possum-preferred tree species (Nugent et al. 2001) showed clear links between possum abundance and foliar cover, and between foliar cover and mortality. It further showed a reduction in mortality following possum control, firstly confirming that possum browse had been resulting in elevated tree mortality at many of the study sites, and secondely, that a modest level of possum control was sufficient to reverse much of that impact. However, Halls totara was most heavily impacted initially and recovered least. That is consistent with large declines in biomass of Hall's totara in three Westland areas (30% in the Taramakau and 44% in Copland rivers over 14 years, and 46% in the Kokatahi over 23 years; Bellingham et al. 1999).

The key implications of the differences between possums and deer in their dietary preferences and impact-density relationships are listed below.

Both deer and possums affect different but overlapping subsets of tree species so control of one but not the other will only partially reduce overall browser impacts.

Moderate or intermediate levels of deer control (i.e. to perhaps 25%–75% of *K*) is likely to improve regeneration only for the least preferred species that can be eaten by deer, whereas moderate levels of possum control appears likely to reduce mortality of almost all tree species with foliage preferred by possums. High levels of deer control are likely to be required to allow widespread regeneration of the species most preferred by deer.

The effect of possum control in slowing or preventing declines in forest C due to possum effects on tree mortality is likely to be more or less immediate (i.e. within a few years). In contrast, the equivalent effect of deer control on forest C declines caused by deer preventing tree regeneration is likely to take many decades or even some centuries.

Reversibility of impacts

A major consideration for management is whether reducing deer density (and/or possum impacts) is achievable and will reverse their ongoing unwanted effects. This is a major, but often untested, assumption underpinning operational decisions in pest management (Allen et al. 2023). However, New Zealand is globally viewed as a conservation leader for large-scale environmental management based largely on invasive species pest control (Simberloff 2019). Predator Free 2050 is one of these initiatives, built largely on island eradications, but increasingly being focused on larger mainland areas (Peltzer et al. 2019). A major synthesis of monitoring data for fenced sanctuaries and unfenced extensive management operations shows that bird (and plant) diversity tends to increase with intensive and long-term (>7 yr) possum, rat and mustelid control (Binney et al. 2021). However, ungulates were not included in that synthesis and impacts on ecosystem properties such as C were not considered.

Apart from the few published exclosure studies mentioned above, there are no direct assessments of the effect of deer and/or possum control on C emissions and sequestration. Instead, the potential responses are typically inferred from observed changes in forest composition over time. However, there are several reasons why reducing or eliminating browsing may not quickly reverse the past and current impacts of deer, or herbivores more generally. Coomes et al. (2003) provided an important synthesis of the interlinked factors potentially preventing the recovery of deer-impacted species following deer control in New Zealand, as follows:

Dietary buffering: As already noted, the food sources of deer in tall indigenous forests can be grouped into three main pools: (i) growing foliage from highly preferred species; (ii) a small or large quantity of fallen leaves from preferred broadleaved trees, depending on forest type; (iii) growing foliage from marginally or unpreferred species that are either browse resistant or browse tolerant. Modest reductions in deer density will benefit the third pool. However, major reductions or eradication are likely to be required to allow the first pool to recover because of the buffering effect of the supply of palatable fallen leaves that (in the short-to-medium term) is unaffected by deer (Nugent, Fraser, Asher et al. 2001). The reduced number of deer still consume almost all of the first pool, but simply leave more of the fallen leaves uneaten at progressively lower deer densities until very low densities are reached.

Expanded niche occupation by unpreferred species: During deer invasion, forest understoreys comprised of shade-tolerant preferred species (including ferns, herbs, and grasses) were often almost completely eaten out, reducing competition for space, light, and nutrients. That typically enabled the increase and spread of the least preferred forest species. That is unlikely to occur where possums – but not deer – are present because possums prefer (and have access) to sunlit foliage (Sweetapple et al. 2016).

Irreversible changes to successional pathways: Herbivores can accelerate, slow, or fundamentally alter the course of succession, depending on which species they choose to eat (Connell & Slayter 1977). For example, the small myrtaceous trees kānuka (*Kunzea ericoides*) and mānuka (*Leptospermum scoparium*) often dominate early successional shrublands following abandonment of agricultural land or burning in New Zealand. These species have small, tough leaves that are avoided by deer but can act as nurse plants by helping the recruitment of other species such as the small, broad-leaved trees māhoe (*Melicytus ramiflorus)* and māpou *Myrsine australis* (Wardle 1991). A crucial question arises if deer browsing leads (on a millennial scale) to a dominance of conifers (as predicted for Waitutu, see Forsyth et al. 2015) with larger forest C than at present. Should restoring (if possible) the original successional pathways through deer and/or possum control (as a conservation objective) take priority over the prospect of increased C?

Lack of seeds required to re-found populations: Deer browsing could eventually eliminate some species from patches of forest. Without local seed sources such species may be unable to re-establish themselves. Seed limitation may be exacerbated by the loss of native pollinators and seed dispersers. Alternatively, other regeneration pathways may persist – at least some of the most palatable species can establish, flower and fruit as epiphytes. For example, in the Pureora Forest Park, kāmahi and broadleaf (often the most important deer foods) often regenerate above the browse tier as epiphytes (Smale & Kimberley 1993), where Nugent et al. (1997) recorded epiphytic broadleaf seedlings and saplings on 18% of 355 plots.

Long-term alteration of ecosystem properties: Browsers can affect below-ground processes and fauna that affect many ecosystem processes such as nutrient cycling and productivity, but little is known about the reversibility of these changes (Wardle et al. 2001; Forsyth et al.. 2010; Kardol et al. 2014).

Interactions among multiple introduced species: Most forests contain not only deer and possums, but also pigs, rats and other mammalian predators as well as invertebrates like wasps. It is not known whether those other species also significantly affect forest composition and forest C directly (e.g. through seed predation by rats, or via increased space for regeneration as a result of pig rooting (Wardle 1984).

Re-establishment of trees in areas invaded by non-native plants: The number of introduced plant species far exceeds that of native plants in New Zealand, with sward-forming grasses now naturalised over extensive areas of deforested land (Brandt et al. 2021). These species can sometimes reduce regeneration of native species with herbivory taking a relatively minor role (Cabin et al. 2000; Bellingham et al. 2016).

Cost-effectiveness of deer control

Determinants of deer control costs in tall forest: If deer are confirmed as having some adverse and reversible effect on forest C sequestration in some forest areas, whether that impact can be reversed cost effectively needs to be considered. That requires an understanding of cost of control compared to the economic value of an increase in forest C.

The cost of deer control varies in relation to carrying capacity. At carrying capacity, deer are abundant so kill rates are high; because deer recruitment rates are zero or low, deer density can be reduced with modest efforts. However, as the intensity of control increases, the removal of deer is increasingly offset by increased reproduction. This occurs until density is reduced to (very broadly) about half of *K*, when kill rate matches the intrinsic rate of increase. Below this level, the cost of reducing deer densities is increasingly inversely related to deer density (Nugent & Choquenot 2010). For example, in the eradication of deer from Secretary Island (Macdonald et al. 2019) (Figure 15) the direct operational costs of killing the last deer (in 2014) exceeded NZ$8,000. That compares to a cost of NZ$411 per deer for ground-hunting in 2006/07, which was the first year of the programme. (Note. These figures assumed a cost of NZ$350/day in 2012). Deer density was c. 6.5 deer per km^2 in that year, and the population was presumably close to carrying capacity in 2006/07given minimal previous hunting efforts.

The cost of deer control also varies hugely between open unforested areas and tall closed-canopy forest. In open areas, where deer lack cover, aerial hunting is highly effective in rapidly reducing deer density. Between 1969 and 1984, commercial hunters in Fiordland reduced deer densities to zero in unforested areas above the timberline, but only by about 60% in contiguous forested areas (Nugent et al. 1987). There was no significant decline in the most fully forested sub area where there was an estimated density of 6.4 deer per km^2, which was 2–3 times higher than in less forested areas. The difficulty of deer control in large areas of tall closed-canopy forest is exemplified by a failure to reduce deer density at all in Waihaha, Pureora Forest Park, despite expenditure of about 150 hunting days over four years to kill 84 deer from an area of 32 km^2 (Forsyth et al. 2013). Given the decline in commercial hunting between the 1990s and early 2000s (Nugent & Forsyth 2021) the deer density probably exceeded the 6 deer per km^2 recorded nearby in the early 1990s (Nugent, Fraser, Asher et al. 2001). Forsyth et al. (2013) wryly concluded that 'reducing the abundances of deer in forests may require substantially more control effort than is currently believed.' Given current broad evidence for increases in the abundance of ungulates nationally (Moloney et al. 2021), the issue of their effects, management and costs or benefits of control is an area of active debate (e.g. Ramsey et al. 2017; Leathwick & Byrom 2023).

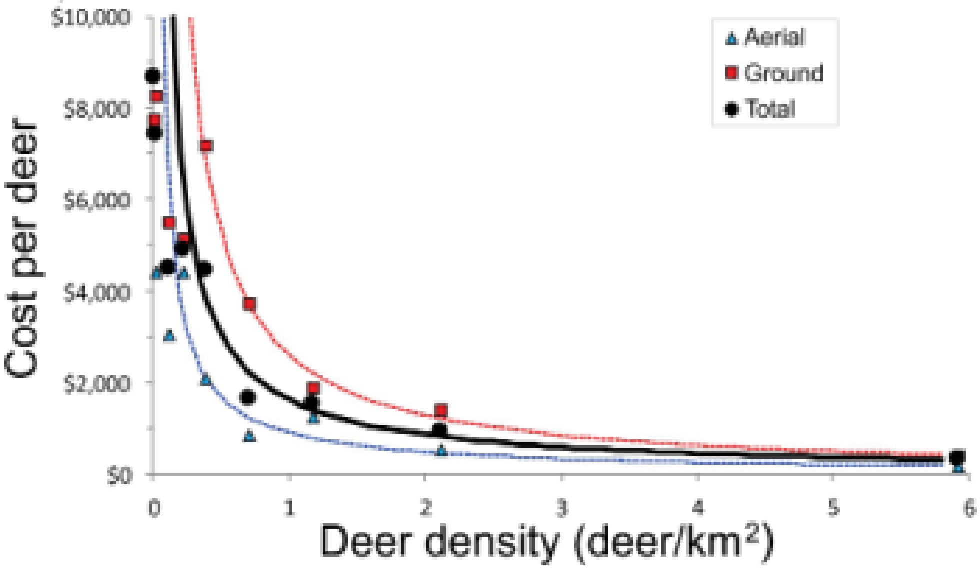


Figure 15. Direct operational costs for aerial and ground-based hunting (in NZ$ in 2012) per deer killed versus deer density for aerial hunting, ground hunting and overall, during the 2007–2014 eradication of deer from Secretary Island, Fiordland. (Source: Macdonald et al. 2019 Figure 3 © 2019 IUCN, International Union for Conservation of Nature and Natural Resources.)

Cost of increasing sequestration of forest C through deer control: Combining the density–impact curves for forest areas (Figure 13) with the density–cost curves (Figure 15) suggests that small reductions in deer density from carrying capacity could be achieved at low cost compared to eradication. These reductions could substantially increase the regeneration of marginally palatable trees that could eventually (over decades or even centuries) grow into major C stores. The reductions would not initially stop any current decline in forest C caused by a historic imbalance between accumulation and loss of C, and would not reduce all browser impacts in kāmahi-podocarp forest unless they were coupled with possum control. This suggests that the greatest imperative is to first reduce high deer densities in successional landscapes to secure C benefits, and in closed canopy forest to insure against future disturbances (where it could slow recruitment of canopy tree species).

Much larger reductions to just 1–2 deer per km^2 would be needed to allow regeneration of the tree species most preferred by deer. The cost of the initial reduction to near zero densities is likely to approach the cost of complete eradication, and the reduction would then need to be maintained through ongoing control in perpetuity to prevent immigration and population recovery. Again, the increase in forest C would be slow and only partial without possum control.

We assume that increases in forest C could attract carbon credits through additionality (discussed in Holdaway et al. 2012; Hackwell & Robinson 2021). However, the relatively slow expected increase in biomass of deer-preferred trees means most economic value of that increase would not accrue until far into the future. This means that the present value of those distant-future credits will be heavily discounted, whereas the costs of the initial deer density reduction will scarcely be discounted at all, and the ongoing costs of maintaining the low density be only modestly discounted for the first decade or so. Any potential benefits of possum control to C sequestration are likely to be realised much more quickly than for deer (e.g. by immediately reducing mortality rates of large trees), and so be far less prone to having a greatly discounted present value. Economic modelling could be used to predict whether the net present value of deer control was likely to be positive. However, at present neither the costs nor benefits can be confidently predicted.

Cost of reducing direct emissions by deer. Hackwell and Robinson (2021) (citing Holdaway et al. 2012) suggest that wild deer cause direct carbon losses of up to 0.49 tC per deer per year as a result of their consumption of foliage. That seems high, given the reported dry matter (DM) intake of 1.8 kg per deer per day of lucerne hay (with DM digestibility of 55%) recorded for c. 97 kg captive red deer feeding on lucerne hay (Domingue et al. 1991). Wild deer would be substantially smaller than that (especially fawns and fallow, sika, and white-tailed deer). These figures suggest deer probably metabolise in the order of 0.36 t of foliar DM annually, which equates to 0.14 tC per deer per year. In large forest areas, much of the foliage consumed is fallen leaves from broadleaved species that would have largely decayed within a year (see Hoorens et al. 2013). The actual net losses therefore appear likely to be less than 0.1tC per deer per year. However, a significant proportion of deer emissions are methane rather than CO_2. Farmed deer are assumed to emit 22.9 kg of methane (c. 0.5 tCO_2e) per deer per year ; MPI inventory 2022).

Can those emissions be cost effectively reduced by killing deer? Assuming wild deer in most New Zealand populations have average age of 3–6 years (based on the age distributions of hunter-killed deer; Nugent, Fraser, Asher et al. 2001), that suggests life-time methane emissions in the range of 1.5–3.0 tCO_2e per deer. Further assuming that the killing of deer by hunters will (on average) halve their life expectancy, would reduce their lifetime emissions by 0.75–1.50 tCO2e per deer. At 31 May 2023 carbon credit prices of NZ$54 per tCO2e, that equates to $40–80/deer. The kill and effort data from Forsyth et al (2013) for the Waihaha forest indicate a kill rate of 0.56 deer per day assuming a 6-hour hunter day and excluding travel time. Contract hunters currently cost NZ$600-700/day (J. Parkes, Kurahaupo Consulting, pers. comm May 2023), suggesting a current cost per kill well in excess of NZ$1000 excluding any additional costs of travel or emissions related to management. The implication is that it will rarely be cost effective to kill deer using ground hunting in tall forest area solely to reduce their direct emissions.

3 Summary of main findings

Key previous conclusions

Holdaway et al. (2012) developed criteria for identifying what areas are most likely to result in measurable C gains from wild animal management. These criteria included: high population density and associated effects (like methane production) in broadleaved forests with palatable species in the understorey (because this offers an opportunity to slow or limit canopy tree regeneration); increased canopy tree mortality (primarily assumed to be associated with possums); and where seed or propagule sources are limited. Their key conclusions from that study are noted below.

The magnitude of responses in terrestrial C stocks to wild animal control is small relative to stock size.

Responses are driven mostly by indirect effects and multiple mechanisms, often causing both positive and negative effects on C stocks at the same time.

There are few data linking individual or population changes in plants to community-level C.

Available data are scarce, but suggest that herbivores can have positive, negative or neutral effects on C.

Despite this complexity, the largest gains are likely to be in areas of highly palatable early successional vegetation having high animal abundance.

Their concluding remarks are consistent with the evidence reviewed here. Holdaway et al (2012) wrote: 'In general, carbon gains are likely to be small, occur through complex indirect mechanisms, and difficult to quantity in practice. However, significant carbon gains may occur in certain situations such as when herbivore control promotes the establishment of high-biomass woody species (in successional forests).' And 'While carbon gains from herbivore control are unlikely to provide a silver bullet for conservation funding at a national scale, there is potential in certain areas of New Zealand's indigenous vegetation for both conservation benefits and carbon gains to go hand in hand.'

Main findings of this review

There was no overall decline in forest C in indigenous forests within the 2002–2014 period (Paul et al. 2021). However, there was a significant decline in C in kāmahi-podocarp forest, and possibly some smaller declines in other kāmahi forest types, which together comprise a fifth of tall forest in New Zealand. Given the reported overall balance in total C stocks between measurement periods, this implies that there was an increase in C in other indigenous forest types, despite the presence of deer and other introduced mammals in most areas.

As there is no published assessment of trends in forest C since 2014, it is not known whether the decline(s) in kāmahi forest types are continuing. The cause(s) of the decline(s) have also not yet been identified. However, it seems unlikely that much, if any, of the recorded declines reflect the removal of previously abundant deer-preferred plant biomass from the browse tier during the initial colonisation of forests by deer because that introduction happened 50–150 years ago in most areas. The biomass declines are more likely to reflect some mix of several processes.

1 Natural mortality of outcompeted or senescent deer- or deer- and possum-preferred tree species without sufficient recruitment and growth of replacements because deer prevent their regeneration.
2 Natural mortality of outcompeted or senescent trees of species not preferred by deer without sufficient recruitment and growth of replacements because of natural changes in forest composition (e.g. conifer to broadleaved forest transitions)
3 Ongoing increased mortality rates of kāmahi, tōtara, and other possum-preferred trees caused by current and ongoing possum browsing.
4 Continued decay of coarse woody debris (standing and fallen) from large trees that were killed by possums some decades previously.
5 Loss of C through mechanisms other than deer- or possum-induced changes in forest composition.

Of the first four processes, only the first could potentially be ameliorated by deer control.

In kāmahi-podocarp forests, much of the plant biomass is typically stored in a relatively small number of large podocarp trees or rātā (*Metrosideros spp)* most of which are not affected at all by deer whereas one of them (Hall's tōtara) can be heavily affected by possums. Overall, most of the biomass is often not preferred by deer or possums, which consume only 1%–3% of foliage. However, continued browsing by deer and possums is likely to result in progressive reductions (over many decades or centuries) of biomass of preferred species such as broadleaf and kāmahi. Both of these species can regenerate epiphytically and in areas inaccessible to deer, so are unlikely to be completely eliminated.

Whilst uncontrolled deer reduce the regeneration of preferred species, they also create light and space for enhanced regeneration of unpreferred species (most notably pepperwood/horopito and, importantly, the podocarps). Similarly, the thinning of kāmahi canopies by a mix of increasing tree age (due to non-replacement) and possum browsing seems likely to further enhance regeneration of least shade-tolerant non-preferred tree species. There is therefore potential for development – in the absence of deer and possum control and on a scale of centuries or millennia – of podocarp-rich browse-resistant forests with substantially increased forest C stores. That process is likely to have already occurred to some extent in forests where deer have long been present, and it seems unlikely that deer (or possum) control would reverse any such changes in overstorey composition quickly.

The reversibility of deer and possum effects on forest C are both timescale- and density-dependent. For deer, changes in forest C after intensive deer control would result mainly from less impeded growth of seedlings to maturity over many decades or centuries. In contrast, possum control is likely to result in a near-total and immediate reduction in foliage use accompanied by the mortality of high-C canopy trees (although the loss of C from already dead trees would continue for some decades.)

For deer, moderate reductions in density from carrying capacity should allow regeneration of most of the least preferred species. However, near-total reductions or eradications are likely to be needed to allow regeneration of the most preferred species, most of which have trivial contribution to C in old-growth forests but which could have key functional roles in succession. For possums, large-scale control is always undertaken by aerial poisoning which typically achieves near-total reductions in density and can significantly reduce deer numbers. The frequency of repeat possum control is likely to be determined by an assessment of the density at which the recovering population resumes browsing of foliage at levels that threaten tree survival.

The assumption that management of deer aimed at maximising forest C sequestration will automatically also benefit conservation may not always be valid, particularly if conservation objectives are focused on fully restoring deer-preferred species. Management of deer at moderate intermediate densities could in some areas allow large-tree (high C) species not highly preferred by deer to increase in relative abundance.

Carbon emissions by wild deer are overall small, probably substantially less than 0.15 tC ha^{-1} yr^{-1} on average. The value of carbon credits from eliminating those emissions might equate to between NZ$3 and NZ$7 per hectare per year. However, elimination of those emissions by eradication of deer over large areas is currently not feasible because immigration of deer from elsewhere cannot be prevented easily. The present value of annual cost of sustained control of deer to low densities is highly likely to exceed the present value of carbon credits that will mostly accrue far into the future.

Key questions for the Game Animal Council (GAC)

It is clear that there are multiple drivers of carbon sequestration in indigenous forests. It is equally clear that the data and models currently available do not provide a clear understanding of those complex processes and the interactions between them. That undermines confidence that deer managers can make robust decisions about if, where and when control of deer might be cost effective in reducing carbon emissions and sequestration.

Some crucial unanswered questions (in addition to Table 2) are listed below.

Are total C stocks in indigenous forest still unchanged nationally (i.e. not different from zero)? For identified forest-types in which declines in C stocks were observed (kāmahi-podocarp forest), have declines continued since the 2002–2014 assessment, and if so, why?

What are the main contributors to changes in forest C and are they ongoing? The key possibilities of greatest interest to the GAC are changes resulting from: (i) regeneration suppression of deer preferred tree species; (ii) gradual (decades-long) decay of dead trees killed by possums (and is that possum-induced mortality ongoing or historical?); (iii) increased recruitment of long-lived large tree species not preferred by deer (and also of those not preferred by either deer or possums).

What deer densities currently prevail? Ideally, this needs to be known in relative terms of closeness to carrying capacity (rather than absolute deer abundance per se) because this determines deer use of the edible but least preferred tree species.

4 Recommendations

Several recommendations emerge from our synthesis. We recommend the GAC take the following actions.

Seek assessment of the trends in forest C based on the most recent remeasurement period of the LUCAS plots. These data are not yet publicly released, but provide crucial information required to evaluate if there are continued trends in C change within indigenous forests. Similarly, the GAC should consider a formal request to make this information publicly available, including decisions surrounding plot selection and data analyses that are essential but not currently provided or easily obtained from the Ministry for the Environment.

Support additional interrogation of the LUCAS data to understand better where positive or negative changes in forest C can be confidently attributed to herbivore impacts, or to differences in sampling effort or analysis between sampling periods; or whether they are changing due to other drivers such as storms or other disturbances.

Support the maintenance and remeasurement of ungulate exclosures and permanent plots across different forest-types as the strongest long-term data available for understanding the potential effects of reducing ungulate populations on both biodiversity and C. For example, local-scale networks of permanents plots containing kāmahi forests (e.g. in Rakiura and Westland) coupled with estimates of ungulate and possum abundance could be used to understand long-term and local-scale effects of management. Ideally, some of the plots should be in areas where possums have been eliminated but deer are still present to help separate possum and deer effects.

Support the development of forest canopy succession models capable of predicting the managed and unmanaged impacts of deer, possums, and of possums and deer combined and the timescales over which these impacts occur. These are needed to assess the cost-effectiveness of potential management action.

Insist DOC, the Ministry for Primary Industries and the Ministry for the Environment (the 'natural resources cluster') collect and maintain information on the distribution and trends in abundance of mammal species. Given the importance of successional forests for C sequestration, biodiversity and animal management, extending data collection to private and Māori lands will be needed. This is essential for understanding both management effectiveness, population responses, and the consequences for forest ecosystems.

Seek clarification on how mammal management is being prioritised for both biodiversity goals and carbon sequestration. This is needed to set clear goals for management, but also where both C and conservation gains could be made from reducing mammal densities. For GAC members, additional consideration of game animal condition under different management regimes will be of interest. Of particular interest is the need to identify locations in which game animals are near carrying capacity and preventing canopy replacement (i.e. situations in which conservation, C storage, and hunter interests are most likely to align).

Seek full C accounting of management and responses. This is needed to evaluate the net effects on emissions. Current consultation on the ETS (see https://www.beehive.govt.nz/release/nz-ets-review-begins-alongside-redesignpermanent-forest-category) seems to be clear that emissions reduction and incentives for C sequestration will need to be separately considered, but linked.

Work to help fill some fundamental capacity gaps for understanding animal ecology, management and impacts in New Zealand that limit the knowledge needed to understand when and where management of animals is needed for C, biodiversity or other goals. Increased training and expertise in animal ecology and management is required either through university training or collaborating with international experts.

Develop a clear position for GAC on the maintenance of biodiversity and ecological integrity should be developed, particularly given the upcoming national policy on indigenous biodiversity, and forthcoming policy on ecological integrity.

Undertake more strategic, long-term planning for management of game animals for C, biodiversity or other goals. This is not a short-term (<5 yr) undertaking, and should be considered as part of implementation of te Mana o te Taiao and the newly launched National Policy Statement for Indigenous Biodiversity in which regional biodiversity plans are to be developed (see https://environment.govt.nz/acts-and-regulations/national-policy-statements/national-policy-statement-for-indigenous-biodiversity/).

These recommendations should provide additional evidence or information required for decisions of when and where control of game and other mammals is needed for a goal of maintaining or increasing C stocks in indigenous forests.

5 Acknowledgements

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6 References

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Appendix A – Published national carbon estimates from LUCAS plots by forest types

Data from Paul et al. (2021) over the first two sampling periods (2002-2007 and 2009-2014). The most recent measurement is completed but not yet analysed. Source: reproduced from Paul et al. 2021 under Creative Commons CC BY license.

Table 5 Estimates of total carbon stocks for each cycle by tall forests and regenerating forests (shrublands) and their assigned alliances as defined by Wiser (2016). Plus-or-minus values are estimated 95% confidence intervals calculated using two methods; the first method is based solely on sampling variation between plots (CI_s); and the second method combines the effects of sampling variation and prediction uncertainty ($CI_{s\&p}$)

Tall forests and their alliances	***N***	**Stocks in 2002–2007**			**Stocks in 2009–2014**		
		tC·ha^{-1}	CI_s	$CI_{s\&p}$	**tC·ha^{-1}**	CI_s	$CI_{s\&p}$
Beech-Broadleaved Forest							
Kāmahi-hardwood forest	75	291.6	± 25.6	± 29.5	298.0	± 26.6	± 30.4
Silver beech-broadleaf forest	70	261.7	± 22.9	± 26.4	262.7	± 23.8	± 27.2
Silver beech-red beech-kāmahi forest	72	360.5	± 29.5	± 34.6	350.1	± 26.4	± 31.7
Subtotal	217	304.1	± 16.2	± 22.2	303.3	± 15.5	± 21.7
Beech-Broadleaved-Podocarp Forest							
Kāmahi-Southern rata forest and tall shrubland	38	205.9	± 37.1	± 38.5	199.3	± 35.7	± 37.1
Pepperwood-hardwood forest and successional shrubland	50	286.7	± 35.4	± 38.2	295.0	± 38.5	± 41.2
Kāmahi forest	59	306.0	± 29.8	± 33.5	296.0	± 30.0	± 33.4
Kāmahi-silver fern forest	42	214.2	± 30.4	± 32.2	198.2	± 32.3	± 33.8
Subtotal	189	260.3	± 17.2	± 21.6	255.6	± 18.1	± 22.2
Beech Forest							
Black/mountain beech forest (subalpine)	28	191.1	± 20.8	± 22.9	203.3	± 23.5	± 25.6
Black/mountain beech-silver beech forest/subalpine shrubland	54	244.9	± 40.8	± 42.6	251.6	± 41.6	± 43.5
Black/mountain beech forest	34	178.3	± 29.7	± 31.0	185.4	± 34.3	± 35.5
Silver beech-red beech-black/mountain beech forest	28	323.2	± 36.7	± 40.1	321.9	± 39.5	± 42.7
Silver beech forest with mountain lacebark and weeping matipo	11	201.5	± 103	± 103	225.7	± 152	± 153
Hard beech-kāmahi forest	21	330.6	± 69.4	± 71.4	324.1	± 78.1	± 79.7
Subtotal	176	243.2	± 20.3	± 23.6	250.1	± 20.9	± 24.4
Broadleaved-Podocarp Forest (including kauri)							
Kāmahi-podocarp forest	86	316.4	± 43.8	± 46.6	301.7	± 41.5	± 44.2
Mahoe forest	61	169.4	± 34.8	± 35.9	166.4	± 29.8	± 31.0
Tawa forest	82	248.6	± 32.2	± 34.5	250.6	± 32.6	± 34.9
Silver fern-mahoe forest	64	147.8	± 19.5	± 20.8	146.1	± 21.3	± 22.5
Pepperwood-fuchsia-broadleaf forest	21	149.1	± 44.0	± 44.6	144.0	± 39.6	± 40.2
Mataī forest	7	178.1	± 153	± 153	202.8	± 209	± 209
Towai-tawa forest	9	240.6	± 121	± 122	260.6	± 136	± 137
Subtotal	330	217.6	± 16.1	± 19.4	216.2	± 15.8	± 19.1
Regenerating forest and shrublands and their alliances							
Shrublands							
Kānuka shrubland with Coprosma and prickly mingimingi	24	75.5	± 18.3	± 18.7	85.5	± 22.6	± 23.0
Grey scrub with kanuka	29	31.3	± 12.4	± 12.5	34.0	± 14.1	± 14.2
Mānuka shrubland	4	22.4	± 58.4	± 58.4	23.6	± 58.1	± 58.1
Matagouri shrubland[a,b]	1	7.6			8.6		
Turpentine scrub-*Gaultheria* montane shrubland	9	6.5	± 11.7	± 11.7	6.3	± 13.0	± 13.0
Gorse shrubland with cabbage trees[a,b]	5	18.3			9.1		
Subtotal	72	42.8	± 10.1	± 10.4	45.5	± 11.7	± 11.9

Table 6 Estimates of carbon stock change in the AGB, BGB and dead wood pools between 2002 and 2007 and 2009–2012 in the tall forest and regenerating forest group as defined by Wiser et al. (2011) and their alliances. Changes in stock values in bold differ significantly from zero. Plus-or-minus values are estimated 95% confidence intervals calculated using two methods; the first method is based solely on sampling variation between plots (CI_s); and the second method combines the effects of sampling variation and prediction uncertainty ($CI_{s\&p}$)

	Change in stocks			
Tall forests and their alliances	***N***	**tC·ha^{-1}**	CI_s	$CI_{s\&p}$
Beech-Broadleaved Forest				
Kāmahi-hardwood forest	75	2.3	± 6.9	± 6.9
Silver beech-broadleaf forest	70	1.1	± 4.6	± 4.6
Silver beech-red beech-kāmahi forest	72	0.8	± 7.4	± 7.4
Subtotal	217	1.4	± 3.7	± 3.7
Beech-Broadleaved-Podocarp Forest				
Kāmahi-Southern rata forest and tall shrubland	38	−0.4	± 3.7	± 3.7
Pepperwood-hardwood forest and successional shrubland	50	1.0	± 7.8	± 7.8
Kāmahi forest	59	−2.4	± 6.4	± 6.4
Kāmahi-silver fern forest	42	−3.0	± 6.6	± 6.6
Subtotal	189	−1.1	± 3.3	± 3.3
Beech Forest				
Black/mountain beech forest (subalpine)	28	4.8	± 5.2	± 5.2
Black/mountain beech-silver beech forest/subalpine shrubland	54	−1.0	± 4.4	± 4.4
Black/mountain beech forest	34	3.0	± 6.6	± 6.6
Silver beech-red beech-black/mountain beech forest	28	1.5	± 9.1	± 9.1
Silver beech forest with mountain lacebark and weeping matipo	11	1.3	± 10.3	± 10.3
Hard beech-kāmahi forest	21	−3.4	± 9.9	± 9.9
Subtotal	176	0.9	± 2.7	± 2.7
Broadleaved-Podocarp Forest (including kauri)				
Kāmahi-podocarp forest	86	−8.0	± 6.1	± 6.1
Mahoe forest	61	2.4	± 4.8	± 4.8
Tawa forest	82	−0.6	± 4.9	± 4.9
Silver fern-mahoe forest	64	−2.2	± 6.8	± 6.8
Pepperwood-fuchsia-broadleaf forest	21	1.6	± 9.9	± 9.9
Mataī forest	7	6.7	± 19.3	± 19.3
Towai-tawa forest	9	0.2	± 22.7	± 22.7
Subtotal	330	−2.0	± 2.7	± 2.7
Regenerating forest and shrublands and their alliances				
Shrublands				
Kānuka shrubland with Coprosma and prickly mingimingi	24	8.3	± 5.6	± 5.6
Grey scrub with kanuka	29	2.9	± 2.8	± 2.8
Mānuka shrubland	4	1.1	± 3.1	± 3.1
Matagouri shrubland	1	1.0		
Turpentine scrub-*Gaultheria* montane shrubland	9	−0.4	± 1.4	± 1.4
Gorse shrubland with cabbage trees	5	−9.2	± 16.0	± 16.0
Subtotal	72	3.3	± 2.6	± 2.6

Appendix B – Glossary of species names used in this report.

Common name(s)	Scientific name
brushtail possum	*Trichosurus vulpecula*
chamois	*Rupicapra rupicapra*
domestic cat	*Felis catus*
goats (feral)	*Capra aegagrus hircus*
Himalyan tahr	*Hemitragus jemlahicus*
mice	*Mus musculus*
pigs	*Sus scrofa*
rats (ship rat)	*Rattus rattus*
red deer	*Cervus elaphus*
sika deer	*Cervus nippon*
stoat	*Mustela erminea*
white-tailed deer	*Odocoileus virginianus*
black maire, maire rau nui	*Nestegis cunninghamii*
black pine, mataī	*Prumnopitys taxifolia*
broadleaf, kāpuka	*Griselinia littoralis*
brown pine, miro	*Prumopitys ferruginea*
creek fern, kiwakiwa	*Blechnum fluviatile*
crown fern, piupiu	*Blechnum discolor*
puahpou (five-finger, puahpou)	*Pseudopanax arboreus*
kāmahikamahi, tawhero	*Weinmannia racemosa* (*Pterophylla racemosa*)
lancewood, horoeka,	*Pseudopanax crassifolius*
long-leaved mapau, toro	*Myrsine salicina*
marbleleaf, putaputawētā	*Carpodetus serratus*
mountain beech, tawhai rauriki.	*Nothofagus solandri var. cliffortioides*
NZ ash, tītoki	*Alectryon excelsus*
NZ cedar, pāhautea	*Libocedrus bidwillii*
NZ olive, hīnau	*Elaeocarpus dentatus,*
pepperwood, (horopito)	*Pseudowintera colorata*
pokaka, pōkākā	*Elaeocarpus hookerianus*
quintinia, tāwheowheo	*Quintinia serrata*
red matipo, māpou	*Myrsine australis*
red pine, rimu	*Dacrydium cupressinum*
rough tree fern, wheki	*Dicksonia squarrosa*
seven finger, pate (seven finger)	*Schefflera digitata*
southern rātā, rātā	*Metrosideros umbellata*
tea tree, kānuka	*Kunzea ericoides*

Common name(s)	**Scientific name**
tea tree, mānuka	*Leptospermum scoparium*
totara, Hall’s tōtara	*Podocarpus spphallii*
tree fuchsia, kōtukutuku	*Fuschia excorticata*
whitey wood, māhoe	*Melicytus ramiflorus*
wineberry, makomako	*Aristotelia serrata*
wire vine, pōhuehue	*Muehlenbeckia complexa*