Implications of experimental design on the detection of herbivore impacts on carbon stocks in a broadleaved-hardwood forest

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CONTENTS

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Abstract

We investigated whether plots established for the Thames Coast Flood Protection Project (TCFPP) could also be used to estimate the impact of herbivores on carbon storage in warm-temperate secondary forests. To establish baseline whole-ecosystem carbon stocks, in 2008/09 we measured coarse woody debris, forest floor and soil carbon pools of 32 permanent forest plots and eight paired exclosure and control plots (20 × 20 m) that had been established in 2005/06. To estimate total carbon stock at the initiation of intensive herbivore control, we combined these data with stem measurements collected at the time of plot establishment. Total carbon stocks (216.3 ± 9.7 t C/ha) in each of five pools were estimated to be: above-ground live—74.7 ± 5.3 t C/ha; below-ground—18.7 t C/ha; coarse woody debris—10.3 ± 1.9 t C/ha; forest floor (fine woody debris + litter + fermentation-humic horizon)—18.8 ± 1.7 t C/ha; and soil (0–30 cm)—93.9 ± 4.3 t C/ha. To provide guidance for future studies, we also conducted a power analysis investigating a range of plausible effect sizes and background variability. Our results indicate that the current plot design is capable of detecting only extremely large (≥ 200%) differences in sequestration rates and will be unable to attribute any changes detected to decreased herbivory unless suitable reference plots can be identified. Future studies of carbon storage in forests should be designed as landscape-scale manipulations with appropriate non-treatment plots and will likely require more plots than are required for studies of tree growth or vegetation composition.

Keywords: carbon sequestration, exclosures, succession, herbivores, pest management, possum control, goat control, sampling design

1. Introduction

Carbon (C) has long been studied as a standard 'ecosystem currency' useful for basic research on energy flows within ecological systems. More recently, carbon storage has attracted political attention as a possible mechanism for mitigating greenhouse gas emissions. Public conservation lands are currently estimated to contain a total of 2578 Mt of C (9461 Mt CO_2 equivalent) across vegetation and soil pools (Mason et al. 2012). This represents the largest carbon stock administered by a single body in New Zealand. Small changes in per-hectare stocks resulting from critical management decisions could, therefore, have a large impact on national totals. Existing research suggests that herbivores play a critical role in ecosystem processes, especially in their mediation of above- and below-ground interactions (Wardle & Bardgett 2004). However, the precise impact of New Zealand's introduced herbivores on forest carbon is difficult to determine (Burrows et al. 2008; Peltzer et al. 2010). Understorey communities, which can respond dramatically to herbivore exclusion (Allen et al. 1984), form such a small proportion of the ecosystem carbon budget that they are excluded from calculations. There is some evidence for a decrease in tree density in the presence of non-native herbivores (Allen et al. 1984; Wardle et al. 2001), but it is also possible that there are instances where the presence of herbivores could increase carbon storage. For example, herbivore-triggered shifts to less palatable species may result in more recalcitrant litter, and thus a net increase in soil carbon (Wardle & Bardgett 2004). The design of experiments to measure the effects of wild animal control on carbon stocks and/or rates of sequestration must therefore cater for complex above- and below-ground interactions, and be able to detect both increases and decreases in carbon at the ecosystem-scale.

Concern about the impact of introduced herbivores on the New Zealand vegetation is not new (e.g. Kirk 1920; Chavasse 1955). However, despite heavy government investment in control programmes, forest overstorey composition and structure do not always respond rapidly or strongly to changes in herbivore populations (Bellingham et al. 1999; Coomes et al. 2003). There are many possible reasons for this; for example, native forests are typically under threat from more than one introduced herbivore, and control of one may increase the populations of another (Coomes et al. 2003); some introduced herbivores, such as possums (*Trichosurus vulpecula*), have indirect impacts on vegetation through their effects on populations of native herbivores and seed dispersers, particularly birds (Clout & Eriksen 2000); and seedling growth and establishment is a function not just of herbivore pressure, but also reflects environmental conditions, seed availability and competition with other plants (Bellingham & Allan 2003). Previous work has shown that although some plant communities respond rapidly to herbivore control (Rogers 1997; Nugent et al. 2010), the recovery of others can take decades after herbivore populations are reduced (Tanentzap et al. 2009; Bellingham et al. 2010). Several authors have suggested that vegetation recovery may require intensive control to be sustained for many years (e.g. Payton et al. 1997; Coomes et al. 2003; Tanentzap et al. 2009).

The Thames Coast Flood Protection Project (TCFPP) is a collaborative project between Environment Waikato, the Thames-Coromandel District Council, the Department of Conservation (DOC) and the Hauraki Maori Trust Board. The Project's main aims are to improve the forest condition and address flood risks on the Coromandel Peninsula. We selected the TCFPP as a test case for investigating changes in carbon pools under an operational animal control programme because it operates at a broad spatial scale, includes control of multiple species, and is committed to regular monitoring of the effectiveness of the control operations and to sustained control at a decadal time scale. Forty-eight already-established plots (see section 3.1) provided data for estimating baseline carbon stocks in the TCFPP. Establishing a clear pre-treatment baseline is critical in repeated-measures designs (Foster 1992; Allen et al. 2003), which have clear advantages over designs that are replicated only in space (Coomes et al. 2002; Allen et al. 2003), given the possibility that herbivore impacts on ecosystem carbon may be relatively subtle in established forests (Burrows et al. 2008). In addition, because primary data on carbon

sequestration in New Zealand forests are lacking, we also investigated the minimum number of permanent plots required to detect the likely level of change in carbon stocks as a result of wild animal control, using Monte Carlo simulations.

Carbon inventories for forests customarily apportion carbon stocks into five pools: above-ground live (AG), below-ground live (i.e. roots; BG), coarse woody debris (CWD), litter and soil (Coomes et al. 2002). However, at present, BG biomass is usually estimated as a proportion of the AG biomass (Hall et al. 2001). Given the possibility that herbivores influence partitioning of carbon within litter and soil pools and, consequently, the rate of turnover of that carbon (Coomes et al. 2003; Peltzer et al. 2010), we further subdivided the litter pool into fine woody debris (FWD), litter proper and fermentation-humic (FH) layers, and the mineral soil into 0–10 cm, 10–20 cm and 20–30 cm depths (Stevenson & St John 2009). For clarity, we refer to the combined FWD, litter and FH pools as the 'forest floor' pool for the rest of this report. We hypothesised that the AG carbon pool would increase with wild animal control and that the litter, FH and FWD pools would be more sensitive to wild animal control than the mineral soil. Thus, tracking changes in these intermediate pools would be key to understanding the complex interactions between AG and BG processes. Note that the present study only reports carbon stocks in all pools at the initiation of wild animal control. Future remeasurement will be required to test our hypotheses.

1.1 Objectives

In using data from the 48 pre-existing plots in the TCFPP operational area, and collecting additional forest floor and soil carbon data we aimed to:

- Estimate carbon stocks in AG, BG, CWD, FWD, litter and FH pools, and in the soil pools (0–10 cm, 10–20 cm and 20–30 cm depths)
- Determine the sampling intensity required to estimate carbon stocks and changes to those stocks for various levels of confidence
- Establish a baseline for future interpretation of changes in carbon stocks, where they may be attributable to goat (*Capra hircus*) and/or possum control

1.2 The TCFPP and animal control

The TCFPP operational area totals 49 123 ha of public conservation land and private land on the western side of the Coromandel Peninsula, North Island, from the Kauaeranga Valley in the south to the Koputauaki Bay in the north. The vegetation in this area is mostly tawa (*Beilschmiedia tawa*) broadleaved forest with some emergent rātā (*Metrosideros robusta*) and kauri (*Agathis australis*). For animal control purposes, the area has been divided into three blocks (Fig. 1):

- Southern block—Kauaeranga Valley–Te Puru (19 409 ha)
- Central block—Te Puru–Manaia (13 918 ha)
- Northern block—Manaia–Koputauaki Bay (15 796 ha)

DOC has been conducting possum and goat control as part of the TCFPP (Table 1).

Aerially applied 1080 and ground-based methods are used for possum control, with each TCFPP block recommended for three-yearly control initially (Broekema 2007). To assess the success of the control programme, possum numbers are monitored pre- and post-control using approximately 600 trap lines (F. Buchanan, DOC, pers. comm.) and the residual trap-catch index (RTCI, National Possum Control Agencies 2008). Control operations aim to reduce possum numbers to ≤ 5% RTCI. Canopy condition is also monitored pre- and post-possum control using palatable indicator species on foliar browse index (FBI) plots (Broekema 2007, 2008), and from permanent forest plots (20 × 20 m) and exclosures (Fig. 1).
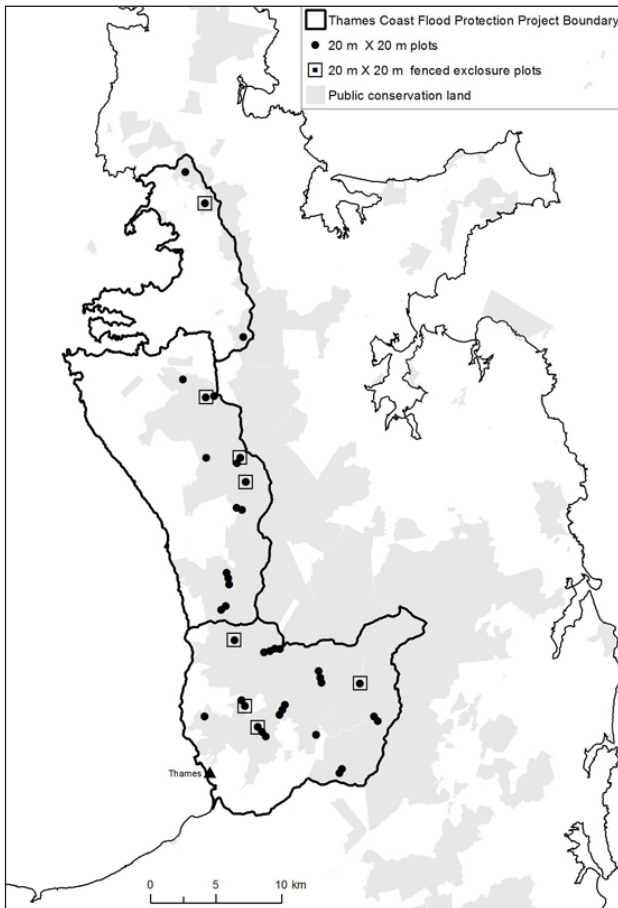
Figure 1.   Location of the 48 permanent forest plots in the TCFPP operational area (control plots adjacent to exclosures are not distinguishable at this scale. (Map courtesy of I. Broekema, Waikato Conservancy, DOC).
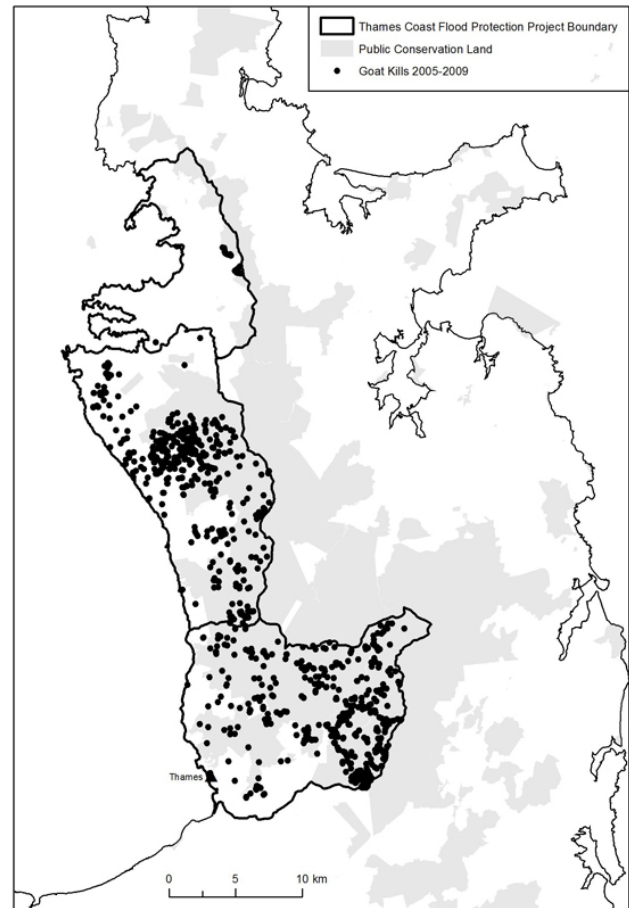
Figure 2.   Location of all goats (*Capra hircus*) killed between 2005 and 2009 and goat-hunting blocks. (Map courtesy of P. Schneider, Waikato Conservancy, DOC).

Goats are intensively controlled by systematic team hunting with dogs (the 'Wall of Death' method). To ensure thorough coverage, each hunt is tracked using a GPS unit to record its location (and the location of any goat kills; Fig. 2) and so that any missed areas can be identified and revisited. Tallies are kept of goats killed per man-day for each goat block hunted (F. Buchanan, DOC, pers. comm.)[1]. Between July 2005 (when official hunting began) and June 2008, the TCFPP goat hunting team removed a total of 2272 goats from 34368 ha (see Table 1).

Pigs (*Sus scrofa*) are present throughout the TCFPP and the DOC goat-hunting team considers that present pig numbers are high, most likely as a result of domestic pigs being released in the bush (I. Broekema, DOC, pers. comm.). There are no data on hunting and/or control history and population trends for pigs. There are reportedly no deer in the area.

1.3   Power analyses and carbon sequestration

The power of a study is the probability that true treatment differences will be detected. Power depends on the magnitude of the change caused by a treatment (effect size), the variability of the effect from plot to plot, and sample size. In studies of rates (such as carbon sequestration), the length of time between successive measurements also plays a role. The observed variability in treatment effect is a combination of true differences in the rate from plot to plot (termed 'process

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[1]   Background information, summaries and maps of areas hunted and numbers of goats killed each year are presented in the Peninsula Project Animal Pest Control Programme Annual Report (DOC 2005, 2006, 2007, 2008). All goat-hunting data are held by the DOC Hauraki Area Office and are available on request.

Table 1. Possum (*Trichosurus vulpecula*) and goat (*Capra hircus*) control operations in the three blocks of the TCFPP (see also Figs 1 & 2). Figures for residual trap-catch indices (RTCIs) are given as pre- to post-control percentages, or just post-control percentages.

	SOUTHERN BLOCK 19 409 ha	CENTRAL BLOCK 13 918 ha	NORTHERN BLOCK 15 796 ha
Possums	**2005**: 12 854 ha, aerial 1080, RTCI 18.1% to 1.0%; 6555 ha, ground-based methods, RTCI 20.4% to 9.8%. **2006**: Mangurehu block, trapping, RTCI to 3.4%; Te Puru South block, trapping, RTCI to 8.2%; Lower Tararu block, trapping to 11.4%. **2008**: Most of block, aerial 1080, no usable comparative data; remainder of block (near townships, the coast and major waterways), ground-based methods, no usable comparative data.	**1995**: Small areas of northern part. **1999**: Small areas of northern part and area between Te Puru and Tapu. **2002**: Area between Te Puru and Tapu. **2003**: Small areas of northern part. **2006**: 7573 ha, aerial 1080, RTCI 12.3% to 1.4%; 6345 ha, ground-based methods, 11.9% to 2.7%.	**1994**: Area around line 30, ground-based methods, no usable comparative data. **2007**: Strip of DOC land, ground-based methods, no usable comparative data; area around line 30, ground-based methods, no usable comparative data.
Goats		**2005/06**: 8453 ha between Waiomu and Manaia, hunting (see text), 470 goats.	
	2006/07: 12 775 ha between Tararu and the 309 Road, hunting (see text), 1324 goats. **2007/08**: 13 140 ha between Manaia and Koputauaki Bay and in Kauaeranga Valley, hunting (see text), 478 goats.		

variability' or 'process error') and measurement error (Bolker 2008). In the short to medium term, a longer study does not affect variability in treatment effect due to process variability, but will diminish the effect of measurement error (as the magnitude of the effect increases). However, extremely long studies may increase both process variability (due to infrequent disturbances, e.g. cyclones) and measurement error (as loss of institutional memory and replacement of equipment makes exact replication of methods difficult).

In order to claim 'carbon credits' arising as a result of management of existing forests (currently covered by an Article not adopted by New Zealand under the Kyoto Protocol), it is necessary to demonstrate the forest sequestration rate in the absence of the specific forest management, such that 'additionality' can be shown to have directly resulted from the management intervention. Therefore, for herbivore control, it is first necessary to calculate carbon sequestration rates in the absence of control, as baseline data. Given the history of disturbance and human modification on the Coromandel Peninsula, it is unlikely that these forests are at equilibrium. However, few studies in New Zealand have measured carbon sequestration rates in natural systems, with or without pest control, so both of the key parameters for determining statistical power—potential effect size and variability of effect—are unknown. We used a Monte Carlo-type simulation to investigate the number of plots required to detect a change in carbon sequestration across a range of likely effect sizes and sample variability.

2. Methods

2.1 Plot establishment for the TCFPP

In 2005/06, 48 permanent forest plots (20 × 20 m) were established on 22 restricted-random transects (Allen 1993) located on public conservation land in the TCFPP area. The primary aim of establishing the permanent plots was to assess herbivore impacts on forest biodiversity and tree recruitment and mortality (Grove 2005). Regular remeasurements are scheduled for the understorey (five-yearly) and trees (ten-yearly).

For each of the three treatment blocks, the number of plots is proportional to the area of indigenous forest and shrubland on conservation land in that block. Because one objective of the TCFPP was to decrease soil erosion, the Tararu catchment in the Southern block, which is an Environment Waikato soil erosion monitoring site, was allocated additional vegetation monitoring plots. For each catchment, a 'back-up' exclosure site and transect were identified prior to researchers going into the field (Grove 2005).

Each transect runs from valley bottom to ridge top from a random origin along a watercourse (Allen 1993). There are 1–3 plots on each transect; the first plot is 50 m from the origin and subsequent plots are 500 m apart. If the origin was not in native bush, the first plot was located 250 m from the bush edge (transects 18, 19, 24, 27, 29, 31, 35 and 36). Plots were placed on the right-hand side of the transect, unless the plot location was dangerous or otherwise unsuitable, in which case the left-hand side was used. If both sides of the transect were unusable, then the transect was extended by 500 m; if that was not possible, a fourth plot was added to another transect; and if that was not possible, the 'back-up' transect was used (Grove 2005).

The 48 plots include eight fenced, ungulate-proof exclosure plots paired with eight unfenced control plots:

Exclosures: 15/3A, 19/1A, 22/2A, 24/1A, 28/2A, 29/1A, 31/1A, 36/1A

Controls: 15/3B, 19/1B, 22/2B, 24/1B, 28/2B, 29/1B, 31/1B, 36/1B

To place the paired plots, eight transects were randomly selected such that the number of transects per block was proportional to the block area. Along each transect, a control plot was randomly selected and then an exclosure plot was located 5 m from, and parallel to, it (Grove 2005). The fenced area was 22 × 22 m and fences were constructed after the design of John Knowlton (Grove 2005). Exclosure plots were required to have a slope of less than 25° within the plot, be comparable to the unfenced plot in landform, aspect, slope and canopy composition, and be reasonably accessible for construction and maintenance purposes. Prior to going into the field, a back-up plot on each transect and an alternate plot location were identified in the event that the plot establishment conditions could not be met (Grove 2005).

DOC reported that, in January 2009, goats were entering exclosure 29/1A after the fence had been damaged by a windfall. The damage was repaired just before the plot was measured in March or April 2009. However, the ground crew considered that goats could still gain access via a large leaning rātā tree (Chris Brausch, Bushworks Contracting, pers. comm.).

2.2 Data collection

2.2.1 Above-ground live carbon

Trees and other vegetation were measured at the time of plot establishment in 2005/06 using standard permanent-plot and Reconnaissance (Recce) methods (Allen 1992, 1993), with the exception of live tree ferns and dead standing trees, which were measured but not tagged.

2.2.2 Coarse woody debris

Coarse woody debris (CWD) was measured using protocols developed for the national land use and carbon analysis system (LUCAS) (Payton et al. 2004) in December 2008 – January 2009. Briefly, CWD was defined as material ≥10 cm in diameter and included trees and tree ferns, subdivided into dead standing trees (>1.35 cm tall), stumps (<1.35 cm tall) and fallen logs. For dead standing trees, diameter at breast height and height were recorded. For stumps and fallen CWD, the length was recorded only for the portion located in the plot and two sets of orthogonal widths were measured only for the portion that was ≥10 cm in diameter. Hollowness was noted and a decay class assigned to indicate state of decomposition.

2.2.3 Fine woody debris, litter, FH and mineral soil

Soil sampling was conducted concurrently with CWD measurement and followed a protocol developed for the WACEM programme (Stevenson & St John 2009). This protocol directly measures carbon in the FWD, litter, FH and 0–10-, 10–20 -and 20–30-cm soil horizons independently, and is optimised for detecting changes between paired and remeasured plots. It is also compatible with LUCAS. In brief, litter, FWD and FH samples were collected at 16 points on the plot and bulked. Litter was defined as distinct plant parts, insect and faecal material that is identifiable as not having undergone decomposition, and included pieces of wood 2.5–10 cm in diameter. FWD includes all twigs <2.5 cm in diameter. The FH pool included partially and fully decomposed organic material that was not readily identifiable. At 12 of the 16 sample points, a soil corer (65 mm internal diameter) was inserted to 10 cm to extract a short core. At the remaining 4 sample points, the corer was inserted to a depth of 30 cm and the entire sample used for determination of both bulk density and soil carbon in 10 cm sections. The uppermost 10 cm portion was pooled with the other 12 samples from the plot, homogenised and sub-sampled to approximately 1 kg.

2.3 Estimation of carbon stocks

The carbon stocks of five pools were estimated, following established practice: AG, BG, CWD, forest floor (combined FWD, litter and FH) and soil (Coomes et al. 2002). All calculations and analyses were done with the software package R, version 2.10. (R Development Core Team 2009).

As our aim was to estimate baseline carbon stocks prior to intensified wild animal control, we included data from all 48 plots (32 standard plots, 8 exclosures and 8 controls) in our calculations. If the TCFPP continues to experience difficulty conducting control operations in the Northern block, it may be more appropriate to consider the two standard plots and one exclosure control pair in the Northern block to represent a 'business as usual' control scenario for future assessments of change in carbon stocks.

2.3.1 Above-ground carbon in live trees

Total AG biomass for each tree was calculated from 2005/06 stem diameter data, using the following formula (Coomes et al. 2002):

$$AG = 0.0000598 \times \rho \times (dbh^2 \times ht)^{0.946} \times (1 - 0.0019 \times dbh) + (0.03 \times dbh^{2.33}) + (0.0406 \times dbh^{1.53}) \quad \text{(Eq. 1)}$$

where ρ = wood density (kg/m^3), dbh = diameter at breast height (cm), ht = tree height (m).

Species-specific wood densities were derived from Beets et al. (2009), supplemented with Russo et al. (2010). If neither source had a species-specific value, we used congeneric values (Beets et al. 2009; Russo et al. 2010), or life-form values (476 kg/m^3 for canopy trees, 197 kg/m^3 for tree ferns, 333 kg/m^3 for shrubs, 493 kg/m^3 for subcanopy trees; Beets et al. 2009) (Appendix 1).

Tree height was estimated using allometric equations developed by Richardson et al. (2009) from the LUCAS Natural Forest plots. These species-specific equations are of the form:

$$\text{Height} = \exp(a + b_1 \times \log(\text{dbh}) + b_2 \times \text{elevation}) \qquad \text{(Eq. 2)}$$

where dbh = diameter at breast height, elevation = height above sea level (m), and a, b_1 and b_2 are species-specific parameters. Six species in the WACEM data, with a total of 227 stems, were not modelled by Richardson et al. (2009). For each of these six species, we identified a species with similar growth habits and used that model to estimate heights. Substitutions were as follows: for *Geniostoma ligustrifolium* (182 stems) and *Toronia toru* (5 stems), we used parameters from *Coprosma robusta*; for *Pinus radiata* (2 stems) and *Syzygium maire* (2 stems), we used parameters from *Weinmannia racemosa*; and finally, for *Hakea saligna* (23 stems) and *H. sericea* (4 stems), we used parameters from *Ulex europaeus*.

The relationship between height and diameter is unreliable for two life-forms common in the Coromandel: tree ferns and lianes. Tree fern heights were measured by field crews (although two tree ferns had no measured height, so we substituted the mean height of all tree ferns recorded: 4 m). The heights of lianes were not measured, but instead estimated as half of the mean canopy height on the plot where they occured (aka mean plot height, *sensu* Allen 1993). We treated *Metrosideros robusta* as a tree and used the allometric equation from Richardson et al. (2009).

Finally, following established practice (e.g. Coomes et al. 2002), half of the tree biomass was assumed to be carbon. Carbon values for each tree were summed by plot and then corrected for plot slope by dividing the carbon stock estimate by the cosine of the slope angle.

2.3.2 Below-ground carbon in live trees

Below-ground carbon was estimated as 25% of the AG live pool (Coomes et al. 2002).

2.3.3 Carbon stocks in CWD

To avoid potential problems with double counting standing dead trees, we used the 2009 survey exclusively for our estimates of dead wood. Five logs in that survey were recorded with a decay status of '0', indicating a living tree touching the ground in two or more places. These trees were added to the AG pool.

For CWD, carbon is a function of the volume, stem density of the tree while alive and a decay-state modifier, which adjusts for the level of decay (Coomes et al. 2002).

The volume of standing dead trees was estimated as for living trees, using the equation:

$$V = 0.0000598 \times (\text{dbh}^2 \times l)^{0.946} \times (1 - 0.0019 \times \text{dbh}) \qquad \text{(Eq. 3)}$$

The volume of stumps was calculated useing the same formula, except that mean diameter of the top of the stump was used in place of dbh. The volume of fallen logs was estimated by:

$$V = pi \times {}^1\!/_{32} \,((a + b)^2 + (c + d)^2) \qquad \text{(Eq. 4)}$$

where a log has length l, large-end orthogonal widths of a and b, and small-end orthogonal widths of c and d (Coomes et al. 2002).

We multiplied the volume of each piece of CWD by its species-specific stem density and then by a decay stage modifier (Coomes et al. 2002). Species-specific decay stage modifiers were available for only two of the species present in the WACEM data (*Weinmannia racemosa* and *Metrosideros umbellata*; Coomes et al. 2002).

Some 283 stems were not identified to species in the field, so we assigned them the mean wood density for indigenous canopy trees (476 kg/m^3; Beets et al. 2008). Two stems were missing a decay class, so we assigned them a decay class of 2 (the middle of the scale) in accordance with the approach used for recent analysis of the LUCAS Natural Forest data (Beets et al. 2009).

As for AG pool, CWD biomass was summed by plot, divided by two and slope-corrected.

2.3.4 Carbon stocks in FWD, litter, FH and mineral soil

Estimation of carbon stocks in FWD, litter, the FH horizon and mineral soil followed the protocols of Stevenson & St John (2009). All samples of litter, FWD and FH were oven-dried to constant mass at 55°C and then sampled for carbon content. All soil carbon samples were oven-dried to constant mass at 105°C and analysed for carbon content on a Leco analyser. Soil carbon content was corrected for bulk density.

2.4 Comparison of control and exclosure plots

As the data analysed in this report were baseline data collected either at the time the exclosures were erected or within 5 years after that, we did not expect to see treatment effects. Instead, we attempted to determine if the carbon stocks of each control and exclosure pair were well-matched. We calculated the difference between the baseline value for the exclosure and control for each pair of plots for each of the five pools, as well as the total ecosystem carbon.

2.5 Power analysis

The two key parameters for a power analysis—effect size and variability of that effect—are unknown. Therefore, we selected a range of plausible values for both parameters based on the available literature. Since Burrows et al. (2008) suggested that the effects of operational control of herbivores on mature forests are likely to be subtle, the range of effect sizes tested in our simulations was biased towards small effects—1%, 5%, 10% and 20% increases above baseline in the annual rate of carbon sequestration with pest control. Using our chosen baseline of 0.513 t $Cha^{-1}yr^{-1}$ (Beets et al. 2009), this translates to absolute effects of 0.005, 0.02, 0.05 and 0.1 t $Cha^{-1}yr^{-1}$. In order to demonstrate the size of effect that this number of plots could detect, we also included a 200% increase (1 t $Cha^{-1}yr^{-1}$) for comparison.

The three estimates of variability in sequestration rates we were able to locate all suggested high variability in baseline sequestration rates. Carswell et al. (2009), in a c. 5 year study of exotic and mānuka (*Leptospermum scoparium*) shrublands, reported a coefficient of variation (CV) of 135%. In a transect across the South Island, Coomes et al. (2002) also found sequestration rates to be hugely variable (CV = 220%). Beets et al. (2009), in looking at the remeasured National Vegetation Survey (NVS) plots included in the LUCAS data, found a CV of 280%. As this study encompassed the whole country, the variability observed should represent an upper bound on plausible values for regional-scale work.

The variability in sequestration rates observed by Beets et al. (2009), Coomes et al. (2003) and Carswell et al. (2009) reflects a mix of process variability and measurement error. Unfortunately, there are no published estimates of measurement error in carbon sequestration studies in natural New Zealand forests. We therefore selected 2% of baseline standing stock as a conservative estimate of measurement error by experienced crews (Dickie et al. 2009) and apportioned the variability observed (t C/ha) into process variability (t $Cha^{-1}yr^{-1}$) and measurement error (t C/ha) using the equation:

Variation observed = time × process variability + measurement error   (Eq. 5)

Where remeasurement intervals varied within studies, we used the smallest reported interval. Applying these adjusted estimates (122%, 184% and 247%) to our baseline rate yielded estimates of process variability: 0.6, 0.95 and 1.3 t $Cha^{-1}yr^{-1}$.

We then simulated different-sized studies by first drawing a sample of size *n* from a normal distribution parameterised from the Thames Coromandel data (mean 216.3 t C/ha, SD 67.3), representing carbon stocks at the initiation of the wild animal control programme. For each combination of effect size and sample variability, carbon gain after *y* years was then simulated for

each plot as a realisation of a normal distribution with mean equal to $y \times$ (baseline rate + effect) and with standard deviation equal to $y \times$ process variability. We simulated measurement error by drawing a value from a normal distribution with zero mean and a standard deviation of 4 t (i.e. 2% of the mean initial standing stocks) and adding this value to the simulated carbon gain .

For each simulated sample, we rounded each 'measurement' to the nearest 10th of a tonne, then conducted a two-sided, one-sample t-test against the null hypothesis of sequestration at the baseline rate (0.513 t Cha^{-1}yr^{-1}; Beets et al. 2009). Power (the probability of correctly rejecting the null hypothesis) was calculated as the proportion of 1000 trials where $P < 0.05$. We assumed that sequestration rate was independent of initial carbon stock, which is a strong assumption that may merit closer examination. We also assumed that sequestration was constant for the duration of the experiment, and that both process variability and measurement error were not affected by the treatment or the initial or final carbon stocks.

3. Results

3.1 Baseline carbon stocks

The mean carbon stock was 216.3 t C/ha (n = 48, SEM = 9.7) for the TCFPP study area (Table 2). The AG pool made up 35% of the total ecosystem carbon stock; soil (all three depths pooled) made up 43%; forest floor, 9%; and CWD, 5% (Figs 3 & 4). Per-plot values varied widely around the mean (Fig. 5). The study forest had a mean stem density of 3399 stems/ha (SEM = 300) and a basal area of 49.3 m²/ha (SEM = 2.2).

Within the largest pool (soil), most of the carbon was in the top two layers (0–100 mm: 34.5 t C/ha, SEM = 1.7; 100–200 mm: 33.4 t C/ha, SEM = 1.9; 200–300 mm: 26.0 t C/ha, SEM = 1.7). Within the forest floor, the FH horizon (11.9 t C/ha, SEM = 1.5) held nearly twice as much carbon as the litter pool (6.2 t C/ha, SEM = 0.4) and 20 times that of FWD (0.6 t C/ha, SEM = 0.1).

3.2 Exclosure versus control

As a group, the exclosure and control plots were not dissimilar from the standard plots, although the mean carbon stocks in the exclosure plots were higher than those of the controls (Fig. 3). As might be expected given the small sample size, estimates of mean carbon in each pool were not precise. The eight pairs of exclosures and controls were not similar in terms of standing stock carbon, despite the physical proximity of the plots of each exclosure/control pair (Fig. 6). The distribution of differences in total carbon was the worst in this respect; it was bimodal, with two pairs differing by over 200 t C/ha. The outlying pair(s) differs for each of the pools, indicating that heterogeneity in carbon is not synchronous across pools.

Table 2. Carbon stocks (t C/ha) in five pools. All values are slope-corrected. n = 48 plots. Below-ground carbon was estimated as 0.25 × above-ground, so no measures of spread are reported.

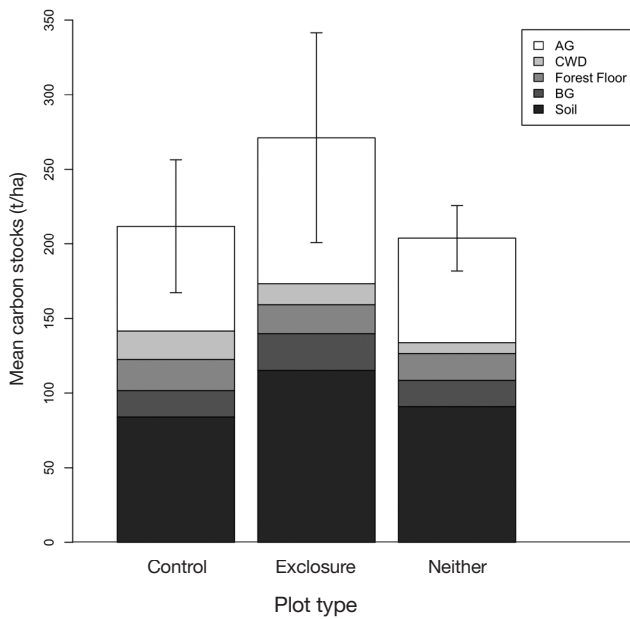| POOL	MEAN	STANDARD DEVIATION	95% CONFIDENCE INTERVAL	COEFFICIENT OF VARIATION (%)
Above-ground	74.7	36.8	10.7	49
Coarse woody debris	10.3	13.2	3.8	127
Litter	18.8	12.1	3.5	64
Below-ground	18.7	NA	NA	NA
Soil	93.9	29.8	8.6	32
Total	216.3	67.3	19.5	31

Figure 3. Mean carbon stocks (t C/ha) ± 95% confidence interval by pool for each of the three plot types (*n* = 8 exclosures, 8 controls and 32 'neither'). The below-ground (BG) pool was not measured independently, but calculated as a fraction of the above-ground (AG) pool. CWD = coarse woody debris.
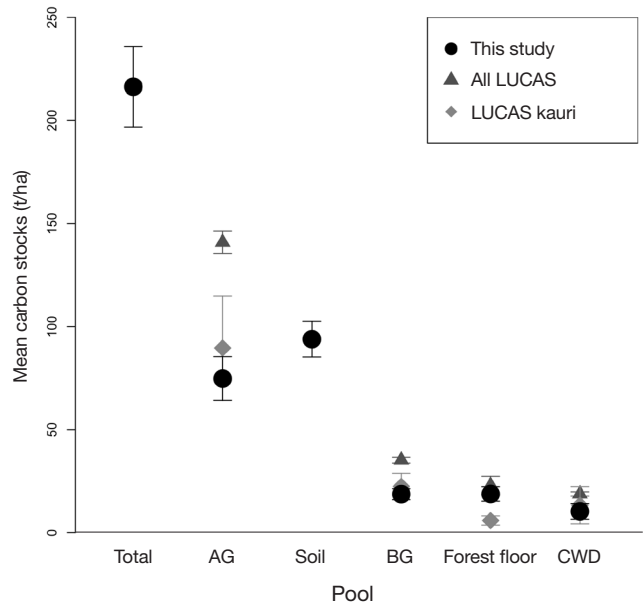
Figure 4. Mean carbon stocks ± 95% confidence interval for total carbon and each of the five pools, compared with other estimates for New Zealand forests. Data from all three plot types have been pooled for this analysis (*n* = 48 plots). Data sources are: 'All LUCAS': Beets et al. (2009), who did not report on the soil carbon component of LUCAS and therefore total carbon could not be calculated. 'LUCAS kauri': Beets et al. (2009). AG = above-ground; BG = below-ground; CWD = coarse woody debris.

Figure 5. Spatial variation in total ecosystem carbon and in two main constituent pools (AG = above-ground pool). Symbols are scaled so that the area of the circle is proportionate to the carbon value (t C/ha) observed. Legends show the minimum value, first quartile, median, third quartile and maximum value of each pool. The Coromandel Peninsula coastline is shown in the background.
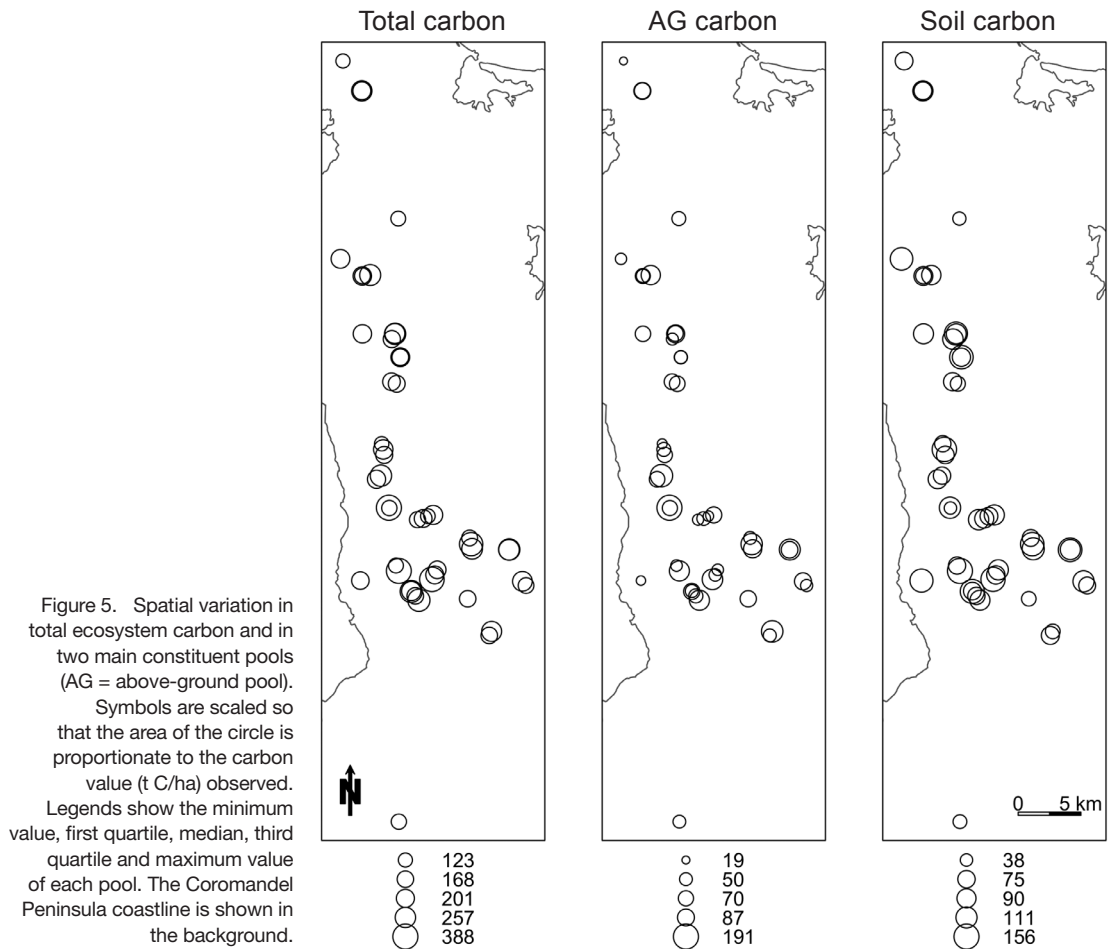
Figure 6. Difference in baseline measurements for eight pairs of exclosures and controls. Plots to the left of the 0 line are those for which control values were greater than exclosure values; plots to the right were the opposite. AG = above-ground, CWD = coarse woody debris; BG = below-ground.

3.3 Power analysis
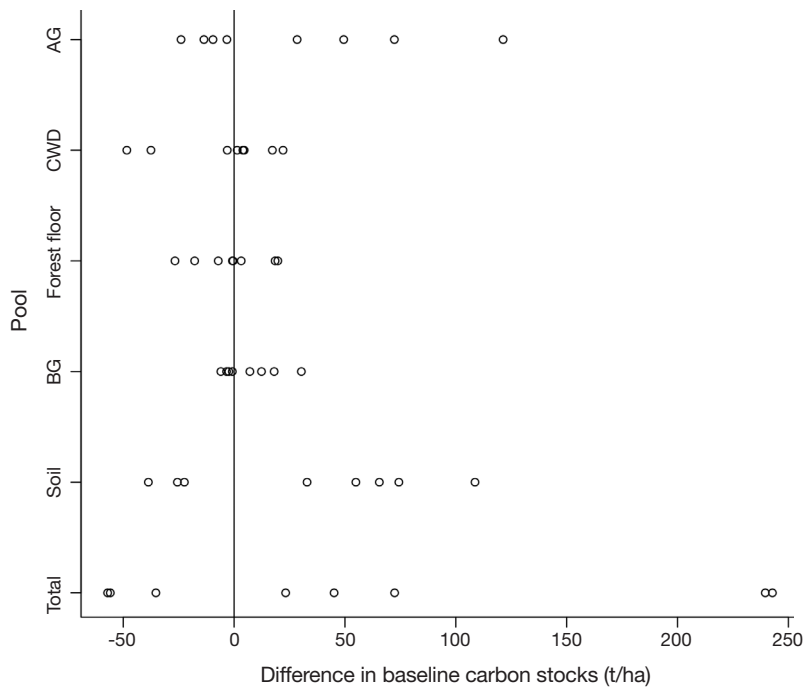
Based on the assumptions that the effect size of operational pest control on carbon sequestration in mature forests is small and the varibility of that effect is large, then even very long-term studies (20 years) with very large numbers of plots (> 400) have low power to detect changes in carbon sequestration (Fig. 7). To have an 80% chance of correctly detecting a difference in an annual carbon sequestration rate of 0.1 t Cha^{-1}y^{-1} (a 20% increase over baseline) with a five-year remeasurement interval, given a process variability of 0.6 t Cha^{-1}y^{-1} and a measurement error of 4 tC/ha, would require more than 500 000 plots (Table 3).

Predictably, larger effects were more detectable, particularly if the variation in sequestration rate was closer to 0.6 t Cha^{-1}yr^{-1} than 1.3 tCha^{-1}yr^{-1} (Table 3 & Fig. 7).
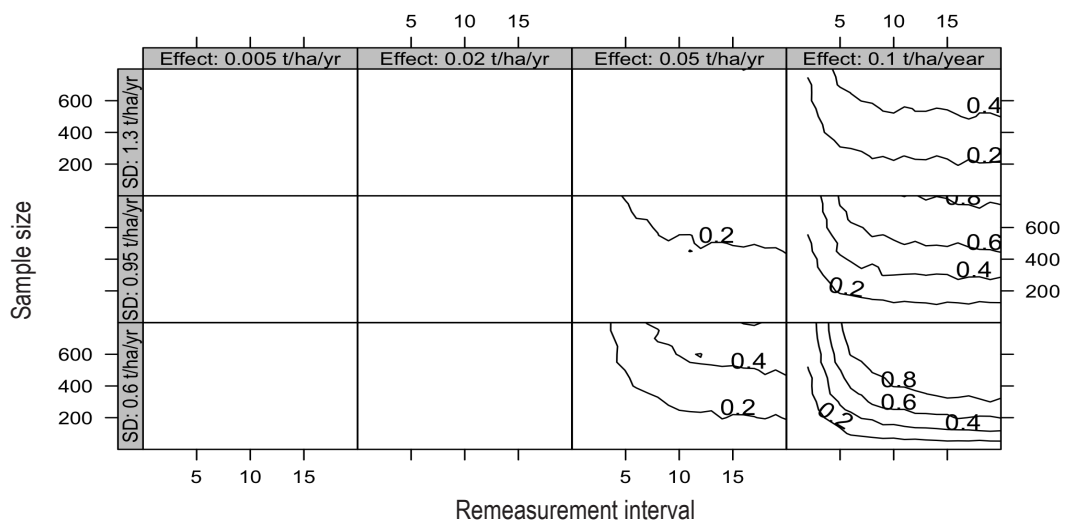
Figure 7. Power as a function of sample size and remeasurement interval, for a range of possible effect sizes (as a percentage increase in the baseline sequestration rate) and measurement precisions (assessed as coefficient of variation, CV). A power of 0.8 means that a study of that size and duration, with the simulated sample variability, has an 80% chance of correctly rejecting the null hypothesis if the effect of the treatment is as large as that simulated.

Table 3.   Number of plots required to have an 80% chance of detecting ($P < 0.05$) an increase in carbon sequestration rate (tha^{-1}yr^{-1}) after 5 years, assuming a measurement error of 2% of initial stock and given various combinations of effect size and variability (tha^{-1}yr^{-1}).

VARIATION IN SEQUESTRATION RATE	INCREASE IN SEQUESTRATION RATE (tha^{-1}yr^{-1})				
	0.005	0.02	0.05	0.1	1
0.6	615355	38462	6156	1541	18
0.95	961490	60095	9617	2406	23
1.3	1384545	86536	13848	3464	28

4.   Discussion

4.1   Baseline carbon stocks

A number of estimates of carbon stocks in indigenous forests have been made for New Zealand (Coomes et al. 2002; Davis 2002; Hart et al. 2003; Beets et al 2009). Our estimates for the forest floor and CWD pools are similar to those estimated in previous work (Fig. 4). In contrast, the soil carbon value is higher than reported elsewhere in New Zealand, and it forms a much higher proportion of the ecosystem carbon (Coomes et al. 2002; Hart et al. 2003). However, soil carbon pools are the most precisely estimated of all our carbon pools (Table 2). Our estimate of AG (stem) carbon (74.7 t C/ha; Table 2) is considerably lower than the national estimate prepared by Beets et al. (2009) from the LUCAS data (140.9 t C/ha). Given the dominance of podocarp-broadleaved trees in the study forest, it may be more appropriate to compare the stocks with values from such forests. Hall et al. (2001) estimated such forest to contain 186 ± 27 t C/ha, whilst Holdaway et al. (2012) estimated 235 ± 139 t C/ha. Our estimate most closely resembles that of Beets et al. (2009) for the 16 plots classified as Kauri forest by ECOSAT (89.6 t C/ha), a satellite-derived vegetation map, which places our plots into the 'kauri' category (Shepherd 2005).

This appears to be the first calculation of a whole-ecosystem carbon budget for a forest of the study type. However, some work has been done on AG and litter pools. Silvester & Orchard (1999) reported AG biomasses equivalent to 368 t C/ha and 767 t C/ha in a regenerating and mature kauri forest, respectively. In contrast, after conversion of Madgwick et al.'s (1982) figures from biomass to carbon, we estimate that they measured only 66.8 t C/ha in AG carbon for a regenerating kauri stand (130 years old). Silvester & Orchard (1999) observed an often deep, but widely variable, litter layer ranging from 38 t C/ha to 225 t C/ha (mean 123 t C/ha, $n = 4$); even their minimum value is substantially higher than the values we observed (Table 2). A litterfall study in podocarp-hardwood forest in the Orongorongo Valley reported litter and CWD stocks of 10.9 ± 0.8 t C/ha in leaf and small (< 20 mm diameter) wood litter, 11.4 ± 2.1 t C/ha in larger (20–250 mm) woody litter, and 49.2 ± 13.7 t C/ha in coarse (> 250 mm) woody debris (Daniel & Adams 1984).

Although the study forest contained a number of large trees (e.g. one 140 cm dbh rimu, one 60 cm dbh kauri, three tōwai (*Weinmannia silvicola*) >50 cm dbh), overall basal area was at the low end of that observed in other regenerating kauri forests. Kauri ricker stands in the Waitakere ranges have stem densities of 2500–6100 stems/ha and basal areas ranging from 49.3 m²/ha to 73.6 m²/ha (Ogden 1983). In contrast, Burns & Smale (1990) reported a basal area for trees ≥10 cm (rather than the 2.5 cm cut-off in our study) of 62.0 m²/ha for a secondary kauri forest on the opposite side of the Coromandel Peninsula from our study area.

In addition to the low total basal area, a large proportion (31%) of that basal area is composed of tree ferns, whose low wood density, and consequent lower carbon content, means that they contribute only 0.5% of the AG carbon stock. Such a high proportion of tree ferns is not uncommon in regenerating warm-temperate forests (Ogden 1983; Burns & Smale 1990) and is again indicative of the relatively high level of recent (c. 50–200 years ago) anthropological disturbance.

Estimates of soil carbon under indigenous New Zealand forests are sparse. Those studies that are available have reached widely varying conclusions on the relative importance of soil carbon to ecosystem totals. Much of the disparity likely results from differences in the forest types under investigation. Coomes et al. (2002) provided data from indigenous humid temperate forests with high clay activity soils on the South Island, which, of the soil types they investigated, most closely matched the soils of our Coromandel plots. They reported an average value of 96.1 t C/ha for the top 30 cm of mineral soil. When combined with forest floor carbon ('fine litter'), this represented 32% of the total ecosystem carbon, compared with approximately 51% as measured in our study. Davis et al. (2003) reported 5–9 t C/ha in the litter layer, 11–29 t C/ha in the FH layer and 30–42 t C/ha in the top 10 cm of mineral soil in a mountain beech (*Nothofagus solandri* var. *cliffortioides*) forest. These figures are similar to our values of 6.22 ± 0.44, 11.92 ± 1.53 and 34.51 ± 1.74 t C/ha, respectively. In terms of total ecosystem carbon, Davis et al. (2003) found 22% to be in the top 10 cm of soil under a mature beech forest compared with our measure of 16% for the same horizon. Another measure of beech forests estimated total carbon at 340 t C/ha, nearly 50% of which was in the AG pool, with only 16% of ecosystem carbon in the top 60 cm of soil (Hart et al. 2003). For comparison with exotic plantations, Davis et al. (2007) measured soil carbon stocks to 30 cm depth in New Zealand pine plantations (*Pinus nigra*) and found nearly identical values to those reported here.

4.2 Exclosure versus control

The eight exclosures and controls were clearly not well paired with respect to their initial carbon stocks (Fig. 6). This may not have impacted on their capability to detect herbivore effects on carbon sequestration because it is the sequestration rate, not standing stock, that is the key parameter for detecting change in permanent plots. If, however, a relationship between sequestration and standing stock is suspected, then we recommend that the exclosures be re-paired with one of the 32 standard vegetation plots—based on similarity in the initial measurement. As long as this re-pairing is done while truly 'blind' to changes after the fences were erected, the results should not be compromised (G. Forrester, Landcare Research, pers. comm.). It would be best, however, to use the same pairing for all pools, so a multivariate approach to minimising differences in initial state would be most appropriate.

The damage to exclosure 29/1A by a windfall and the ongoing difficulty with conducting possum control operations in the Northern block around exclosure and control plots 31/1A and 31/1B with the same intensity as in the Southern and Central blocks underscores the vulnerability of small studies to 'nondemonic intrusion' (Hurlburt 1984).

4.3 Power analysis

The results of the power analysis suggested that there is little ability to detect effects of pests on carbon in mature forests, given current estimates of the expected effect size and the variability in sequestration rates. While it may be tempting to initiate a small study 'just in case' the effects are larger than estimated, this can lead to deeply misleading results. If a study has too few plots, it will only return significant results when the difference between treatments is anomalously large—giving a false impression of system dynamics (Gelman & Weakliem 2009). Thus, putting in a study that is too small at best wastes money and at worst gives an overly optimistic estimate of the carbon gains that can be expected.

Because of the lack of empirical estimates of effect sizes and variability, our power analysis relied on a number of strong assumptions—that neither the background sequestration rate nor the treatment effect varied with initial carbon stocks and that measurement error and process variability were similarly un-influenced by initial carbon stocks, forest structure or treatment. To explore the impact these assumptions have on power, it may be profitable to make use of a forest model. Simulating intensive pest control in a modelling framework may give more reliable estimates of baseline sequestration rates, effect sizes and variability than the simplistic estimates used here. It would also allow investigators to determine which forest types are likely to show large effects under intensive animal control.

Even if a significant effect is detected, it will be impossible to distinguish between effective pest control and faster-than-average growth, because of other features of the study area such as productive soils, successional age or simply good growing conditions during the remeasurement interval—unless the WACEM data can be compared with the general trajectory for the region. Given the difficulties encountered in sustaining possum control in the Northern block, it may be more reasonable to consider the four plots contained there as comparison plots experiencing 'business as usual' sporadic wild animal control, rather than the sustained, intensive control of the other two blocks. Four plots (three controls and one exclosure) are not enough to base rigorous comparisons on, but could provide useful context for any observed changes if coupled with a retrospective analysis of historical data, to establish the background trend. They could also be useful in wider comparisons with the LUCAS Natural Forest plots and the permanent plots in the NVS Databank.

Despite the concerns expressed above, large-scale studies such as the present one are urgently required in order to more accurately assess the variability in rates of forest carbon sequestration and the potential impact of wild animal control. Our study is among the first to quantify the detectability of wild animal control on carbon sequestration; therefore, efforts to identify or establish appropriate non-treatment plots, so that robust conclusions can be drawn, would be well worthwhile. In addition, assessing changes in pig populations and activity may be useful for understanding soil carbon dynamics and could illuminate interactions between herbivore populations.

4.4 Future study design

The carbon calculations presented here rely heavily on estimates of tree height, volume, wood density and decay rates. Refining these estimates should improve the precision and accuracy of the ecosystem carbon budget. The most obvious improvement would be to measure tree height in the field, rather than estimating it from diameter. The next biggest improvement in the calculations would come from replacing estimates of stem wood density based on life-form with species-specific values. These data could easily be gathered during the next remeasurement by coring trees adjacent to the plots. Developing life-form-specific equations to estimate biomass from height and diameter is the next priority. Lianes are the most difficult in this respect, but they can be a significant component of forests, particularly in the lowlands (Wardle 2002; Jiménes-Castillo et al. 2007), and their architecture differs radically from that of canopy trees (Isnard & Silk 2009). Because of their low wood density, tree ferns and palms (such as nīkau, *Rhopalostylis sapida*) are unlikely to be a large fraction of the AG carbon, but as they can be quite prevalent, more precise estimates of their biomass should reduce plot-to-plot variability. Finally, CWD is a small component of the total carbon for this system but its variability is enormous (Table 2), so it will have a disproportionate impact on variability in total carbon. This variability is because tree fall and/or mortality are highly patchy in their distribution—adjacent areas of the forest floor can have a lot or no CWD.

Along with improving the calculation of ecosystem carbon from field data, selecting a study area with lower natural heterogeneity would theoretically improve the chances of isolating the effect of introduced herbivores on ecosystem carbon. In practice, this is likely to be quite difficult, as the present study showed wide variability in carbon stocks despite it being limited to a confined geographic area (Fig. 5). Understanding the drivers of that variability is critical for selecting future study sites where we will be able to detect change on management-relevant timescales.

In studies of forest response to removal or introduction of herbivory, the choice of baseline is critical. Growth or decline of a species is always relative, and past land-use or disturbance can influence composition and structure for centuries (Foster 1992; Foster et al. 2003). The forests of the Coromandel were logged and burned soon after European settlement (Masters et al. 1957; Molloy 1980), and thus it is critical to establish how much compositional turnover and canopy tree mortality is related to successional state. Since possums reached the Coromandel only in the latter half of the 20th century (Clout & Eriksen 2000), after forest surveys were begun in New Zealand, we suggest a comparison of the current data with historical data archived by the NVS Databank, particularly the data collected under the auspices of the National Forest Survey (NFS) immediately after World War II. These historical data are insufficient to estimate total carbon, but would give insight into overstorey composition and structure prior to possum colonisation. An analysis of them would have to deal explicitly with the successional nature of the Thames Coast forests.

Building and maintaining exclosures is costly and laborious. Therefore, it is critical that study design be robust. Before erecting fences, it would be helpful to map out the possible outcomes to help ensure that the exclosures will yield unambiguous conclusions. We suggest that addressing the following questions may be useful in the design of future studies: If the exclosure and control are significantly different, is that because (a) the process of fence building created gaps in the canopy; (b) the exclosures were located in an atypical stand; (c) a big disturbance affected one or two plots? Conversely, if the exclosure and control are not different, is that due to (a) lack of sensitivity to introduced herbivores; (b) strong impacts by a herbivore that is not affected by the exclosures; (c) the exclosures not working as designed; (d) pest populations in the unfenced portion of the forest falling below the levels necessary to sustain damage (because of other control efforts or natural causes, e.g. disease); (e) the experiment being too short to detect a difference; (f) pests only affecting vegetation in particular circumstances (e.g. early succession) that did not occur in the exclosures?

Once the number and distribution of exclosures has been identified, particular care should be exercised in locating them. The experience of this study indicates that mere physical proximity may not be sufficient to secure a good pairing. We recommend setting criteria for site homogeneity before the crew heads into the field, and then identifying (in the field) a homogeneous area large enough to hold two plots (e.g. with a 50 m radius) and, finally, randomly locating two plots within it and flipping a coin to see which one gets the fence. It is likely that homogeneity will need to be assessed by measurements, rather than by field crew judgement. This will involve more work for the field crews setting up the exclosures, but given the long-term commitment such exclosures represent and the difficulty of obtaining robust results from small sample sizes, we suggest that it would be money and time well spent.

As noted in section 1, carbon stocks are the integrated result of many forces, not just foliar removal (Burrows et al. 2008). An ecosystem approach to their quantification, such as that deployed by the current study, is strongly recommended. Future research on the use of operational herbivore control on carbon stocks in indigenous forests should maximise the number of plots installed and sustain pest control for long periods of time. Consideration of the following factors will maximise the robustness of the study and the interpretability of its findings:

1. **Disturbance history**   Expectations of future carbon sequestration depend on the successional state of the forest. Interpretation of study results will depend on knowing how the current carbon stocks compare with potential ones.

2. **Scale**   The forces controlling carbon act at broad spatial scales, so the controlled area needs to be large enough to encompass the relevant interactions. We recommend the whole-ecosystem experiment approach of Carpenter et al. (1995).

3. **Reference system**   As with fenced exclosures, whole-ecosystem experiments need non-treatment plots to be compared with either a reference catchment (Carpenter et al. 1995) or a regional network of permanent plots.

5.   Conclusions

- Total baseline carbon for the Thames Coast study area is 216.3 ± 9.7 t C/ha comprising:
  – Above-ground live—74.7 ± 5.3 t C/ha,
  – Below-ground live—18.7 t C/ha,
  – Coarse woody debris—10.3 ± 1.9 t C/ha,
  – Forest floor: fine woody debris + litter + fermentation-humic horizon—18.8 ± 2.7 t C/ha
  – Soil 0–30 cm—93.9 ± 4.3 t C/ha.

- Total carbon (216.3 ± 9.7 t C/ha) and above-ground live carbon (74.7 ± 5.31 t C/ha) in the Thames Coast study area appears to be lower than in most other New Zealand forests, perhaps due to the high abundance of tree ferns (31% of total basal area).

- Carbon stocks are highly variable, even within a small geographic area. This makes study of the incremental impact of introduced herbivores difficult without exceptionally intense sampling. It is unlikely that plot networks set up for monitoring biodiversity will be adequate for assessing impacts on carbon.

- Robust conclusions about the impact of intensive pest control on carbon stocks in the Thames Coast study area will require a comparison with the trajectory of carbon accumulation in forests of similar composition, growing conditions and successional state that have experienced little or no pest control. Existing permanent plots in the NVS databank may be able to provide the necessary context.

6.   Recommendations

- Future studies of carbon storage in forests would be improved by field measurements of tree height, and the development of life-form-specific allometrics for tree ferns and lianes. Developing species-specific decay curves for CWD would greatly improve estimates of the contribution of dead wood to ecosystem carbon budgets.

- The expected effect size is one of the key unknowns for the WACEM project. A historical analysis of NVS and NFS data collected before possums arrived on the Coromandel Peninsula could help determine how sensitive the forests in the present study are to possum browsing and thus how great an effect intensive control might have.

- Studies of ecosystem carbon in areas with known disturbance history (natural or anthropogenic) would help identify the causes of fine-scale spatial heterogeneity, enabling future study designers to accurately assess the heterogenity they are likely to observe.

- There is little the experimenter can do to affect either the effect size or the sample variability. Poor decisions about field methods can worsen the precision of the measurement, but the natural variability of the underlying process is not under the experimenter's control. Study designers should, therefore, resist a strongly optimistic

estimate of the key parameters. Forest models offer an opportunity to incorporate knowledge of herbivore impacts on individual species and density-dependent carbon sequestration into estimates of ecosystem-level impacts. These may support more robust power analyses that would ensure that furture studies have enough plots to draw robust conclusions about the phenomenon of interest.

- Studies of ecosystem-level impacts of introduced herbivores should be designed as landscape-scale manipulations, with known control histories and either reference catchments, where possible, or a regional network of existing permanent plots in order to isolate the impact of the treatment from other sources of change. Making multiple pre-treatment measurements may make more robust conclusions about treatment effects possible even when reference catchements are difficult to identify.

7. Acknowledgements

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Appendix 1

Stem wood density values used for estimation of above-ground and coarse woody debris carbon stocks, along with source

S = species-specific, G = congeneric value, T = typical value based on life-form.

SPECIES	SELECTED VALUE	SOURCE
AGAAUS	435	Beets et al. 2009* - S
BEITAR	527	Beets et al. 2009 - S
BEITAW	505	Beets et al. 2009 - S
BRAKIR	333	Beets et al. 2009 - T
BRAREP	333	Beets et al. 2009 - T
CARSER	668	Russo et al. 2010† - S
CLEPAN	333	Beets et al. 2009 - T
COPARB	333	Beets et al. 2009 - G
COPGRA	333	Beets et al. 2009 - S
COPLUC	333	Beets et al. 2009 - G
COPROB	333	Beets et al. 2009 - T
CORBAN	197	Beets et al. 2009 - T
CORLAE	476	Beets et al. 2009 - T
CYACUN	197	Beets et al. 2009 - T
CYADEA	197	Beets et al 2009 - T
CYAMED	197	Beets et al 2009 - T
CYASMI	199	Russo et al. 2010 - S
DACCUP	433	Beets et al. 2009 - S
DACDAC	351	Beets et al. 2009 - S
DICSQU	197	Beets et al. 2009 - T
DRALAT	333	Beets et al. 2009 - T
DYSSPE	424	Beets et al. 2009 - S
ELADEN	526	Beets et al. 2009 - S
GENLIG	333	Beets et al. 2009 - T
GRILIT	632	Beets et al. 2009 - T
GRILUC	493	Beets et al. 2009 - T
HAKSAL	333	Beets et al. 2009 - T
HAKSER	333	Beets et al. 2009 - T
HEDARB	465	Beets et al. 2009 - S
IXEBRE	493	Beets et al. 2009 - T
KNIEXC	503	Beets et al. 2009 - S
KUNERI	736	Beets et al. 2009 - S
LAUNOV	341	Beets et al. 2009 - S
LEPSCO	614	Beets et al. 2009 - S
LEUFAS	333	Beets et al. 2009 - T
LOPBUL	333	Beets et al. 2009 - T
LYGART	197	Beets et al. 2009 - T (tree fern)
MACEXC	333	Beets et al. 2009 - T
MELMAC	333	Beets et al. 2009 - T
MELRAM	358	Beets et al. 2009 - S
METALB	333	Beets et al. 2009 - T

SPECIES	SELECTED VALUE	SOURCE
METDIF	333	Beets et al. 2009 - T
METFUL	333	Beets et al. 2009 - T
METPER	333	Beets et al. 2009 - T
METROB	632	Beets et al. 2009 - S
MYRAUS	493	Beets et al. 2009 - T
MYRSAL	493	Beets et al. 2009 - T
NESCUN	770	Beets et al. 2009 - S
NESLAN	493	Beets et al. 2009-T
OLEFUR	400	Russo et al. 2010 - G (OLEPAN)
OLERAN	400	Russo et al. 2010 - G (OLEPAN)
PHYTRI	489	Beets et al. 2009 - S
PINRAD	420	Beets et al. 2009 - S
PITTEN	400	Russo et al. 2010 - S
PODHAL	577	Russo et al. 2010 - S
PRUFER	482	Beets et al. 2009 - S
PSEARB	490	Russo et al. 2010 - S
PSECRA	493	Beets et al. 2009 - T
PSEDIS	493	Beets et al. 2009 - T
QUISER	427	Beets et al. 2009 - S
RAUEDG	493	Beets et al. 2009 - T
RHOSAP	197	Beets et al. 2009 - T
RUBCIS	333	Beets et al. 2009 - T
SCHDIG	490	Russo et al. 2010 - S
SYZMAI	476	Beets et al. 2009 - T
TORTOR	333	Beets et al. 2009 - T
VITLUC	476	Beets et al. 2009 - T
WEIRAC	469	Beets et al. 2009 - S
WEISIL	476	Beets et al. 2009 - T
BEIROA	516	Beets et al. 2009 - G
CORAUS	197	Beets et al. 2009 - T
CYATHE	197	Beets et al. 2009 - T
PODTOT	370	Beets et al. 2009 - S

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