Century-scale effects of invasive deer and rodents on the dynamics of forests growing on soils of contrasting fertility

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Abstract. Understanding the long-term impacts of invasive mammalian browsers and granivores in mixed forests is difficult due to the many processes potentially affecting the demography of long-lived trees. We constructed individual-based spatially explicit simulation models of two mixed conifer–angiosperm forests, growing on soils of contrasting phosphorus (P) availability, to investigate how browsing by invasive red deer (*Cervus elaphus scoticus*) and granivory by invasive rodents (primarily house mouse *Mus musculus*) might alter forest dynamics. Models were parameterized with field data. Seedling growth and survival rates were estimated inside and outside deer exclosures. Seed predation rates were estimated at high and low rodent densities in mast and non-mast seeding years. For the alluvial terrace forest, which grew on P-rich soil, our model contained 15 tree species dominated by angiosperms; our model of the P-poor marine terrace forest contained seven species dominated by conifers. The two forest models were used to explore four 500-year scenarios: deer and rodents present, deer present and rodents absent, deer absent and rodents present, and deer and rodents absent.

Our field studies revealed that the highest probabilities of seed predation by rodents occurred for two canopy species in mast years and in neighborhoods of high species-specific basal area, and that deer browsing had the greatest negative effects on the growth and survival rates of angiosperm seedlings. Our simulation models predicted that the presence of deer and rodents would reduce the abundances of canopy codominants, and hence total basal area, in the alluvial terrace forest. The presence of deer increased the dominance of conifers in both forests, but effects of deer and rodents were much stronger in the alluvial terrace forest. Our study revealed two emergent properties. First, rodent- and deer-induced reductions in seedling abundances did not always translate into reduced sapling and adult tree abundances. Second, when deer changed the abundance of a canopy dominant, other species were affected by altered interspecific competition.

We conclude that the effects of invasive deer and rodents will be greatest in forests growing on P-rich soils. Exclusion of deer is predicted to have greater long-term effects on forest dynamics than exclusion of rodents.

Key words: angiosperms; conifers; emergent properties; granivory; herbivory; house mouse; invasive species; New Zealand; red deer; seed predation; SORTIE; terrace forests.

INTRODUCTION

Forest ecosystems have critical roles in global carbon, water, and energy cycles (Waring and Schlesinger 1985) and are important habitats for biodiversity (Lindenmayer and Franklin 2002). Biological invasions are a major driver of global change (Vitousek et al. 1997, Mack et al. 2000), and many forests have been invaded by multiple species (Long 2003). Understanding the long-term (i.e., century-scale; Strayer et al. 2006) impacts of invasive species on forest ecosystems is particularly difficult due to tree longevity, the potential for multiple successional pathways (Coomes et al. 2003, Nuttle et al. 2014), and the legacies of historical disturbances and environmental change resulting in

transient nonequilibrium dynamics (Chesson and Case 1986, Davis 1986, Hastings 2004).

Rodents are the world's most widespread mammal invaders and commonly invade forest ecosystems (Long 2003). Ungulates, particularly deer (Family: Cervidae), have also invaded many forests and are frequently sympatric with invasive rodents (Long 2003). The effects of these invasive mammals on forest ecosystems are likely to vary with soil fertility, a key driver of forest dynamics (Vitousek et al. 1995, Wardle et al. 2004, Peltzer et al. 2010). More fertile ecosystems have a greater proportion of palatable, nutrient-rich plants that support more intensive browsing relative to less fertile ecosystems (reviews in Bardgett and Wardle 2003, 2010). Seed production also increases with soil fertility (Kelly and Sork 2002, Smaill et al. 2011), but it is unclear how the effects of seed predation vary with soil fertility. Although a higher proportion of net primary productivity is consumed by herbivores in more productive ecosystems relative to less productive ecosystems (McNaughton et al. 1989), interactions among soil fertility, forest composition, and invasive species are likely to be complex. For example, Kuijper et al. (2010) showed that soil fertility was the dominant factor affecting early stages of tree regeneration, but browsing by ungulates was more important in later stages of tree regeneration.

Mammalian herbivores were absent from New Zealand until the arrival of Pacific rats (kiore, *Rattus exulans*) with Polynesian settlers ~AD 1280 (Wilmshurst et al. 2008). Norway rats (*R. norvegicus*), ship rats (*R. rattus*), and house mice (*Mus musculus*) arrived on European ships after 1770 (King 2005). At least 14 ungulate species were deliberately introduced to New Zealand during 1851–1926 (Forsyth and Duncan 2001), and of those that established, the red deer (*Cervus elaphus scoticus*) is now the most widespread (Nugent and Fraser 2005). Although considerable resources have been expended controlling invasive deer and rodents in New Zealand forests (e.g., Parkes and Murphy 2003, King 2005), there is much debate about the long-term effects of these taxa on forest dynamics; for deer, e.g., see Forsyth et al. (2010) and Peltzer et al. (2014).

Rodents may impact tree populations through seed predation (Janzen 1971, Price and Jenkins 1986, Hulme 1998, Hulme and Kollmann 2005). Ship rats and house mice are common and widespread on the New Zealand mainland (Innes 2005, Ruscoe and Murphy 2005), and undergo extreme fluctuations in abundance in response to the availability of seeds from some canopy tree species that exhibit periodic mast seeding (King 1983, Choquenot and Ruscoe 2000, Ruscoe et al. 2005). For example, in some years house mice eat the entire annual seed crop of the mast-seeding *Nothofagus solandri* var. *cliffortioides* (Ruscoe et al. 2005). Although effects of rodents on grassland succession have been well demonstrated with exclosure studies (Brown and Heske 1990, Ostfeld et al. 1997), century-scale demographic effects of

rodents on populations of long-lived trees have not been evaluated (Hulme 1998, 2002, Hulme and Kollmann 2005). The biological significance of seed predation for tree species and forest communities will partly depend on the extent to which tree populations are seed limited (Hulme 1998, 2002, Hulme and Kollmann 2005, Clark et al. 2007, Zwolak et al. 2010, Maclean et al. 2011); seed predators may have little consequence for adult recruitment if most of the seeds they eat would die from other causes as seeds, seedlings, and saplings (Harper 1977).

In contrast to rodents, deer alter the growth and mortality rates of tree seedlings through browsing (Côté et al. 2004, Tripler et al. 2005, Long et al. 2007). Globally, the impacts of invasive deer in forest ecosystems have been evaluated mostly in short-term (<40-year) studies of vegetation change using data collected inside and outside deer exclosures that do not exclude rodents. Those studies have demonstrated that deer can significantly reduce plant diversity and vegetation density in the browse layer of forests (Gill 1992a, b, Augustine and McNaughton 1998, Wardle et al. 2001, Côté et al. 2004, Spear and Chown 2009), although the effects may vary with the stage of forest development (Mason et al. 2010, Wright et al. 2012) and soil fertility (Kuijper et al. 2010).

A structured approach is required to evaluate the long-term effects of invasive browsers and granivores within the context of other processes driving forest dynamics (Gill 1992a, b, Wisdom et al. 2006). Field experiments are impractical for evaluating the century-scale effects of invasive species on forest dynamics, but advances in computational power and the design of individual-based forest simulation models (Pacala et al. 1996, Coates et al. 2003, Uriarte et al. 2009) enable forecasting of these effects (e.g., Didion et al. 2009). Individual-based models also enable emergent properties of the system (i.e., higher-level dynamics that are not linearly related to lower-level dynamics) to be identified (Reuter et al. 2005).

In this paper, we combined field studies and individual-based spatially explicit simulation models of two conifer–angiosperm forests growing on soils of contrasting fertility on a New Zealand geologic chronosequence to investigate how folivory by invasive red deer and granivory by invasive rodents might alter forest dynamics. The models are powerful tools for predicting effects of invasive species on forest dynamics over long timescales. Our models descend from SORTIE (Pacala et al. 1996) and use an open-source platform for spatially explicit stochastic simulation of the neighborhood dynamics of forest ecosystems (SORTIE-ND; Uriarte et al. 2009). Our study addressed four key questions: (1) Will the proximate effects of invasive deer (on seedlings) and rodents (on seeds) translate into altered abundances of adult trees? (2) Does preferential feeding by invasive deer on angiosperm seedlings alter the competitive hierarchy between angiosperm and conifer seedlings such that conifers become more

dominant as saplings and adults? (3) Are the effects of invasive deer and rodents greater in forests growing on more fertile soils? (4) Are there any emergent properties of the modeled systems that include invasive deer and/or rodents?

This paper is organized as follows. We first describe our study system. We next outline the structure of our SORTIE/NZ models and their parameterization using field data collected during 2001–2009. We describe in detail field studies conducted to determine the effects of invasive rodents and red deer in our study area. One field study estimated seed predation by rodents at high and low densities in mast and non-mast years. Another field study estimated seedling growth and mortality rates in the presence and absence of red deer. We then use the parameterized SORTIE/NZ models to simulate the century-scale effects of adding and removing deer and/or rodents on seedlings, saplings, and adult trees in each of the two forests. The key components of our SORTIE/NZ models and their parameterizations are described in *Methods*, with details either published elsewhere or provided in Supplemental Material. The key results from our field studies and SORTIE/NZ simulations, and comparison of the short- and long-term predictions of the models with independent observations of rodent and deer impacts in New Zealand forests, are provided in *Results*; more detailed descriptions of results (including uncertainties in model predictions) and evaluation of model predictions are provided in Supplemental Material.

Methods

Study area and plant species included in the SORTIE/NZ models

We conducted our study in two mixed conifer–angiosperm forest types growing on the Waitutu geologic chronosequence (Mark et al. 1988, Ward 1988) located at Waitutu Forest, Fiordland National Park, southwestern South Island, New Zealand (~46.4° S, 167.2° E; Fig. 1). Annual rainfall is 1600–2400 mm (Mark et al. 1988) and the mean January (summer) and July (winter) temperatures are 12°C and 5°C, respectively (Coomes et al. 2005).

We contrasted forests growing on recent alluvial outwashes (<25 000 years old; "alluvial terrace forest") with those growing on uplifted marine terraces (~80 000 years old; "marine terrace forest"). The marine terrace soils were significantly less fertile and more poorly drained than the alluvial terrace soils (Wardle et al. 2004, Coomes et al. 2005; see Appendix A: Table A1). There is strong evidence that plant growth is limited by phosphorus (P) rather than nitrogen (N) on the Waitutu marine terraces, with soil P depletion on the marine terraces, but similar soil N concentrations on the alluvial and marine terraces (Wardle et al. 2004, Coomes et al. 2005, 2009, Parfitt et al. 2005; Appendix A: Table A1). Foliar N and P concentrations reflected soil N and P availability; plants growing on the marine terraces had

about one-half the foliar P concentrations of conspecific plants growing on nearby alluvial terraces, but foliar N concentrations were similar (Wright et al. 2010). The two forests contained the same seven canopy-tree species (three conifers and four angiosperms; Mark et al. 1988, Coomes et al. 2005, Kunstler et al. 2013; Table 1; Appendix B: Table B1). However, whereas the alluvial terrace forest was dominated by two angiosperms, *Nothofagus menziesii* and *Weinmannia racemosa*, the marine terrace forest was dominated by the conifer *Dacrydium cupressinum* (species names follow the New Zealand plant names database, *available online*).[11] The alluvial terrace forest also contained six angiosperm subcanopy tree species, and a dense layer of ground-ferns dominated by *Blechnum discolor* (Mark et al. 1988, Coomes et al. 2005); see Table 1; Appendices B (Table B1) and C (Fig. C1A). In contrast, the understory of the marine terrace forest was characterized by a sparse cover of the ferns *Blechnum procerum*, *B. discolor*, and *Hymenophyllum* spp. (Coomes et al. 2005); see Appendix C: Fig. C1B.

Our alluvial terrace forest model contained 15 species (three conifers, two southern beeches (*Nothofagus* spp.), eight other angiosperms, and two tree ferns; Table 1) that together constituted >98% of the total adult basal area of this forest (Coomes et al. 2005), and our marine terrace forest model contained seven tree species (three conifers, two southern beeches, and two other angiosperms; Table 1) that together also constituted >98% of the total basal area of plots sampled in marine terrace forest (Coomes et al. 2005, Kunstler et al. 2013).

Differences in dynamics between the two forests growing on soils of contrasting fertility are also driven by competition for light. Field studies showed that the floor of the alluvial terrace forest was more deeply shaded (≥2% light transmission) than the marine terrace forest (≥5% light transmission) (Coomes et al. 2005) and that there were more shade-tolerant tree species in the alluvial terrace forest (Coomes et al. 2009).

Invasive deer and rodents in Waitutu Forest

Red deer (Appendix D: Fig. D1A) invaded Waitutu Forest in about 1920 (Holloway 1950) and heavy browsing by deer on seedlings of some angiosperm subcanopy tree species was evident in 1925 (Lovelock 1985). There was no government-funded control of deer in the area and Holloway (1950) thought that red deer abundance was at that time declining from an initial peak as preferred foods declined within the browse layer. Commercial harvesting of deer has been common in the study area since the late 1960s, and recreational hunting is a popular activity (Lovelock 1985). Fecal pellet counts conducted at Waitutu Forest in 1978, 1984, 1996–1998, and 2010–2011 indicate that red deer densities have changed little over that period (Forsyth et al. 2011). Red deer at Waitutu Forest preferentially eat the foliage of

[11] http://nzflora.landcareresearch.co.nz/

angiosperm species (which are most abundant in the alluvial terrace forest), but avoid eating the foliage of conifer species (which are most abundant in the marine terrace forest) (Forsyth et al. 2005).

House mice (Appendix D: Fig. D1B) were the most abundant rodents at Waitutu Forest, but Pacific rats and ship rats were also present (Ruscoe 2004, Ruscoe et al. 2004). The density of house mice in Waitutu Forest reached 17–28/ha (minimum number alive) in 2003 as a result of increased reproduction following heavy seed production by *Dacrydium cupressinum* (Ruscoe et al. 2004). In other years between 2001 and 2007, mouse densities fluctuated between undetectable and intermediate levels (Ruscoe et al. 2004, Wilson et al. 2007; W. A. Ruscoe et al., *unpublished data*). Ship rat and Pacific rat captures also peaked in 2003, but too few rats were caught for density to be estimated (Ruscoe 2004, Ruscoe et al. 2004; W. A. Ruscoe et al., *unpublished data*). In a seed predation study at Waitutu Forest, the probability of predation on seeds of *D. cupressinum* and *Nothofagus solandri* var. *cliffortioides* by rodents was highest in neighborhoods dominated by those species and by *N. menziesii*, particularly in a mast year with plentiful seed rain from these species (Wilson et al. 2007). The probability of predation on these seeds was also related to local mouse density. These relationships suggest that the highest local abundances of mice were concentrated in neighborhoods where the seed rain supplied plentiful food. Predation on *Prumnopitys ferruginea* seeds, which are eaten by rats but not mice, was low (Wilson et al. 2007).

The SORTIE/NZ models

Our SORTIE/NZ models are structured like previous SORTIE applications in temperate and tropical forests (Pacala et al. 1996, Coates et al. 2003, Uriarte et al. 2009, Tatsumi et al. 2012) and were implemented using the SORTIE-ND software. The elements of the two SORTIE/NZ models that we developed are submodels that simulate the population dynamics of canopy and subcanopy trees in each of the two forests, and tree ferns in the alluvial terrace forest (Fig. 2). Trees have three life-history stages (seedlings, saplings, and adults). The annual growth and mortality rates of seedlings and saplings vary with available light, which is a function of crown size and species-specific light transmission of neighboring adult trees. The annual growth and mortality rates of adult trees are size dependent. Adult trees produce seeds that are dispersed onto a variety of substrate types, and some of the seeds recruit into seedlings (Fig. 2). Granivory by invasive rodents potentially reduces the number of dispersed seeds (i.e., is post-dispersal; Janzen 1971) that can recruit into seedlings, and browsing by invasive deer can alter seedling growth and mortality rates (Fig. 2). Many modeled processes (i.e., seeding, seed dispersal, seedling growth, and seedling, sapling, and tree mortality) are stochastic.

The relationships describing each submodel were parameterized by fitting statistical models to data collected in the study area, and are fully described in Appendix B of this paper (alluvial terrace forest) and Appendix A of Kunstler et al. (2013) (marine terrace forest). Key features of the submodels and the data used to parameterize them are briefly summarized here. The compiled software, the source code, programmer's guides, user guides, and documentation of all submodels are *available online*.[12]

Light submodel.—As in the original SORTIE (Pacala et al. 1996), light availability was estimated for individual saplings and adult trees, and in a 2×2 m cell for seedlings, as a function of sky brightness distribution and the species, crown size (from allometry functions), and spacing of trees (≥ 10 cm diameter at breast height, dbh) and tree ferns (≥ 1 m height), using species-specific parameters for canopy light transmission estimated from hemispherical photographs of identified tree crowns (Canham et al. 1999). The predicted distribution of light was in agreement with light distribution measured in six mapped stands ranging in area from 1.5 to 2.5 ha (Coomes et al. 2005, Kunstler et al. 2013) in Waitutu Forest.

Recruitment submodel.—Spatial dispersal functions for large-seeded canopy species in the alluvial forest were based on densities of seeds collected from 0.28-m² seed trays within the mapped stands (Canham et al. 2014). Spatial dispersal functions for small-seeded and understory species in the alluvial terrace forest, and for all species in the marine terrace forest, were based on the densities of short seedlings counted in 1-m² quadrats established along transects within the mapped stands, following methods in LePage et al. (2000). These seed or seedling densities were related to the spatial distribution and sizes of neighboring parent trees, using inverse models (Canham and Uriarte 2006) to estimate the shape and size of tree dispersal kernels and fecundity parameters (annual production of seedlings), which were then scaled to yield densities of seedlings consistent with field data. For each species, a probability of establishment (range 0–1) on each substrate type (mineral soil, fresh logs, decayed logs, litter, and moss) was estimated from seedling densities and substrate cover recorded in the seedling quadrats. Substrates are created following tree mortality (uprooted trees create mineral soil, and uprooted and fractured trees create fresh logs), and decay into other substrates (e.g., raised fresh logs decay into ground-level litter and moss).

Growth submodel.—Seedling (<1.35 m in height) growth rates were estimated in the presence and absence of deer in a field study (see *Herbivory by invasive red deer*). Sapling (<10 cm dbh) growth rates were estimated from the analysis of tree rings from 293 individuals (Coomes et al. 2009). Adult (≥ 10 cm dbh) growth rates in the marine terrace forest were estimated from changes
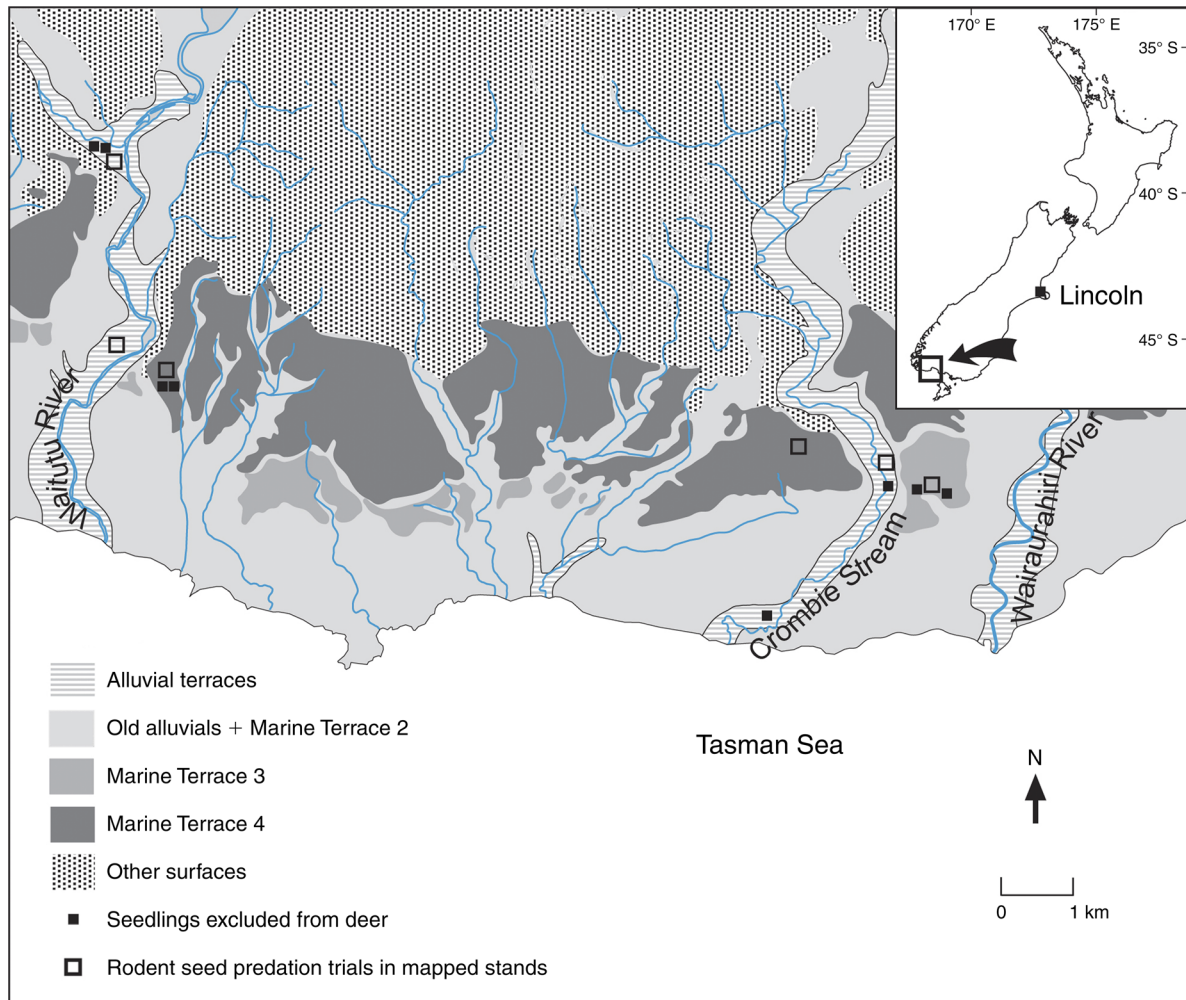
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[12] http://www.sortie-nd.org/

FIG. 1.   Location of study area, Waitutu Forest, southwestern South Island, New Zealand (adapted from Ward 1988). Streams have dissected the marine terraces and deposited alluvial surfaces; the youngest alluvial surfaces border the rivers shown. Marine Terrace 2 has been extensively reworked by rivers during the antepenultimate and penultimate glaciations. Numbering of marine terraces follows Ward (1988).

in dbh as a function of the basal area of neighbors (i.e., local crowding) using data for >10 000 tagged trees in 560 National Vegetation Survey (NVS) plots (Wiser et al. 2001, Hurst and Allen 2007) on low to moderately fertile soils in the southwestern South Island. The smaller sample sizes (11–107 NVS plots per species) for alluvial terrace forest meant that local crowding effects could not be considered in the estimation of adult growth rates in this forest.

Mortality submodel.—Seedling mortality rates were estimated in the presence and absence of deer in the field study used to estimate seedling growth rates (see *Herbivory by invasive red deer*). Sapling mortality rates were estimated using data from the 560 NVS plots (Kunstler et al. 2009). Adult mortality rates were estimated as a function of tree size using data from the 560 NVS plots and the mapped stands in Waitutu Forest. Our statistical models showed that seedling

mortality was determined by light availability (and not density of seedlings) but, within the range of light and sizes captured by the data, the effect was small for large seedlings (Kunstler et al. 2009). Density-dependent seedling mortality is a key process regulating tree populations (Harper 1977), and the absence of an effect of seedling density in our analyses was probably an artifact of the low densities of seedlings currently present in the alluvial (Coomes et al. 2005) and marine (Kunstler et al. 2009) terrace forests. We therefore included density dependence in seedling and sapling mortality to prevent unrealistically high densities of those age classes in some modeled scenarios.

Initial conditions submodel.—The results of individual-based models such as SORTIE/NZ are sensitive to initial (or "starting") conditions (Pacala et al. 1996). We addressed this issue by including the present variability in forest composition and structure in the initial

TABLE 1. Plant species in SORTIE/NZ models of alluvial and marine terrace forest of Waitutu Forest, southwestern South Island, New Zealand, with presence and inclusion in the deer browsing field study (Deer) or seed predation trials (Seed) indicated.

Family, species, and acronym	Alluvial (n = 15 spp.)			Marine (n = 7 spp.)			Life span (yr)	Max. height (m)
	Present	Deer	Seed	Present	Deer	Seed		
A) Conifers (canopy)								
Podocarpaceae								
Dacrydium cupressinum (DACCUP)	x		x	x	x	x	600–1200	25.28
Podocarpus hallii (PODHAL)	x			x			780	20.95
Prumnopitys ferruginea (PRUFER)	x		x	x	x	x	650–770	26.48
B) Angiosperms (canopy)								
Myrtaceae								
Metrosideros umbellata (METUMB)	x			x	x		400–500	24.19
Nothofagaceae								
Nothofagus menziesii (NOTMEN)	x	x		x	x		600	28.93
Nothofagus solandri var. *cliffortioides* (NOTCLI)	x		x	x		x	300–360	30.12
Cunoniaceae								
Weinmannia racemosa (WEIRAC)	x	x		x	x		450	18.26
C) Angiosperms (subcanopy)								
Roussaceae								
Carpodetus serratus (CARSER)	x						310	8.07
Onagraceae								
Fuchsia excorticata (FUCEXC)	x	x					300	3.81
Griseliniaceae								
Griselinia littoralis (GRILIT)	x	x	x				340	8.92
Winteraceae								
Pseudowintera colorata (PSECOL)	x	x					180	5.94
Araliaceae								
Raukaua simplex† (RAUSIM)	x		x				310	7.37
Schefflera digitata (SCHDIG)	x	x					320	5.67
D) Tree ferns								
Cyatheaceae								
Cyathea smithii (CYASMI)	x						150	8.27
Dicksoniaceae								
Dicksonia squarrosa (DICSQU)	x						90	7.25

Notes: Life span data are from Wardle (1991), and Lusk and Ogden (1992), or are modeled estimates (Appendix B).
† The surrogate species used in seed predation trials was *Pseudopanax colensoi*.

conditions of the model and propagating it in our simulations. We generated 100 composite 300 × 300 m stands with tree spatial distribution, density, and size patterns for species similar to the three mapped stands on each terrace. The spatial distribution of trees was generated with a Neyman-Scott cluster process (Diggle 1983, Cressie 1991) to create a spatial structure similar to that of trees sampled across all mapped stands. The density of trees of each species was drawn from a normal distribution with a species-specific mean and variance. Tree size was randomly drawn from the observed dbh distribution. The dbh distributions and the ranges of variability generated over 100 draws are shown in Appendix B (Fig. B25) for the alluvial terrace forest and in Fig. A25 of Appendix A in Kunstler et al. (2013) for the marine terrace forest. The initial abundances of saplings (in four size classes: dbh of 0–3, 3–5, 5–7.5, and 7.5–10 cm) were randomly drawn from species-specific exponential distributions sampled from the NVS plots in Waitutu Forest. Initial seedling densities and substrate covers were fixed to mean values recorded in the NVS plots.

Granivory by invasive rodents

The century-level effects of granivory by invasive rodents on the dynamics of the two forests were evaluated by adding two submodels to SORTIE/NZ that affected the supply of seeds and their recruitment to seedlings. A masting submodel simulated variable tree fecundity (i.e., annual seedling production) due to mast seeding, and was used in all of our modeled scenarios, both with and without rodents. After seed dispersion and before seedling establishment, a seed-predation submodel removed a proportion of seeds at different rates in mast years (i.e., years with high seedfall of at least one tree species) and non-mast years.

The masting and seed predation submodels were parameterized with data collected in a field study at Waitutu Forest during 2002–2009. The methods used in the field study are described fully in Ruscoe et al. (2004), Wilson et al. (2007), and Canham et al. (2014). Here we outline the key features of the masting and seed predation submodels and the field data used to parameterize them.
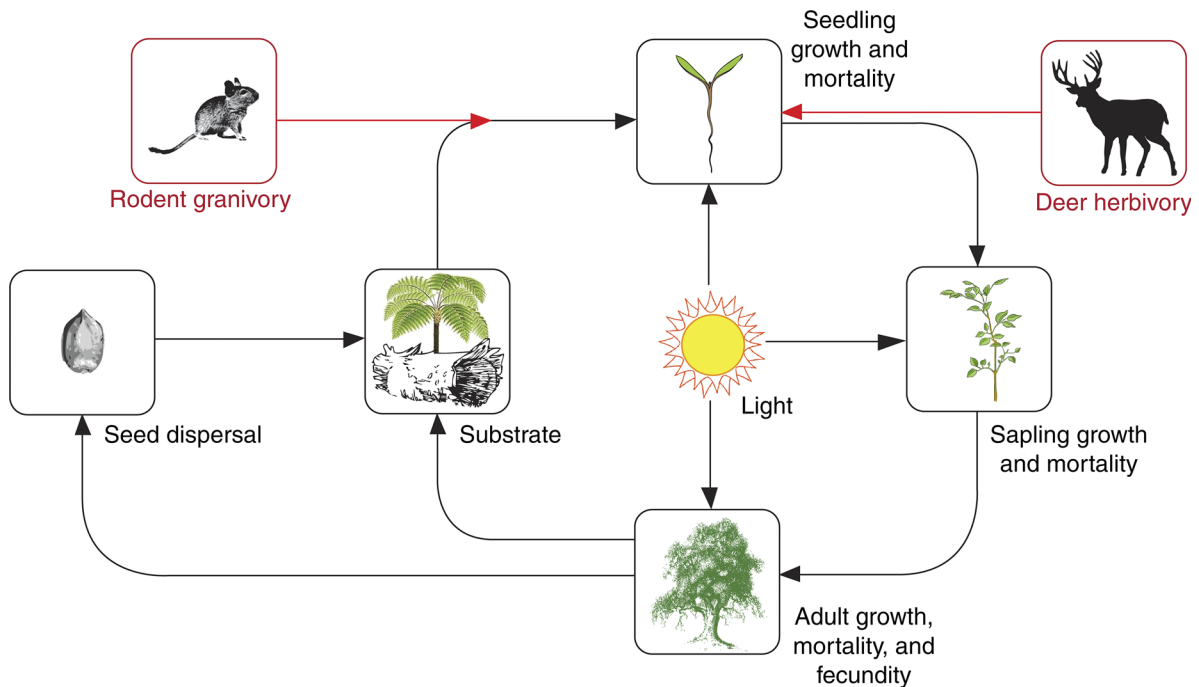
FIG. 2. Schematic diagram showing the major elements of the SORTIE/NZ models that we constructed for alluvial and marine terrace forests at Waitutu Forest, New Zealand. Invasive deer potentially modify the growth and mortality rates of seedlings and invasive rodents potentially reduce the number of seeds that recruit into seedlings.

Mast seeding submodel.—Pulsed fecundities (i.e., annual seedling production) of adults of the masting species (*Dacrydium cupressinum* and *Nothofagus* spp.) present in the alluvial and marine terrace forests were generated with a logistic probability distribution function. The probability of masting in the present year, $f(x)$, was a function of the number of years since the previous mast year for that genus

$$f(x) = \frac{1}{1 + \left(\frac{x}{X_0}\right)^B} \quad (1)$$

where x is the number of years since the last mast, X_0 is the value of x at which $f(x) = 0.5$, and B determines the steepness of the curve. Because we had only eight years of seedfall data in Waitutu Forest, the submodel was parameterized to generate mast years every 3–5 years, corresponding to seedfall patterns observed in New Zealand *Nothofagus* spp. (Allen and Platt 1990, Schauber et al. 2002). Values of $X_0 = 3$ and $B = -5$ generated a mean probability of a mast year of 0.29 (i.e., every 3.43 years; Appendix E). We used identical parameters for *D. cupressinum*, for which fewer historical data were available. The masting function was applied independently to the two genera because they mast asynchronously (Schauber et al. 2002).

We calculated the ratios of mean seedfall of each masting genus in above-average seedfall years to mean seedfall in below-average seedfall years from eight years of seed rain data collected on the alluvial and marine

terrace forests during 2002–2009 (Canham et al. 2014). Fecundity parameters of *D. cupressinum* and *Nothofagus* spp. in mast and non-mast years were then calibrated, based on these ratios and the probability of a mast year (0.29), to their mean fecundities (annual seedling production) in the alluvial (Appendix B) and marine (Appendix A in Kunstler et al. 2013) terrace forests.

Seed predation submodel.—We developed a submodel to calculate the proportion of dispersed seeds that were destroyed by rodents in each modeled 10×10 m grid cell in each time step, and to reduce the number of seeds in that cell by this proportion, prior to seedling establishment. We estimated species-specific parameters from data collected in a seed predation trial conducted in Waitutu Forest in a mast (high seedfall) year (May 2003) and a non-mast (low seedfall) year (June 2004) (Wilson et al. 2007). *Dacrydium cupressinum* seedfall in 2002 and 2003 and *Nothofagus* spp. seedfall in 2003 were above the average 2002–2009 seed rain (Canham et al. 2014). House mice were numerous from November 2002 to August 2003 and then declined to low densities (Ruscoe et al. 2004, Wilson et al. 2007). Seeds of *D. cupressinum*, *N. solandri* var. *cliffortioides*, *Prumno-pitys ferruginea*, and *Griselinia littoralis* were trialed in both years (Wilson et al. 2007). As a surrogate for *Raukaua simplex*, seeds of *Pseudopanax colensoi* (Araliaceae) were trialed in 2004 only. These two species have similar seeds (Appendix F: Table F1) and until recently both were in the genus *Pseudopanax*. Seed predation rates were initially related to the composition of the

neighboring forest canopy, which was described by principal components analysis scores (Wilson et al. 2007). We reanalyzed these spatial patterns in seed predation in relation to the local abundance of five common tree species with seeds known to be eaten by rodents (Appendix F): *D. cupressinum* and *N. menziesii* in the alluvial terrace forest, and *D. cupressinum*, *N. menziesii*, *N. solandri* var. *cliffortioides*, *Podocarpus hallii*, and *Prumnopitys ferruginea* in the marine terrace forest. We used logistic regression to model seed predation on each seed species as a function of the relative basal area (RBA) of these tree species within a radius of 15 m of each seed dish in the trial. Parameters were estimated by maximum likelihood using simulated annealing (Goffe et al. 1994), a global optimization routine implemented with the *likelihood* package in R (R Development Core Team 2007). This approach identified the characteristics of predation hotspots (and refugia) for seeds in the alluvial and marine terrace forests.

The probability of predation, Y_i, on seeds of each focal species i trialed on each terrace was modeled as

$$logit(Y) = p0_s + \sum_{n=1}^{N} p_n RBA_n \qquad (2)$$

where $p0_s$ are intercepts fitted for each of the three sites s on each terrace where field trials were conducted (Fig. 1), and p_n is the coefficient for the relative basal area RBA_n of neighbor tree species n. We then chose a parsimonious model using AIC_c (Akaike's information criterion adjusted for small samples; Burnham and Anderson 2002) by eliminating neighbor species from the full model if doing so reduced AIC_c, beginning with the neighbor species with the least precise estimated coefficient. Similarly, we tried to eliminate site parameters by fitting a single intercept $p0$ to all of the data. For most seed species, differences between sites in seed predation rate meant that separate intercepts for each site were retained on the basis of AIC_c. Either $p0$ or the mean of the three values of $p0_s$ was used in our SORTIE/NZ models.

Parameters for the neighborhood seed predation submodel (which simulated the proportion of dispersed seeds that were destroyed by rodents) were estimated for each species in mast years (when the mast-seeding submodel generated mast seeding in either or both of the masting genera, *Nothofagus* and *Dacrydium*) and in non-mast years. For the seeds of species for which we did not have empirical data, we used parameters from surrogate species with similar fruit and seed characteristics and with empirical or published seed predation data (Appendix F). We set predation to zero for four species for which predation had not been recorded and with seeds weighing <1 mg (*Carpodetus serratus*, *Fuchsia excorticata*, *Weinmannia racemosa*, and *Metrosideros umbellata*; Appendix F), because seeds <1 mg were ignored by captive mice and often passed

undamaged through the digestive systems of captive ship rats (Williams et al. 2000).

Herbivory by invasive red deer

Deer are thought to influence the structure and composition of New Zealand forests primarily by altering the growth and mortality rates of seedlings (Forsyth et al. 2010). The century-level effects of herbivory by invasive red deer on the dynamics of the two forests were evaluated using seedling growth and mortality rates estimated in the presence and absence of deer in the growth and mortality submodels previously described. The data used to parameterize those submodels were collected in a field study at Waitutu Forest during 2002–2008.

Field study methods.—We used two methods to collect data to estimate seedling growth and mortality rates in the presence and absence of deer at Waitutu Forest. First, we tagged $n = 2003$ and $n = 7970$ seedlings on the alluvial and marine terraces, respectively, in February–March 2003 (Coomes et al. 2005, Kunstler et al. 2009, 2013). Seedlings were sampled within 1-m^2 quadrats located to include a range of light conditions and seedling sizes. The fate (alive/dead) and stretched height (mm) of each seedling were remeasured in January 2005. Light over each quadrat was quantified from a hemispherical image taken 1.2 m above each quadrat with a digital camera (Nikon Cool-Pix, 1.3 Megapixel resolution). The percentage of full light received was then estimated using the GLA software (Frazer et al. 1999).

Second, we planted seedlings inside deer exclosures to estimate growth and mortality rates in the absence of deer, because deer were present throughout Waitutu Forest. A random 50% of these exclosures were removed to estimate the effects of deer herbivory on the growth and mortality rates of seedlings of species highly preferred by red deer (e.g., *Griselinia littoralis* and *Schefflera digitata*; Forsyth et al. 2005), because these seldom grew more than ~10 cm tall in Waitutu Forest (Gaxiola et al. 2008) and it was desirable to obtain unbiased estimates of the effects of deer on seedlings of a range of heights. In May 2002, ~4700 seedlings of nine angiosperm and conifer species (six species on each terrace, including three present on both terraces; Table 1) were collected from the alluvial and marine terraces at Waitutu Forest and transported to Lincoln, New Zealand (43.65° S, 172.48° E; Fig. 1), where they were individually potted in soil collected from the seedling's terrace of origin and grown in glasshouse conditions for 26 months. Four replicate samples of the soil from each terrace used in the potting were analyzed by the Environmental Chemistry Laboratory (Palmerston North, New Zealand) for the following nine variables, using the methods outlined in Blakemore et al. (1987): pH, % total C, % total N, C:N, Bray II P, and exchangeable Ca, Mg, K, and Na. A summary of these data (Appendix G) matches

documented differences between soils on those terraces (Parfitt et al. 2005). In December 2003 we identified eight pairs of sites on each terrace that were potentially suitable for planting seedlings. The percentage of full light that each site received was quantified from a hemispherical photograph taken in the center of the site using a digital camera as described previously. Soil samples were also collected (four subsamples aggregated into one sample per site) and analyzed as described previously. We used the soil chemistry and light data to select the four most similar sites on each terrace for this study. In July–August 2004, the seedlings were removed from their pots, their roots were cleaned of all soil (to minimize the risk of introducing glasshouse pathogens to the study area), and were transported in wet newspaper for planting. Seedlings were planted 50 cm apart in a Latin-square design (i.e., each species occurred the same number of times in each row and column, with the order decided randomly). We dug a 10×10 cm hole to a depth of ~15 cm and then covered the roots with soil up to the base of the stem. Seedlings were uniquely tagged. We planted ~25 seedlings of each species in each of the 16 12×12 m plots. Concurrent with the seedlings being planted, all 16 plots were fenced using 2-m posts and 10×10 cm mesh. We waited two years for seedlings to recover from transplanting before we removed fences from a randomly selected eight plots in July 2006, exposing those seedlings to potential deer herbivory. For each seedling, we measured (1) stretched height (mm) from the base of the stem to the tallest living bud, and (2) light above the seedling using a pair of quantum sensors (LI-1905B, LI-COR, Lincoln, Nebraska, USA), as detailed in Coomes et al. (2005). Estimates of light from quantum sensors and hemispherical photos have a 1:1 relationship (Canham 1988) and hence both types of data could be used in SORTIE/NZ. One quantum sensor was used to measure light above each seedling and this measurement was paired to a concurrent measurement of light under open-sky conditions in a nearby clearing or beach. Light was calculated as the percentage of open sky transmitted to each seedling. Seedling mortality and height growth (as previously described) were remeasured each July–August of 2006–2008.

Seedling growth rates in the presence and absence of deer.—Annual seedling growth rates (cm/year) in the presence and absence of deer were estimated using a modified Michaelis-Menten function

$$\frac{\Delta H}{\Delta t} = \frac{\alpha L}{(L + \alpha/\beta)} - \gamma + \text{SF} \qquad (3)$$

where ΔH is change in seedling height (cm), Δt is the time interval (years), L is the light available for the seedling (0–100% of daylight), α and β are parameters describing the asymptotic growth in high light and the slope of the function at zero light, respectively, γ is the intercept that allowed for negative growth, and SF is a

stochastic factor. Accounting for intraspecific variability in growth rates is important because it can allow some seedlings to "escape" from the height tier in which they can be browsed by deer. We estimated the standard deviation (SD) of growth residuals simultaneously with parameters α, β, and γ and used it to implement variability in seedling growth during simulations. This was done by drawing, for each seedling in each simulation step, random deviations from a normal distribution with mean zero and SD as defined previously, and combining them with the deterministic component of growth from the Michaelis-Menten function. Because slow growth in some years tends to compensate for rapid growth in other years, uncorrelated random-growth stochasticity rapidly converges with deterministic growth. Autocorrelation in growth stochasticity generates more realistic predictions of growth and age trajectories (Brienen et al. 2006). We introduced growth autocorrelation by retaining the previous growth deviation when a random number, drawn for each simulation step, was smaller than a predefined autocorrelation value (Appendix B). Seedling growth parameters were estimated using simulated annealing, with the algorithm run for at least 40 000 iterations to maximize the chance of finding a global optimum.

Seedling mortality rates in the presence and absence of deer.—Annual seedling mortality rates (M) in the presence and absence of deer were estimated using a negative exponential function (Kunstler et al. 2009)

$$M = M_{\max} e^{-aH^b - cL^d} \qquad (4)$$

where $M_{\max}$ is the maximum mortality rate and a, b, c, and d are estimated parameters describing how mortality changes with increasing seedling height (H) and light (L) at first measurement. As for seedling growth rates, the parameters describing seedling mortality were estimated by maximum likelihood using simulated annealing run for at least 40 000 iterations.

With the sample sizes required to sensibly estimate mortality rates, it was logistically impossible to include sufficient seedlings of all tree species present in the alluvial terrace forest model in our field study. We estimated parameters for those species using data from surrogate species based on leaf morphophysiology (Appendix B: Fig. B3) and information on deer diet selection in Waitutu Forest (Forsyth et al. 2005) and elsewhere (review in Forsyth et al. 2002). For species avoided by deer (i.e., *Dacrydium cupressinum*, *Prumnopitys ferruginea*, and *Podocarpus hallii*), we used mortality parameters estimated in the presence of deer as surrogates because deer would be unlikely to significantly alter mortality rates. For species preferred or not selected by deer (i.e., *Carpodetus serratus*, *Raukaua simplex*, *Nothofagus solandri* var. *cliffortioides*, and *Metrosideros umbellata*) we used the closest species

from the principal components analysis of leaf morpho-physiology (Appendix B: Fig. B3) as a surrogate.

Model simulations and scenarios

All simulations used the modeled 300×300 m stands and ran for 500 years. Model projections were calculated in one-year time steps. To account for variability in initial conditions, we ran each scenario with 100 different initial conditions generated as described previously. We evaluated four mammalian browser/granivore control scenarios for each forest: +deer +rodents (i.e., ambient browsing and granivory), +deer −rodents, −deer +rodents, and −deer −rodents. All submodels were run simultaneously within each scenario, and the eight SORTIE/NZ parameter files (i.e., one for each scenario in each of the two forests) are provided in the Supplement. The consequences of deer browsing were assessed by comparing the −deer +rodents and +deer +rodents scenarios, and the consequences of rodent granivory by comparing the +deer −rodents and +deer +rodents scenarios. The consequences of both deer browsing and rodent granivory were assessed by comparing the −deer −rodents scenario with the three other scenarios.

Because there were strong temporal (i.e., transient) dynamics in both forests during the 500-year period of interest, we present the results temporally rather than as summaries at any particular time step. The range of variability over 100 replicate runs, representing the variability in initial conditions, was represented by plotting the median and 40–60%, 25–75%, and 2.5–97.5% percentiles for each scenario.

Evaluation of model predictions

We constructed our two forest models to evaluate century-scale consequences of invasive deer and rodents on forest dynamics precisely because field data are unavailable on this timescale. Similarly, no other study has partitioned out the effects of deer and rodents on the dynamics of New Zealand forests. Although quantitative validation of model predictions was impossible, some short-term predictions were evaluated using data collected in other New Zealand forests following colonization by deer and rodents (e.g., Wardle et al. 2001, Mason et al. 2010, Wright et al. 2012), and some long-term predictions were evaluated against palynological trends (e.g., McGlone et al. 1996) and the predictions of a forest gap model simulator (Hall and Hollinger 2000, Hall and McGlone 2006). Our SORTIE/NZ alluvial and marine terrace forest models would be supported if their predictions for the trajectories of seedling and sapling densities in the presence and/or absence of deer and rodents were consistent with those observed in New Zealand forests in the presence and/or absence of deer and/or rodents. Similarly, our models would be supported if their long-term predictions for the trajectories of canopy dominants (i.e., their basal areas) in the absence of deer and rodents were consistent with

those observed in palynological studies conducted near our study area. Conversely, our models would not be supported if their predictions for the trajectories of seedlings, saplings, and adults were inconsistent with these short- and long-term observations.

RESULTS

We first report the results of the field studies estimating probabilities of seed predation by rodents in mast and non-mast years and seedling growth and mortality rates in the presence and absence of deer. We then report the results of the SORTIE/NZ model simulations evaluating the four rodent/red deer scenarios in each of the alluvial and marine terrace forests.

Field study of seed predation by invasive rodents in mast and non-mast years

Alluvial terrace forest.—The highest probabilities of seed predation by invasive rodents observed in our field study (0.5–0.9) occurred in a mast year (when rodents were abundant) in two canopy species, the conifer *Dacrydium cupressinum* and the angiosperm *Nothofagus solandri* var. *cliffortioides* (and hence also for the conifer *Podocarpus hallii* and the angiosperm *N. menziesii* for which they were surrogates) (Fig. 3; Appendix H: Fig. H1). Although the probabilities of seed predation were substantially lower (<0.4) for these four canopy species in a non-mast year (when rodents were scarce), they were nearly always higher than for the other three species trialed (Fig. 3; Appendix H: Fig. H1). Only for *Griselinia littoralis* was the probability of seed predation by rodents lower in a mast compared with a non-mast year (Fig. 3; Appendix H: Fig. H1).

Relative basal areas of up to two neighboring tree species were important predictors of the probability of seed predation for some species, confirming that there were spatial patterns in seed predation; other tree species were discarded from fitted models based on AIC_c (Appendix H: Table H1). There were spatial patterns of predation on *Dacrydium cupressinum* seed (and hence on *Podocarpus hallii*) seed in a mast and non-mast year, and also on *Raukaua simplex* (and hence on *Pseudowintera colorata* and *Schefflera digitata*), based on trials conducted in a non-mast year only. In both the mast and non-mast years, the probability of *D. cupressinum* and *Podocarpus hallii* seeds being eaten by rodents increased as the relative basal area of *Nothofagus menziesii* increased (Appendix H: Table H2). In the non-mast year, the probability of *D. cupressinum* and *Podocarpus hallii* seeds being eaten by rodents also decreased as the relative basal area of *D. cupressinum* increased. The probability of *Raukaua simplex*, *Pseudowintera colorata*, and *Schefflera digitata* seeds being eaten by rodents also decreased in mast and non-mast years as the relative basal area of *D. cupressinum* increased (Appendix H: Table H2).

Marine terrace forest.—As in the alluvial terrace forest, the highest probabilities of seeds being eaten by rodents in our field study (≥ 0.8) occurred in mast years
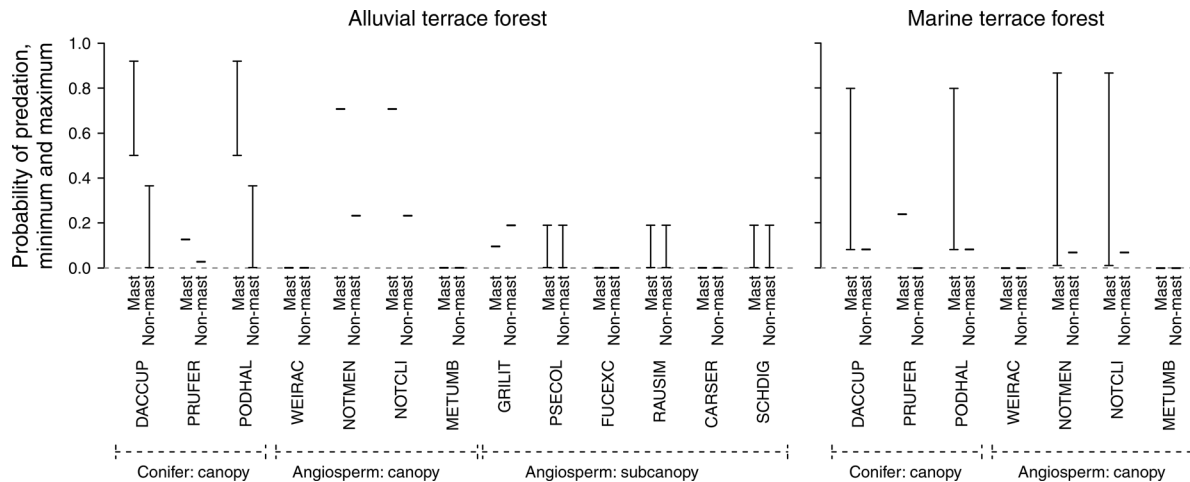
Fig. 3. Minimum and maximum probabilities of rodents eating seeds in mast and non-mast years for tree species in the alluvial (left panel; $n = 13$ species) and marine (right panel; $n = 7$ species) terrace forests at Waitutu Forest, New Zealand. Probabilities for five species were from seed predation trials; probabilities for other species were inferred from surrogate species (Appendix H). Minima and maxima indicate spatial variation in seed predation probabilities as a function of relative basal areas of neighboring tree species (Appendix H). Within tree classes, species are listed left to right in descending order of abundance based on current adult basal areas. For species' acronyms see Table 1.

in the canopy conifers *Dacrydium cupressinum* and *Podocarpus hallii* and the canopy angiosperms *Nothofagus solandri* var. *cliffortioides* and *N. menziesii* (incorporating assumptions based on surrogate species; Fig. 3; Appendix H: Fig. H2). However, there were strong spatial patterns of seed predation for these four species in mast years: predation on *N. solandri* var. *cliffortioides* and *N. menziesii* seeds declined with increasing relative basal areas of both *N. solandri* var. *cliffortioides* and *Podocarpus hallii*, and predation on *D. cupressinum* and *Podocarpus hallii* seeds declined with increasing relative basal area of *Podocarpus hallii* (Appendix H: Table H3). Seeds of the other canopy conifer, *Prumnopitys ferruginea*, experienced a constant (i.e., nonspatial) probability of rodent predation (0.22) in mast years. Probabilities of seed predation by rodents were low (≤0.08) and nonspatial for all species in non-mast years (Fig. 3; Appendix H: Fig. H2).

Field study of seedling growth and mortality in the presence and absence of invasive deer

Our field study revealed that the three conifer species present in both the alluvial and marine terrace forests had low growth rates (<3 cm/yr) that changed little with height, light, and the presence or absence of deer (Fig. 4; Appendix I: Figs. I1 and I2). A similar pattern was evident in the mortality rates of conifer seedlings, except that *Podocarpus hallii* in the marine terrace forest had higher mortality at heights < 30 cm in the absence of deer (Appendix I: Figs. I1 and I2). There were stronger effects of height and light on conifer mortality in the alluvial terrace forest, with small seedlings in low light having the highest mortality (Appendix I: Fig. I1).

Growth rates of all angiosperm species were greater in the absence of deer in both terrace forests, except for *Pseudowintera colorata* (Fig. 4; Appendix I: Figs. I1 and I2). However, differences were relatively minor for *Nothofagus solandri* var. *cliffortioides* (both terrace forests) and *N. menziesii* (marine terrace forest). The negative effect of deer on growth rates was particularly marked for the following six species in the alluvial terrace forest: *Weinmannia racemosa* and *N. menziesii* (both canopy species), and *Fuchsia excorticata*, *Raukaua simplex*, *Carpodetus serratus*, and *Schefflera digitata* (all subcanopy species). Deer had a strong negative effect on the growth rates of two angiosperm canopy species in the marine terrace forest (*Metrosideros umbellata* and *W. racemosa*; Fig. 4; Appendix I: Fig. I2). Maximum growth rates of 10–25 cm/yr were attained at highest light availability in the absence of deer by the angiosperm subcanopy species *F. excorticata*, *R. simplex*, *C. serratus*, and *S. digitata* in the alluvial terrace forest (Fig. 4; Appendix I: Fig. I1).

The mortality rates of angiosperm seedlings were nearly always highest at small heights and/or low light (Fig. 4; Appendix I). The mortality rates of *N. solandri* var. *cliffortioides*, *F. excorticata*, *G. littoralis*, *R. simplex*, *C. serratus*, and *S. digitata* in the alluvial terrace forest were substantially lower in the absence of deer (Fig. 4; Appendix I: Fig. I1). The effects of deer on the mortality rates of angiosperm seedlings in the marine terrace forest were less marked than on the alluvial terrace, but were lower in the absence of deer for the angiosperm canopy species *W. racemosa*, *N. menziesii*, and *N. solandri* var. *cliffortioides* (Fig. 4; Appendix I: Fig. I2). The mortality rates of the angiosperm subcanopy species *S. digitata* (and hence *C. serratus* and *F. excorticata*, for which it
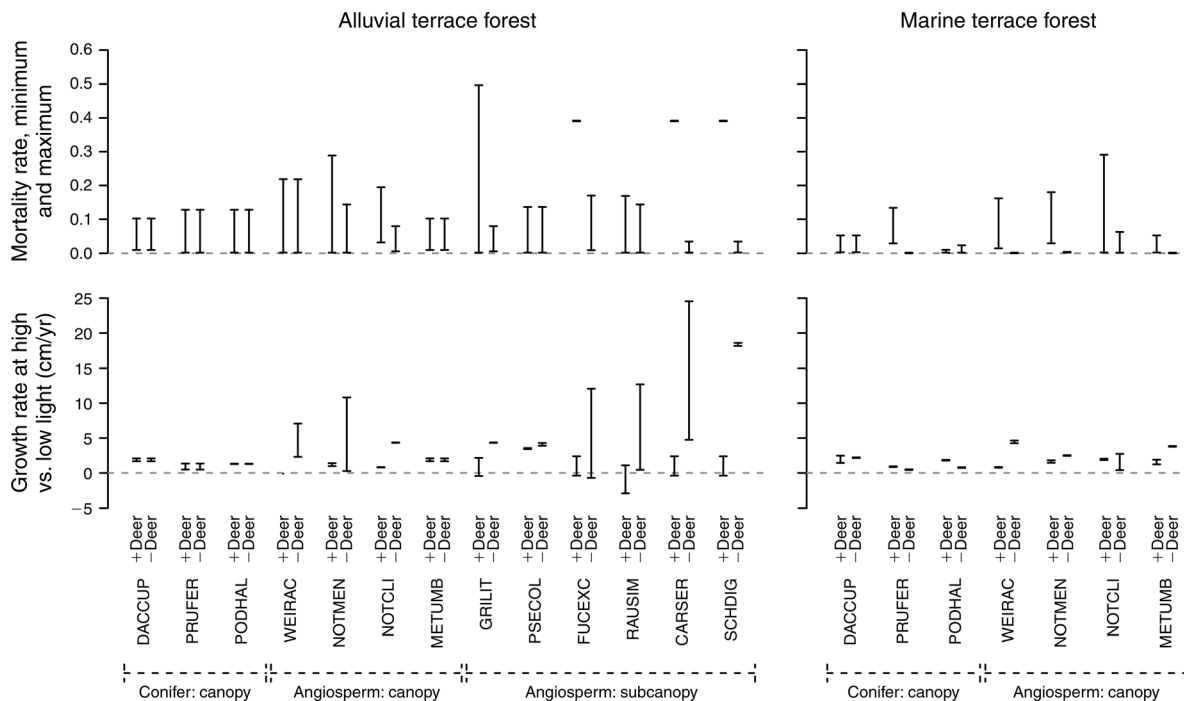
FIG. 4. Minimum and maximum annual mortality (upper panels) and growth (lower panels) rates of seedlings of tree species in the alluvial (left panels; $n = 13$ species) and marine (right panels; $n = 7$ species) terrace forests in the presence (+) and absence (−) of deer at Waitutu Forest, New Zealand. Mortality and growth rates varied with light and seedling height for some species (Appendix I). Minimum and maximum growth rates are presented for the 10th and 90th percentiles of light recorded for all seedlings in the alluvial terrace forest, i.e., at low (3%) and high (15%) light transmission, respectively. Mortality and growth rates of some species were inferred from surrogate species (Appendix I). Species are listed in descending order of abundance within tree classes based on current adult basal areas. For species' acronyms see Table 1.

was a surrogate) were particularly high in the presence of deer (Fig. 4, Appendix I: Fig. I1; Appendix J: Fig. J1 B).

Modeled century-scale effects of invasive deer and rodents on total seedling densities, total sapling densities, and total adult basal areas

Our SORTIE/NZ models predicted that the trajectories of total seedling densities, total sapling densities, and total adult basal areas varied with terrace forest and herbivory scenario (Fig. 5; Appendix K). In the alluvial terrace forest, the presence of deer led to higher total seedling and sapling densities, but substantially lower adult basal areas (Fig. 5; Appendix K: Fig. K1). Most of the increase in sapling densities in the absence of deer was due to the angiosperm subcanopy species *Schefflera digitata*, the seedlings of which were strongly negatively affected by deer browsing (as we will describe). The highest basal areas (~125 m²/ha) occurred at ~450 years in the absence of both deer and rodents (Fig. 5; Appendix K: Fig. K1). Compared with deer, the presence of rodents had much weaker and more variable effects on total seedling and sapling densities in the alluvial terrace forest (Fig. 5).

Rodents had a negative effect on seedling densities in the marine terrace forest, but the magnitude of the rodent effect was weaker than in the alluvial terrace forest and did not translate into decreased sapling densities and adult basal areas (Fig. 5; Appendix K: Fig. K2). The presence of deer had no consistent effects on seedling or sapling densities relative to the absence of deer in the marine terrace forest. Neither rodents nor deer had any effect on adult basal areas in the marine terrace forest.

Modeled century-scale effects of invasive rodents and deer on conifer vs. angiosperm dominance

Our SORTIE/NZ models predicted that the presence of deer would lead to increased proportions of conifer seedlings, saplings, and adults in the alluvial and marine terrace forests. The presence of rodents was predicted to have the opposite effect, leading to increased proportions of angiosperm seedlings, saplings, and adults in the marine terrace forest only; there was no consistent effect of rodents in the alluvial terrace forest (Fig. 6; Appendix L: Fig. L2 cf. Fig. L1). Hence, in the marine terrace forest, conifers were most dominant in all three life-history stages in the presence of deer and absence of rodents, and were least dominant in the absence of deer
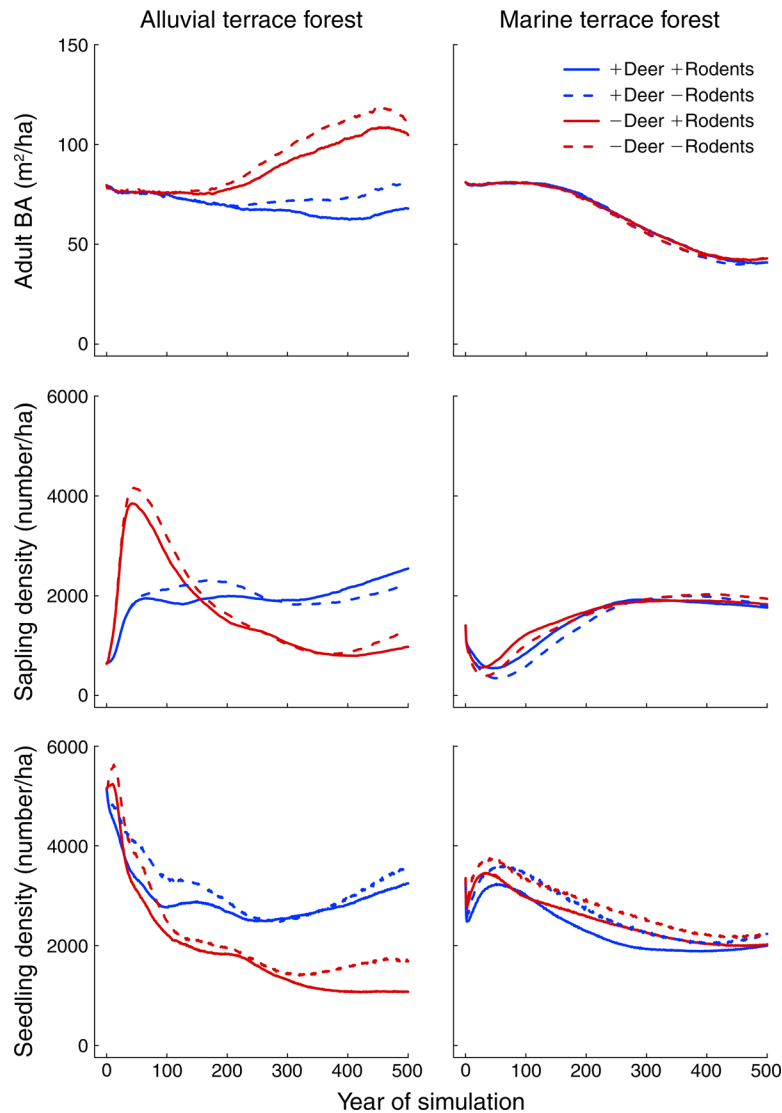
FIG. 5.   Graphs of 500-year trends in total adult basal area (BA, upper panels), total sapling density (center panels), and total seedling density (lower panels) in four herbivory scenarios (presence (+) and absence (−) of deer and rodents) for the alluvial and marine terrace forests at Waitutu Forest, New Zealand. The medians of 100 simulations are shown for each scenario; for uncertainties see Appendix K.

and presence of rodents. In the alluvial terrace forest, conifers were similarly more dominant in all three life-history stages in the presence of deer than in the absence of deer, irrespective of whether rodents were present or absent.

The predicted effects of deer and rodents on the relative dominance of conifers and angiosperms varied with time and life-history stage, occurring first in seedlings, then in saplings, and finally in adults (Fig. 6). For example, the increasing dominance of adult conifers in the marine terrace forest in the presence of deer began at ~350 years (cf. 150 years in the alluvial terrace forest) and conifers were still increasing at 500 years (Fig. 6; Appendix L: Fig. L2 cf. Fig. L1).

Modeled century-scale effects of invasive rodents on tree populations

Alluvial terrace forest.—Our alluvial terrace forest model predicted that the removal of rodents would lead to substantially increased seedling densities, moderately increased sapling densities, and weakly increased adult basal areas (after ~400 years) of the canopy codominant *Nothofagus menziesii*, and also of *Dacrydium cupressinum* and *N. solandri* var. *cliffortioides* (Fig. 7; Appendix M). In contrast, the removal of rodents would reduce seedling and sapling densities and adult basal areas of *Prumnopitys ferruginea*, *Schefflera digitata*, and *Pseudowintera colorata*. Rodents were predicted not to affect the densities of seedlings (or any other life-history stage)
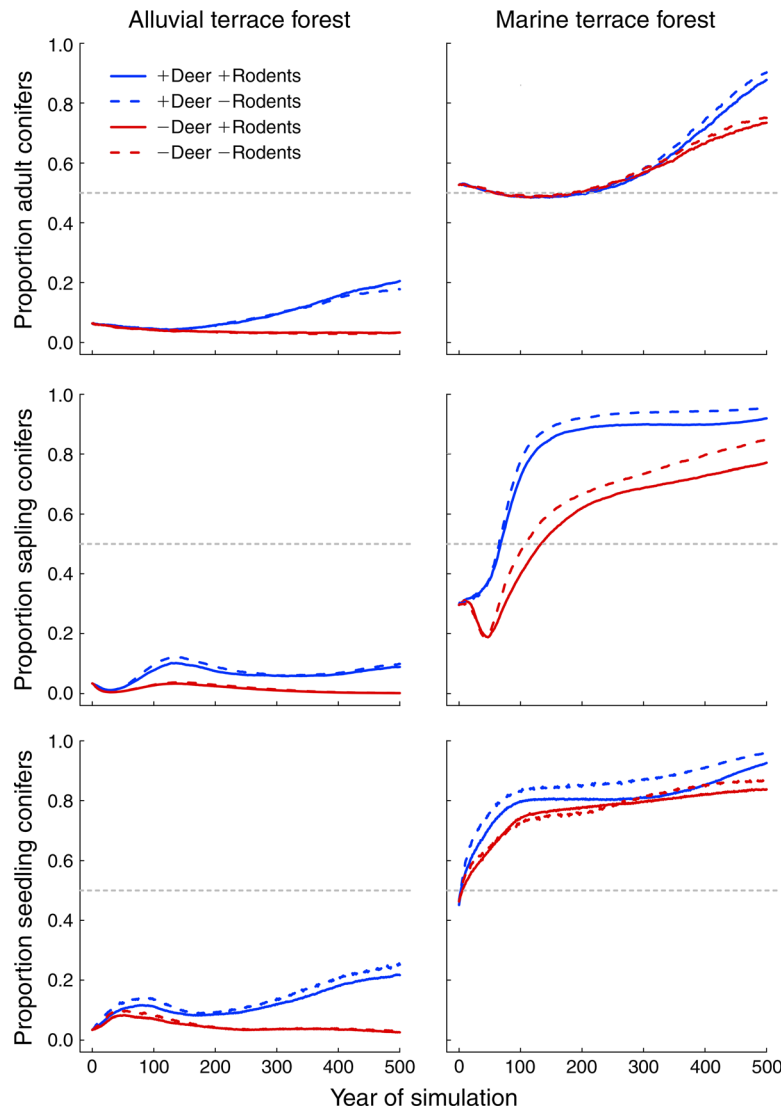
FIG. 6. Graphs of predicted 500-year trends in conifers as a proportion of adult basal area (upper panels), sapling density (center panels), and seedling density (lower panels) in four herbivory scenarios for the alluvial and marine terrace forests at Waitutu Forest, New Zealand. The horizontal gray dashed line indicates equal proportions. The medians of 100 simulations are shown for each scenario; for uncertainties see Appendix L.

of the codominant *Weinmannia racemosa*, or of any other tree species in the alluvial terrace forest (Fig. 7; Appendix M).

Marine terrace forest.—Our marine terrace forest model predicted that the absence of rodents would lead to increased seedling and sapling densities of the canopy dominant *Dacrydium cupressinum*, and weakly increased adult basal areas after ~450 years (Fig. 8; Appendix N). Removing rodents also weakly increased *Nothofagus menziesii* seedling densities, but these increases did not translate into increased sapling densities and adult basal areas. Conversely, densities of *Podocarpus hallii*, *Prumnopitys ferruginea*, *Metrosideros umbellata*, and *Weinmannia racemosa* seedlings and saplings decreased in the absence of rodents. Rodents

were predicted not to affect the abundances of *N. solandri* var. *cliffortioides* seedlings, saplings, or adults.

Modeled century-scale effects of invasive deer on tree populations

Alluvial terrace forest.—Our alluvial terrace forest model predicted that deer would have a substantial negative effect on seedlings, saplings, and eventually adults of the codominant canopy species *Weinmannia racemosa* (Fig. 7; Appendix M): in the absence of deer, the basal areas of *W. racemosa* increased, attaining densities greater than the codominant *Nothofagus menziesii* after ~300 years. In the presence of deer, seedlings and saplings (but not adults) of the angiosperm subcanopy tree *Pseudowin-*
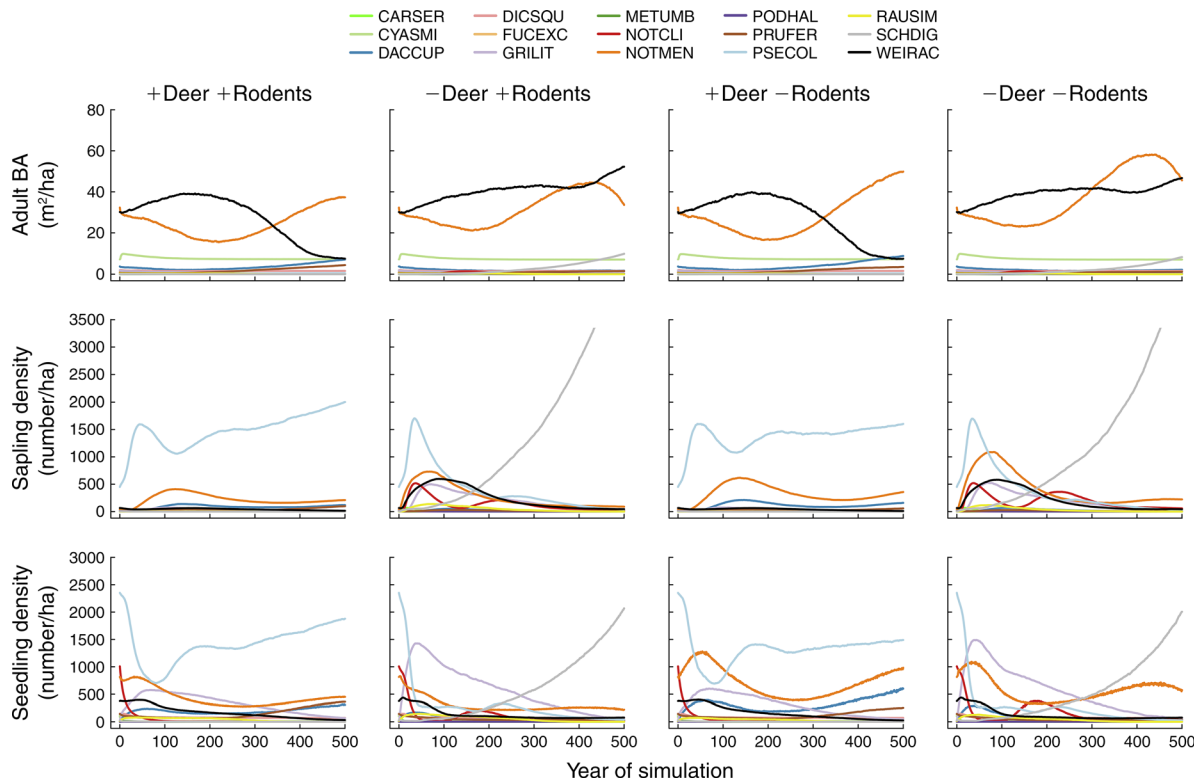
Fig. 7. Graphs of predicted 500-year trends in adult basal area (upper panels), sapling density (center panels), and seedling density (lower panels) for each of the 15 tree species in four herbivory scenarios for the alluvial terrace forest at Waitutu Forest, New Zealand. The medians of 100 simulations are shown; for uncertainties see Appendix M. For species' acronyms see Table 1.

tera colorata became increasingly abundant after ~300 years, with a concomitant decline in other angiosperm species except *N. menziesii* and *Metrosideros umbellata* (Fig. 7; Appendix M). The seedlings and saplings of five angiosperm subcanopy tree species (*Carpodetus serratus*, *Fuchsia excorticata*, *Griselinia littoralis*, *Raukaua simplex*, and *Schefflera digitata*) became more abundant in the absence of deer, but these increases translated into increased adult basal areas for *S. digitata* only. Seedlings, saplings, and adults of the angiosperm canopy tree *N. solandri* var. *cliffortioides* also became more abundant in the absence of deer, whereas seedlings, saplings, and adults of the two most dominant conifers, *Dacrydium cupressinum* and *Prumnopitys ferruginea*, and seedlings of *Podocarpus hallii*, were all much less abundant in the absence of deer. Deer did not affect the abundances of any life-history stage of either of the two tree fern species, *Cyathea smithii* and *Dicksonia squarrosa* (Appendix M).

Marine terrace forest.—Our marine terrace forest model predicted that the presence of deer would not affect the abundances of any life-history stage of *Dacrydium cupressinum*, the dominant tree species in this forest (Fig. 8, Appendix N). The presence of deer had a negative effect on all *Weinmannia racemosa* and *Nothofagus menziesii* life-history stages, although the effect of deer on *W. racemosa* was weaker than in the alluvial terrace forest. Seedlings, saplings, and adult

basal areas of *N. menziesii* increased in the absence of deer. Seedlings and saplings of one conifer, *Prumnopitys ferruginea*, also increased in the absence of deer. In contrast, seedling and sapling densities, and to a much lesser extent adult basal areas, of the conifer *Podocarpus hallii* were predicted to decline in the absence of deer. Deer were predicted not to have an effect on *Metrosideros umbellata* basal areas.

Interactive effects of invasive rodents and deer on forest dynamics

The temporal dynamics inherent in both terrace forests make assessment of interactions between the predicted effects of invasive rodents and deer difficult. However, our models did not predict strong interactive effects of invasive rodents and deer on total seedling densities, total sapling densities, or total adult basal areas (Fig. 5; Appendix K), or on the demography of individual tree species (Figs. 7 and 8; Appendices M and N).

Evaluation of model predictions

A detailed evaluation of the short- and long-term predictions of the alluvial and marine terrace forest models is provided in Appendix O. Briefly, the predicted increasing dominance of the canopy tree *Nothofagus menziesii* in all four scenarios for the alluvial terrace

forest (Fig. 7) is consistent with the palynological record showing that this species is still expanding in southwestern South Island (McGlone et al. 1996). The predicted decreasing abundances of *N. menziesii* and *N. solandri* var. *cliffortioides* in the marine terrace forest relative to the conifer *Dacrydium cupressinum* (Fig. 8) are consistent with the hypothesis that these species are competitively excluded by podocarps on less fertile and poorly drained soils (Urlich et al. 2005), and are also in agreement with simulation studies using an ecosystem process model showing a dominance of *D. cupressinum* at some sites in the southwestern South Island (Hall and Hollinger 2000, Hall and McGlone 2006). Our short-term predictions of the effects of deer on seedlings and saplings are consistent with the results of national exclosure studies (Wardle et al. 2001, Mason et al. 2010, Wright et al. 2012), and our predictions in the presence and absence of rodents are in broad agreement with a study that showed increased recruitment of *Nothofagus* spp. seedlings after *Rattus norvegicus* were removed, in the absence of deer (Allen et al. 1994).

DISCUSSION

Our individual-based SORTIE/NZ models enabled us to evaluate the century-scale consequences of red deer browsing and rodent granivory on the dynamics of two temperate forest communities in a structured way. The predictions of our models were consistent with empirical data from exclosure and palynological studies, and with a forest process model, implying that our models captured the essential dynamics of the systems. There were six key findings. (1) Effects of invasive deer and rodents will be greater in the forest growing on the more P-rich soil. (2) Preferential browsing by deer on seedlings of angiosperm canopy and subcanopy species alters the competitive hierarchy among angiosperm and conifer seedlings such that conifers will become more dominant as saplings and adults. (3) Deer browsing and rodent granivory are both predicted to reduce the adult basal areas of canopy dominants, but to varying extents. (4) Deer- and rodent-induced reductions in seedling densities do not always translate into reduced sapling and adult tree abundances. (5) Effects of invasive deer on forest dynamics are predicted to be greater than those of invasive rodents. (6) Effects of invasive deer and rodents on forest dynamics will be largely distinct from each other because they impact different tree species and different life-history stages of trees.

Invasive mammal impacts and soil fertility

Soil fertility is a key determinant of forest composition globally (Vitousek et al. 1995, Wardle et al. 2004, Peltzer et al. 2010) and soil fertility gradients such as the Waitutu Forest geologic chronosequence are typically accompanied by plant species replacement (Wardle et al. 2004, Coomes et al. 2005). This makes it difficult to partition responses that are due to soil fertility from those due to species replacement. However, our objective was to forecast the century-scale effects of invasive mammals on forests growing on soils of contrasting fertility rather than to understand the fundamental causes of changes in forest composition. We believe that using forests of differing composition along a soil fertility gradient is a more useful approach to understanding how the impacts of mammals vary with soil fertility than developing a model that holds species identity constant and allows only soil fertility to change (see also Allison and Goldberg 2002). In particular, trends shown in a subset of species may not be the same as those shown by a whole community, due to differences in intra- and interspecific responses to changes in soil fertility.

In agreement with the observation that mammals consume a greater proportion of net primary productivity in more productive ecosystems (including those that are more fertile) (McNaughton et al. 1989), we found that invasive deer had greatest impacts on sapling densities and adult basal areas in the more fertile alluvial terrace forest. Rodents had weaker impacts that were similar in both terrace forests.

There are several reasons for invasive deer having a substantially greater effect in the alluvial terrace forest relative to the marine terrace forest. First, a greater proportion of species were more strongly affected by deer browsing in the alluvial terrace forest. The alluvial terrace forest contained more angiosperm species (Table 1) that were substantially more dominant by basal area (Fig. 6) than did the marine terrace forest (Table 1), and the seedlings of some of these species had substantially reduced growth rates and increased mortality rates in the presence of deer (e.g., *Schefflera digitata*; Fig. 4, Appendix I: Appendix J: Fig. J1). Second, the initial basal areas of the species strongly affected by deer were greater in the alluvial terrace forest. For example, although *Weinmannia racemosa* occurred in both forests, it was more abundant in absolute and relative terms in the alluvial terrace forest, and was substantially negatively affected by the presence of deer (Fig. 7; Appendix M). Third, the higher growth rates of the seedlings, saplings, and adults of most species in the alluvial terrace forest (Fig. 4; Appendices B and I; see also Kunstler et al. 2013) meant that forest turnover was more rapid there compared with the marine terrace forest, providing more opportunity for forest structure and composition to change (e.g., for conifer seedlings to establish and grow into saplings and then adults). The low growth rates observed in the marine terrace forest were at least partly due to P limitation (Wardle et al. 2004, Coomes et al. 2005, Parfitt et al. 2005).

Our study highlights the difficulties of making generalizations about the long-term effects of multiple mammalian herbivores on forests growing on soils of contrasting fertility. The tree life-history stage(s) affected by each herbivore (Fig. 2), and the magnitude of those effects, will clearly be important, but the myriad subsequent processes that might prevent the short-term
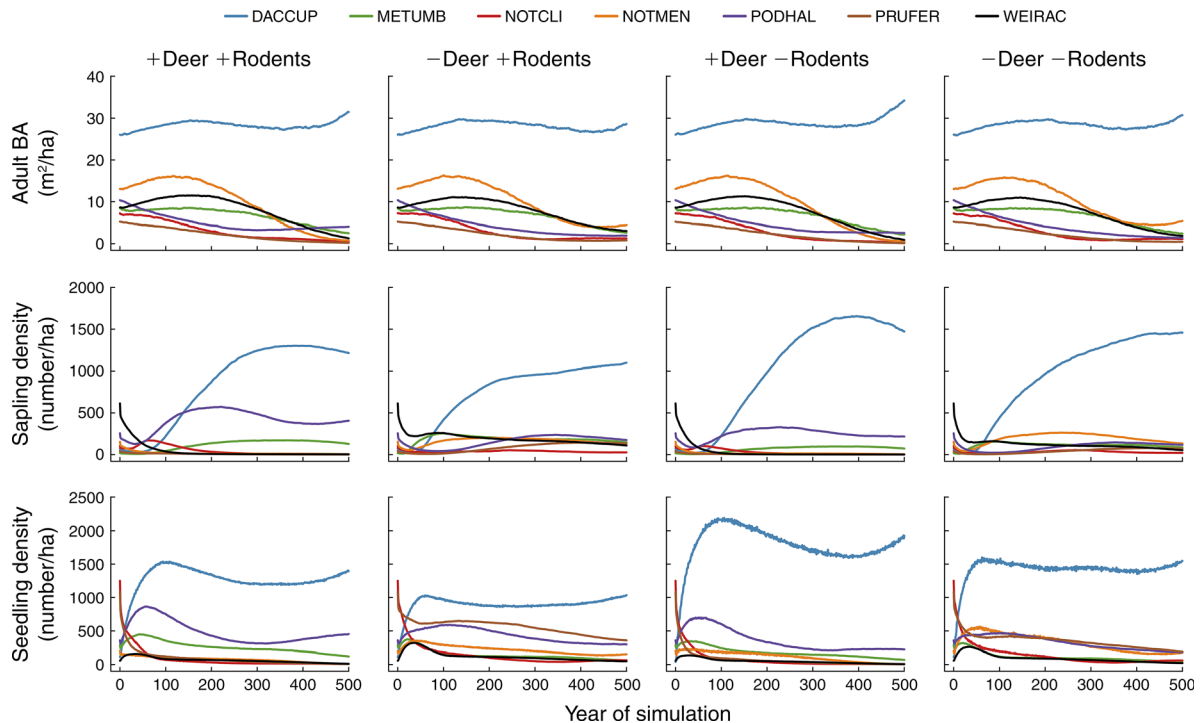
Fig. 8. Graphs of predicted 500-year trends in adult basal area (upper panels), sapling density (center panels), and seedling density (lower panels) for each of the seven tree species in four herbivory scenarios for the marine terrace forest at Waitutu Forest, New Zealand. The medians of 100 simulations are shown; for uncertainties see Appendix N. For species' acronyms see Table 1.

effects of herbivores translating into longer-term changes in forest structure and composition also need to be considered (Pacala et al. 1996, Rees et al. 2001, Hulme and Kollmann 2005).

Century-scale effects of invasive deer and rodents on conifer vs. angiosperm dominance

The role of herbivory in mediating competition between conifers and angiosperms has received little attention (Bond 1989, Becker 2000, Coomes et al. 2005). At Waitutu Forest, the presence of deer was predicted to strongly alter competition in favor of conifers in both forests by reducing the growth rates, and increasing the mortality rates, of angiosperms relative to conifers (Fig. 4, Appendix I), as predicted by Holloway (1950). This finding mirrors the replacement of angiosperm trees by spruce (*Picea glauca* and *P. mariana*) that occurred following the colonization of Isle Royale by moose (Pastor et al. 1988, 1993). However, our models predict that it will take several more centuries for the altered competitive hierarchies among seedlings at Waitutu Forest to translate to increased dominance of conifers in the canopy, due to the slow growth rates and longevity of New Zealand conifers.

In contrast to deer, the presence of rodents altered conifer/angiosperm dominance only in the marine terrace forest. The presence of rodents led to increased dominance of angiosperm seedlings, saplings, and adults in the marine terrace forest because they consumed large proportions of seeds of the dominant species, *Dacrydium cupressinum*, a conifer, and the reduction in seedlings of that species was not compensated for in later competitive stages (e.g., increased growth of seedlings that did recruit). Although tall ferns and deep shade reduce regeneration opportunities for conifers in forest on the more fertile alluvial terraces relative to forest on the less fertile marine terrace (Coomes et al. 2005, 2009; Appendix C: Fig. C1A), our results indicate strong, but opposing, roles of invasive deer and rodents in mediating the outcome of conifer–angiosperm dominance, but these effects may take several hundred years to become apparent in the adult life-history stage. The role of herbivory in determining the outcome of conifer–angiosperm competition deserves wider consideration.

Century-scale effects of invasive rodents on tree populations

Despite rodents being a widespread invasive taxon (e.g., they have reached >80% of the world's major islands; Atkinson 1985), the century-scale demographic effects of invasive rodents on long-lived tree populations and forest dynamics have not been investigated. Norghauer and Newbery (2011) used stage-based population matrix projections to show that excluding mammalian granivores would increase the population growth rates of two tree species in tropical lowland forest, but their approach did not account for the myriad other forest dynamic processes (e.g., compensatory growth by

conspecifics and/or competitors) that may occur. Rodents at Waitutu Forest were predicted to substantially reduce seedling densities (and sometimes sapling densities) of several canopy tree species in both terrace forests, but in the marine terrace forest these translated into weakly reduced adult basal areas for only one species (*Dacrydium cupressinum*). In contrast, in the alluvial terrace forest, the basal areas of three species (*Prumnopitys ferruginea*, *Pseudowintera colorata*, and *Schefflera digitata*) increased, owing to reduced competition from species with seeds preferred by rodents.

Generalist seed predators such as house mice can persist in non-mast years and are not readily satiated by mast seed crops (Janzen 1971, Hulme 1998, Wilson et al. 2007). Rodents can affect the demography of trees that lack vegetative reproduction and persistent seed banks (Hulme 1998, 2002, Hulme and Kollmann 2005), as is the case for most tree species in our study (Beveridge 1967, Wardle 1984). Hulme (1998) and subsequent workers considered a demographic effect of seed predators to be shown if the recruitment of seeds into seedlings is reduced (e.g., Zwolak et al. 2010). However, our results indicate that such consequences often may not translate into altered abundances of saplings or adult trees due to intraspecific (e.g., self-thinning; Harper 1977) and competitive effects among and between seedlings, saplings, and adults (e.g., Kobe 1996, 1999, Pacala et al. 1996).

Spatial and temporal variation in patterns of rodent seed predation may be important for the persistence of plant populations (Hulme and Kollmann 2005). Seed predation rates at Waitutu Forest varied strongly for several canopy tree species as a function of neighborhood community composition and whether it was a mast or a non-mast year. These results suggest that the spatial arrangement of mast-seeding species, and the dispersal distances of their seeds, will be important determinants of the long-term effects of rodents in other mixed forests (Kelly and Sork 2002, Wilson et al. 2007; review in Terborgh 2012).

The diet of the house mouse is dominated by invertebrates and seeds, with other plant parts seldom present (Smith et al. 2002, Ruscoe and Murphy 2005, Angel et al. 2009). Although the Pacific rat may browse newly germinated seedlings (Campbell and Atkinson 2002), this species is uncommon at Waitutu Forest relative to house mice (Ruscoe 2004). Hence, rodent browsing on seedlings is likely to be unimportant relative to rodent seed predation. However, the dietary preferences of invasive rodents (especially house mice) in New Zealand for seeds of native species, whether rodents destroy or disperse the seeds, and rodents' rates of seed consumption, are poorly known (Appendix F). We used only five species of seeds in our seed predation trials because we could not obtain sufficient seeds of other species. This shortcoming meant that some parameters used in the seed predation submodel were estimated from surrogate species with similar seed and fruit characteristics, or from published data (Appendix F). Our findings should therefore be extrapolated cautiously until those parameters can be confirmed in field studies.

Little is known about seed predation by invertebrates in New Zealand forests, and ground beetles (Coleoptera: Carabidae) and weta (Orthoptera: Anostostomatidae) may have removed some smaller seeds at Waitutu Forest (Wilson et al. 2007). However, the few other studies of seed predation in New Zealand forests have confirmed that rodents are much more important predators of larger seeds than are invertebrates (Beveridge 1967, Berry 2006).

Finally, we are convinced that the seed removal observed in our field study was predation rather than hoarding (Vander Wall et al. 2005) for two main reasons (Wilson et al. 2007). First, the rodent species in our study area were not scatter-hoarders, and larder-hoarding by these species has been observed only in captivity (Vander Wall 1990; review in Wilson et al. 2007). Further, any larder-hoarding that may occur in the wild is unlikely to favor germination (Hulme 2002). Second, husks of *Dacrydium cupressinum* and *Nothofagus* spp. seeds usually remained in our seed dishes, indicating that the seeds had been eaten (Wilson et al. 2007).

Century-scale effects of invasive deer on tree populations

Seedling shade tolerance is a critical determinant of the dominance of adult trees in mature temperate and tropical forests (Kobe et al. 1995, Kobe 1996, 1999, Pacala et al. 1996, Rees et al. 2001), and browsing by deer can alter the competitive growth–mortality hierarchies among species (Côté et al. 2004, Tripler et al. 2005, Long et al. 2007, Krueger et al. 2009). At Waitutu Forest, browsing by invasive red deer differentially altered the relationships between light and seedling growth and mortality, particularly in the more fertile alluvial terrace soil (Fig. 4; Appendix I). Our simulation models, parameterized with these seedling growth and mortality relationships, predicted that the presence of deer would lead to lower sapling densities (within the first 150 years) and adult tree basal areas in the alluvial terrace forest. Although the effects of deer on seedlings and saplings have been well documented (reviews in Gill and Beardall 2001, Côté et al. 2004), long-term effects on adult trees have been less well quantified. The most striking effect of invasive red deer on an adult life-history stage at Waitutu Forest was the codominant alluvial terrace forest tree, *Weinmannia racemosa*, which is also New Zealand's most numerous canopy species (Peltzer and Payton 2006) and is highly preferred by red deer (Forsyth et al. 2002, 2005). Basal areas of adult *W. racemosa* were substantially reduced after ~300 years in the presence of deer relative to the absence of deer.

Deer were also predicted to have significant effects on angiosperm subcanopy trees, consistent with observations from short-term (i.e., ≤40 years) exclosure studies

(e.g., Wardle et al. 2001, Mason et al. 2010, Wright et al. 2012). In particular, deer reduced the growth rates, and increased the mortality rates, of some angiosperm seedlings (e.g., *Schefflera digitata* [Appendix J] and *Fuchsia excorticata*) such that none "escaped" to grow into saplings and then adults. The seedling growth and mortality rates of one angiosperm subcanopy tree, *Pseudowintera colorata*, were unaffected by deer, and all life-history stages of this species increased in abundance in the presence of deer due to alteration of the seedling competitive hierarchy (see also Wardle et al. 2001, Forsyth et al. 2010, Mason et al. 2010). More generally, the effects of deer on a tree species depend on the extent to which other tree species in the community are affected by these processes.

This is the first study to evaluate the effects of deer browsing on seedling growth and mortality in New Zealand using seedlings planted inside and outside exclosures (Appendix J). The rarity of tall seedlings of species preferred by deer in the study area (Coomes et al. 2005, Forsyth et al. 2005, Gaxiola et al. 2008) required us to grow seedlings in a glasshouse for two years before planting. However, it was logistically impossible to plant sufficient numbers of seedlings of all tree species inside and outside deer exclosures, and for those species we used relationships from surrogate species of similar preference to deer (Forsyth et al. 2002, 2005) and leaf morphophysiology (Appendix B: Fig. B3). We encourage others to estimate the effects of herbivory by invasive mammals on key life-history stages in order to parameterize forest models, but the logistical difficulties of doing this should not be underestimated.

Century-scale effects of invasive rodents and deer on forest dynamics

Deer and rodents had different predicted absolute and relative effects on forest dynamics, particularly in the alluvial terrace forest. This occurred because deer and rodents impacted different tree life-history stages and different tree species, and explains why our models did not predict strong interactive effects of rodents and deer on forest dynamics. For example, in the alluvial terrace forest, seedling growth and mortality rates of the canopy dominant *Weinmannia racemosa* were strongly reduced by deer browsing, but the very small seeds (<1 mg) of this species were not eaten by rodents. Conversely, the two species with seeds subject to the highest predation rates, *Nothofagus solandri* var. *cliffortioides* and *Dacrydium cupressinum*, had seedling growth and mortality rates that were little affected by deer. Browsing by deer on seedlings was a stronger demographic filter than seed predation by rodents at Waitutu Forest, consistent with short-term experimental findings from African savannah woodland (Maclean et al. 2011).

Our models predict that exclusion of invasive red deer would have greater benefits for restoring pre-invasion forest dynamics than exclusion of invasive rodents, and that removing both deer and rodents would not have substantially greater benefits than removing only deer. Rodents have other significant effects in New Zealand's forests—including direct predation on native wildlife and supporting larger populations of invasive predators such as stoats (*Mustela erminea*; King 1983, 2005, King and Moller 1997)—that should also be considered when prioritizing control actions. Importantly, excluding deer is predicted to most benefit the forest growing on the relatively fertile soils of the alluvial terrace, which occur on only a small proportion of the landscape at Waitutu Forest (Fig. 1). The feasibility and costs of excluding deer or rodents would also need to be considered in the planning of management actions (Parkes and Murphy 2003, Forsyth et al. 2013).

Emergent properties

Individual-based models such as SORTIE/NZ enable the identification of higher-level dynamics that are not linearly related to lower-level dynamics of the system (Reuter et al. 2005). Our study revealed two important emergent properties. First, gains and losses in seedlings caused by deer and rodents do not always translate into gains or losses in subsequent life-history stages (i.e., saplings and adults). Most seeds and seedlings do not survive to become adults (Harper 1977), and many forest species recruit infrequently (e.g., after disturbance; Pickett and White 1985). Infrequent recruitment of both angiosperm and conifer canopy dominants following disturbance is a feature of New Zealand forests (Wardle 1984, Ogden and Stewart 1995), and growth–survival trade-offs among species at Waitutu have been shown to change with life-history stage (Kunstler et al. 2009). Hence, inferences about the effects of herbivory on forests from studies that assess only seeds, seedlings, and saplings should be restricted to those life-history stages and it should not be assumed that changes will have a proportional impact on subsequent life-history stages. Second, when deer changed the abundance of one canopy dominant, the abundances of other canopy dominants changed. This dynamic was most apparent in the alluvial terrace forest, where adult conifers became much less abundant in the absence of deer, owing to increased interspecific competition from the angiosperms that increased in abundance.

Limitations and future opportunities

Our SORTIE/NZ models have several limitations. First, they did not include all impacts of invasive mammals. For example, ring-barking by deer may cause some mortality of sapling and adult angiosperm subcanopy trees (Mark and Baylis 1975). Deer may also avoid patches of the landscape where unpalatable plants are abundant (McNaughton 1978), such that palatable seedlings may be less likely to be browsed if they were in a vegetation patch dominated by seedlings of species avoided by deer (Bee et al. 2009). Feral pigs (*Sus scrofa*) are also present in parts of Waitutu Forest

(Lovelock 1985). Two years of monitoring in alluvial terrace forest indicates that feral pigs tend to re-disturb the same areas, but that this disturbance has little effect on seedling regeneration (Parkes et al. 2015). These impacts and animal behaviors could be tested in future models.

Second, some estimates of parameters describing the deterministic and stochastic components of species-specific life-history stages may be inaccurate and/or overly precise. Trees can exhibit substantial individual variation in their responses to light and other resources (Clark et al. 2003, 2010). Hence, there was sometimes substantial unexplained variation and uncertainty when parameters were estimated from field data. Our simulations accounted for some of the variability in individual responses (e.g., through a stochastic factor describing variability in seedling growth), but they did not account for the uncertainty in parameter estimation. This limitation could be addressed in future work by first using a Bayesian mode of inference to estimate the uncertainty associated with individual parameters (Clark et al. 2010) and then accounting for this parameter uncertainty by sampling parameter values from distributions for each SORTIE simulation.

Third, assuming that parameterized processes will be constant for centuries is a simplification because of the potential effects of disturbances, altered nutrient availability, and changes in mammalian herbivory. Flooding could differentially affect the establishment, growth, and mortality of seedlings in the alluvial terrace forest (Mark et al. 1988, Duncan 1993, Ogden and Stewart 1995, Gaxiola et al. 2010), and wind disturbance (Martin and Ogden 2006) and earthquakes (Allen et al. 1999, Kunstler et al. 2013) could create a "regeneration window" for light-demanding species in both forests. The deer-induced replacement of angiosperm tree species that have low foliar fiber concentrations by conifer species that have high foliar fiber concentrations may reduce litter decomposition rates and, hence, soil nutrient availability (Pastor et al. 1993, Hobbs 1996, Wardle et al. 2002). Mammalian herbivory could also alter as forest composition changes (e.g., reduced food availability will eventually cause red deer abundances to decline; Holloway 1950, Caughley 1970, Forsyth and Caley 2006).

Summary

Our spatially explicit individual-based forest models predict that invasive deer and rodents will have distinct century-scale effects on the structure and composition of forests and that these effects will be most rapid and of greatest magnitude in the forest growing on relatively P-rich soil. Browsing by deer and granivory by rodents altered the abundances of the codominant canopy species in the more fertile alluvial terrace forest, with the codominant canopy species *Weinmannia racemosa* and *Nothofagus menziesii* becoming significantly less abundant in the presence of deer and rodents, respec-

tively. Although the long-term impacts of deer on forest structure and composition have been hypothesized for many decades (review in Côté et al. 2004), our study predicts that invasive rodents will also have long-term effects on the abundances of adult canopy trees through seed predation.

Browsing by invasive red deer reduced growth rates and increased mortality rates of many angiosperm seedlings relative to conifer seedlings. Hence, the presence of deer (but not rodents) led to an increased dominance of conifers in the alluvial terrace forest.

Two main emergent properties were evident. First, rodent- and deer-induced reductions in seedling abundances did not always translate into reduced sapling and adult tree abundances. Second, when deer changed the abundance of a canopy dominant, other tree species were affected by altered interspecific competition.

Finally, our conclusions highlight the usefulness of individual-based models, such as SORTIE (Pacala et al. 1996), for forecasting the long-term effects (sensu Strayer et al. 2006) of multiple invasive mammalian herbivores on forest dynamics while accounting for tree longevity, the potential for multiple successional pathways, and nonequilibrium dynamics (Coomes et al. 2003). We encourage others to investigate the long-term effects of other modes of invasive mammalian herbivore impacts on forest dynamics using this approach.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–O and the Supplement are available online: http://dx.doi.org/10.1890/14-0389.1.sm

Data Availability

Data associated with this paper have been deposited with New Zealand's National Vegetation Survey: http://dx.doi.org/10.7931/V1WC75