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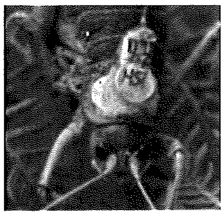
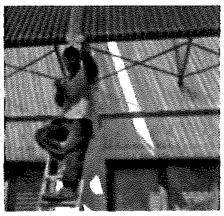
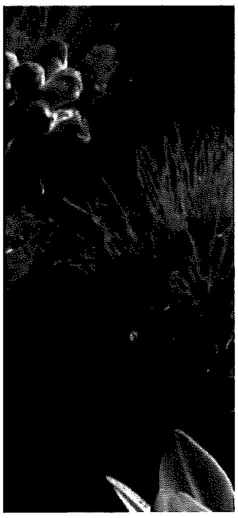
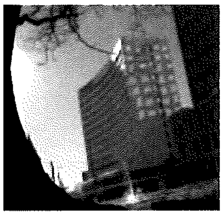
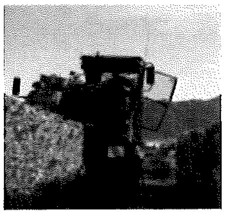
Changes in forest vegetation on Stewart Island over the last 30 years and the influence of white-tailed deer (Odocoileus virginianus)

Richard P Duncan, Wendy A Ruscoe and E. Pen Holland

Landcare Research
Manaaki Whenua

Changes in forest vegetation on Stewart Island over the last 30 years and the influence of white-tailed deer (*Odocoileus virginianus*)

INVESTIGATION NO.: SIFC09/1

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Contents

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ABSTRACT

We examined changes since 1979 in the woody vegetation of permanent plots on Stewart Island, where white-tailed deer have been present for over 100 years, and compared this with changes on Bench and Ulva islands, where deer are absent. Forest composition was stable on Bench and Ulva islands over the study period but not so on Stewart Island. In plots in northern Stewart Island and around Port Pegasus tree populations of many species declined, but these declines could not be linked to deer impacts, and successional processes may be important. There was evidence that deer were suppressing seedlings of palatable species, but were not causing significant declines in seedling numbers. In plots around Port Adventure and Chew Tobacco Bay there was evidence that historically high deer densities on these more fertile sites, probably in combination with possums, had shifted tree composition towards less palatable species. Since the plots were established in 1979, however, there has been a marked recovery in the seedling and sapling tiers with all species increasing in abundance, most likely in response to lower deer densities in recent years. Exclosure plots in this area showed a significant response of deer-preferred species to deer exclusion. Our results suggest that white-tailed deer affect seedling and sapling dynamics in the understorey, but that their impacts vary spatially, most likely due to variation in deer density and the interaction with forest composition, which is influenced by site factors such as fertility. Deer browsing appears to impact tree populations most apparently on higher fertility sites having a greater proportion of deer-preferred hardwood species, where deer densities are also likely to be high.

Keywords: browse; exclosure; herbivory; mortality; recruitment; regeneration

1 Introduction

In 1905, nine white-tailed deer (*Odocoileus virginianus*) from New Hampshire, USA, were released at Cook's Arm, Port Pegasus, at the southern end of Stewart Island. By 1926 the population had expanded across the island to the northern tip (Caughley 1963; Harris 1984) and by 1949 white-tailed deer were reported in all coastal forests in high numbers (Corboy 1949). Since then white-tailed deer densities have fluctuated, but were reduced in the 1970s with studies in the 1980s showing the animals to be in poor condition (Nugent & Challies 1988). By the late 1990s faecal pellet densities had almost doubled compared with densities in 1981 (Bellingham & Allan 2003).

On Stewart Island white-tailed deer inhabit coastal and lowland mixed podocarp–hardwood forest with an extensive subcanopy of deer-preferred species such as *Griselinia littoralis*, *Brachioglottis rotundifolia* and *Weinmannia racemosa.* As early as 1920 severe modification of Stewart Island vegetation by deer was observed (Nugent 2005) with forest dieback noted in the 1950s becoming more extensive along the north and eastern coastlines by the late 1970s. Although it was thought that this was initiated by salt-laden winds, the introduced brushtail possum (*Trichosurus vulpecula*) was also implicated, and recruitment into both the dieback zones and intact forests was thought to have been inhibited by white-tailed deer (Veblen & Stewart 1980). Studies in the 1980s suggested that in areas where deer-preferred species formed the forest canopy, understorey browsing by white-tailed deer threatened the maintenance of canopy species and there was concern that forest composition may shift to more-browse-tolerant or less-deer-preferred species (Stewart & Burrows 1989). However, the most recent analysis of changes in permanent forest plots on Stewart Island (Bellingham & Allan 2003) found no evidence that browsing by white-tailed deer was causing a long-term shift in canopy tree composition, although deer appeared to be affecting the survival of seedlings and saplings in the understorey.

White-tailed deer have been present on Stewart Island for over 100 years, with red deer (*Cervus elaphus*) also present but locally distributed and rare. In contrast, Bench Island, a small island about 5 km east of Stewart Island, has remained free of deer, and Ulva Island, located in Paterson Inlet, had deer eradicated in 1976 with numbers having been held low for some decades prior to eventual eradication (Clayton et al. 2008). These two islands, where white-tailed deer have been completely absent or absent for at least 30 years, provide a baseline against which to compare long-term changes in forest composition that have occurred on Stewart Island in the long-term presence of white-tailed deer.

2 Objectives

The Stewart Island plot network comprises 172 permanent plots (20 × 20 m) located on Stewart Island and two deer- and possum-free offshore islands, Bench Island and Ulva Island. The plots were established over several surveys dating back to the mid-1970s. The primary objective of these surveys was to establish what effect introduced herbivores, in particular white-tailed deer and possums, were having on forest health. These permanent plots have been remeasured at various times throughout the 1980s, 1990, and most recently in 2009. The dataset includes eight deer exclosure plots on Stewart Island (each paired with a non-exclosure control plot), and 13 plots from the two deer- and possum-free offshore islands. The surveys used in this analysis, the number of plots per survey, and the years in which survey plots were measured are shown in Table 1, with the plot locations shown in Fig. 1.

The objective of this analysis is to determine the extent to which white-tailed deer are shifting the density and composition of woody plant species and influencing forest structure on Stewart Island (Port Pegasus, Port Adventure, Chew Tobacco Bay and Stewart Island North surveys; Table 1) by comparing these data with data from deer-free islands (Ulva Island and Bench Island surveys; Table 1). We focus on changes through time in the understorey seedling and sapling tiers, changes in tree basal area, and mortality and recruitment rates of tree species.

In addition to comparing forest changes on Stewart Island relative to the two offshore islands, we use two measures of deer impact to help interpret these changes: (1) a measure of the degree to which species have responded to deer exclusion following their long-term presence, quantified as the relative performance of species in plots where deer were excluded relative to plots where deer were present, using exclosure plot data on Stewart Island (Table 1); (2) an index of ungulate preference taken from Forsyth et al. (2002). We link these two measures to changes in forest composition on Stewart Island.

3 Methods

The data analysed in this report comprise measurements from permanent 20 × 20 m plots within which seedlings, saplings and trees were measured following the methods described in (Allen 1993). The data were extracted from the National Vegetation Survey database held at Landcare Research (Table 1). There are an additional 24 permanent plots that were established on Stewart Island in 2002. Data from these were not included in our analyses because the plots have not been remeasured.

TABLE 1. SUMMARY OF THE SURVEY DATA FROM STEWART ISLAND ANALYSED IN THIS REPORT (ALL DATA AVAILABLE IN NVS: HTTP://NVS.LANDCARERESEARCH.CO.NZ/).

Survey	Date established & no. of plots	Dates remeasured	Comments
Port Pegasus	1998 21 Plots	2008	
Port Adventure	1979 33 Plots	1981, 1985 & 1999, 2009	Only 8 plots were remeasured in 1999 and 2009
Chew Tobacco Bay	1979 31 Plots	1981, 1985, 1996 & 1999, 2009	Only 9 remeasured in 1999 and 2009
Ulva Island	1999 8 Plots	2008	Seedlings only were measured in 1991, 1993 &1994 but these data were not used in this analysis
Bench Island	1979 5 Plots	1985, 1999, 2008	
Stewart Island North	1976 58 Plots	1980, 1985 & 1999, 2009	47 plots remeasured in 1999 1976 RECCE only
Exclosure plots	1979 16 Plots	1980, 1982, 1984, 1999 & 2007	8 paired exclosures. Seedlings only remeasured in 1980 and 1982

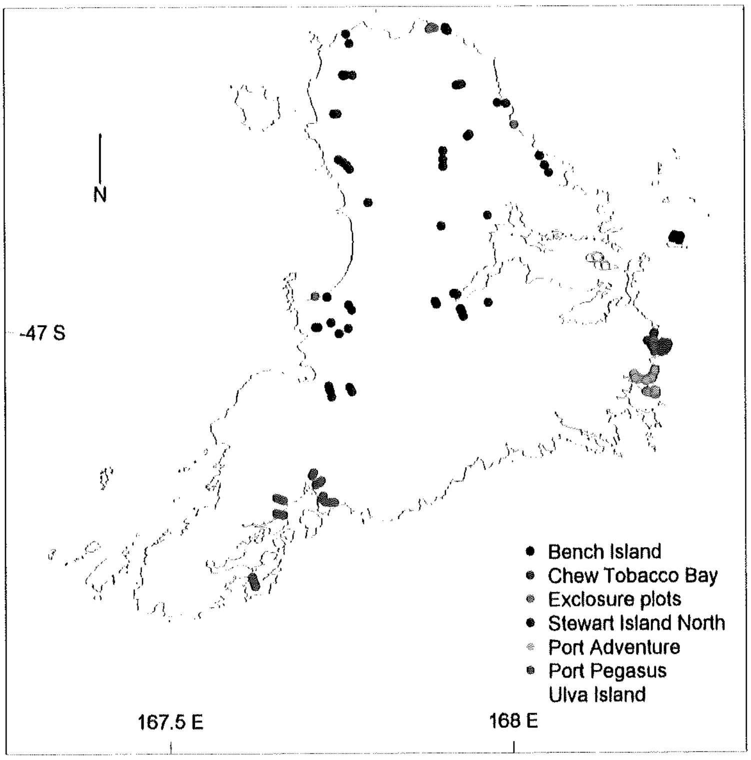

Figure 1. Locations of the permanent plots on Stewart, Bench and Ulva islands that were analysed in this report, coloured by survey (see Table 1).

After downloading from the NVS database, the data were treated as follows:

1. We restricted our analyses to woody tree and shrub species (listed in Appendix 1), excluding tree ferns (because these were measured only in recent surveys) and lianas.

2. Species names were checked and updated to follow Wilson (1987b), and then updated to follow more recent name changes (see Appendix 1). In particular: *Coprosma parviflora* and *C. decurva* were treated as *C.* sp. p 'dumosa'; *Pittosporum colensoi*, *P. tenuifolium* and *P. tenuifolium* supsp. *colensoi* were all treated as *P. tenuifolium* supsp. *colensoi*; *Brachyglottis buchananii* (= *Senecio benettii*) was treated as *B. rotundifolia* (= *Senecio reinoldii*).

We analysed tree, sapling and seedling data separately using the following definitions:

Trees were stems ≥ 2.5 cm in diameter at 1.35 m above the ground (diameter at breast height; dbh). Trees in plots were individually tagged and measured.

Saplings were stems < 2.5 cm dbh and ≥ 1.35 m tall. Saplings in plots were counted by species.

Seedlings were stems > 0.15 m and < 1.35 m tall. Seedlings were counted by species in 24 seedling-plots (each 0.75 m^2 in area) per 20 × 20 m plot.

Permanent plots on Stewart Island cover a wide geographic area grouped by survey (Fig. 1). We first describe compositional variation in tree species across plots to provide a context for understanding changes in the woody vegetation. Our analysis revealed a gradient in forest composition that separated plots at Port Adventure and Chew Tobacco Bay from those at Port Pegasus and northern Stewart Island. We then examined changes through time in seedling and sapling abundance and tree basal area in Stewart Island plots (separating those at Port Adventure and Chew Tobacco Bay from those at Port Pegasus and northern Stewart Island) where deer have been continuously present, and compared this with changes in seedling and sapling abundances and basal area on offshore islands that have remained deer-free (Bench Island) or have had deer eradicated (Ulva Island).

To determine the effects of removing deer on forest regeneration we compared trends in seedling and sapling abundance between deer exclosure plots (surrounded by 2-m-high fences) and adjacent control plots to which deer have access. Each exclosure plot was located adjacent to a control plot that was judged to be similar in vegetation. Previous work showed that the exclosures and controls did not differ in basal area or densities of trees and saplings in 1979 when these plots were established (Stewart & Burrows 1989).

The exclosure plots allow us to asses how seedling and sapling numbers have recovered following deer exclusion on Stewart Island relative to sites where deer have been continuously present. We also used a measure of the degree to which species were selected by ungulates, taken from Forsyth et al. (2002), as a further measure of the susceptibility of species to deer impact.

4 Analysis and Results

4.1 COMPOSITIONAL VARIATION

For trees, we calculated the total basal area (in $m^2 ha^{-1}$) of each species in each plot at the first measurement, and then calculated the dissimilarity in composition and basal area among plots using the Bray–Curtis measure of dissimilarity. This dissimilarity matrix was then analysed using non-metric multidimensional scaling to produce a two-dimensional ordination showing the major gradients in tree species composition across plots (Fig. 2). In the ordination diagram, plots located close together have similar basal area composition relative to plots located further apart. Appendix 2 shows a species-by-plot matrix with basal area in four categories, and with the species and plots ranked by their ordering along the first ordination axis in Fig. 2. The five plots on the far left of the ordination diagram occur in northern Stewart Island and differ from the rest in having a canopy dominated almost exclusively by *Leptospermum scoparium* (see Appendix 2), most likely having colonised following major disturbance. The remaining plots cluster together but with a distinct geographical pattern. Plots in northern Stewart Island and Port Pegasus, along with Ulva Island, tend to occur to the left of the ordination while those in Port Adventure and Chew Tobacco Bay, along with most of the exclosure plots, to the right, with Bench Island intermediate. Plots in northern Stewart Island and Port Pegasus have canopies dominated by mixtures of the conifers *Dacrydium cupressinum*, *Prumnopitys ferruginea* and *Podocarpus halli*, and the hardwoods *Metrosideros umbellata* and *Weinmannia racemosa*, but are also characterised by species such as *Halocarpus biformis*, *Leptecophylla juniperina*, *Dracophyllum longifolium*, and *Neomyrtus pedunculata*. To the right of the ordination, plots in Port Adventure and Chew Tobacco Bay tend to have much lower conifer basal area and range from plots dominated by *Metrosideros umbellata* and *Weinmannia racemosa* to those where the canopy is formed by a diverse range of hardwood species including *Griselinia littoralis*, *Carpodetus serratus*, and *Fuchsia excorticata*. Overall, the major gradient in tree species composition appears to reflect a gradient in fertility with sites in northern Stewart Island and Port Pegasus having species characteristic of lower fertility sites such as *Lepidothamnus intermedius*, *Leptospermum scoparium*, *Dracophyllum longifolium* and *Neomyrtus pedunculata* (see Wilson 1987a). Sites at Port Adventure and Chew Tobacco Bay are characterised by species typical of more fertile sites, including hardwood species such as *Griselinia littoralis*, *Carpodetus serratus*, *Fuchsia excortica* and *Coprosma areolata*, however no quantitative studies of soil fertility have been done on Stewart Island.

On the basis of these differences in forest composition, we separated plots on Stewart Island into two groups: plots in the northern Stewart Island and Port Pegasus surveys formed one group (termed main Stewart Island) and plots in the Port Adventure and Chew Tobacco Bay surveys a second group (termed east Stewart Island).

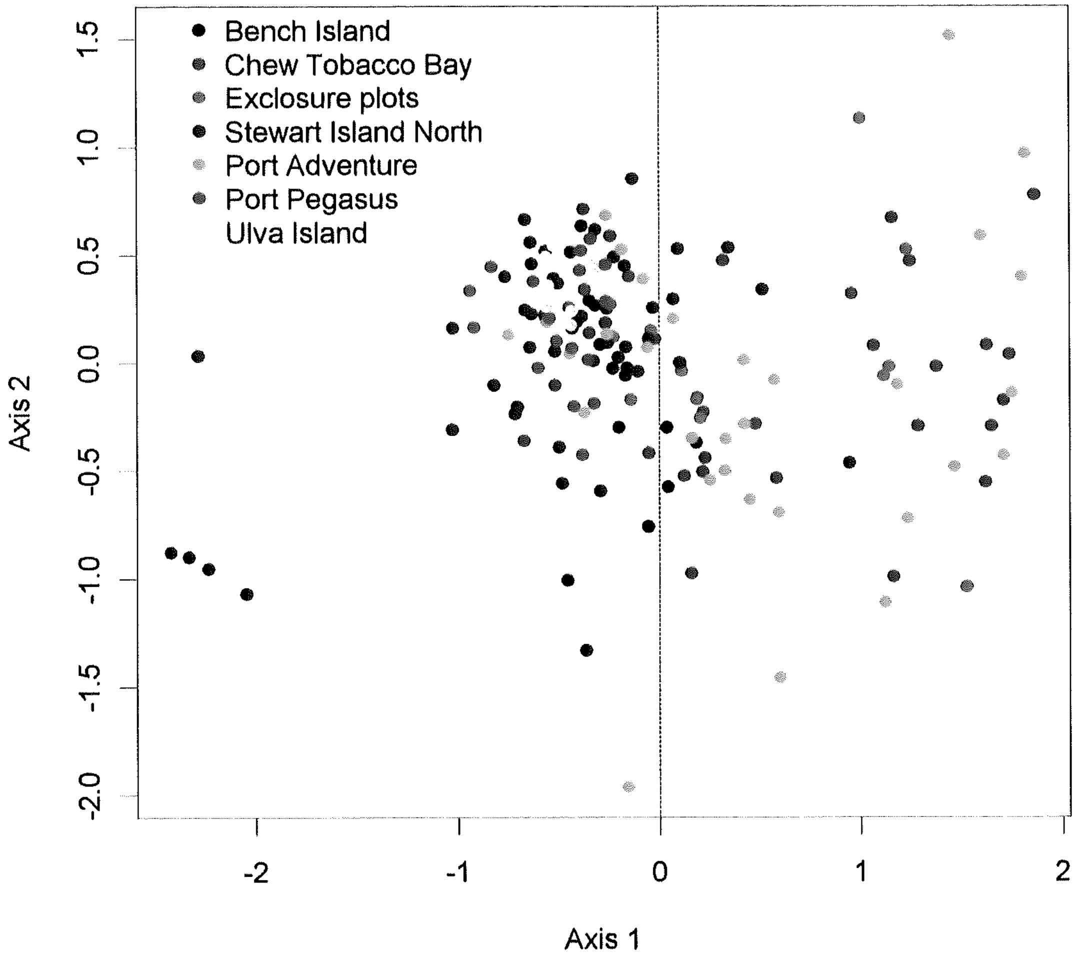

Figure 2. Non-metric multidimensional scaling ordination of Stewart Island permanent plots. Axis 1 represents the dominant compositional gradient, which tends to separate plots in the Port Adventure and Chew Tobacco Bay surveys from those in the Port Pegasus and Stewart Island north surveys.

4.2 INITIAL DIFFERENCES IN SEEDLING AND SAPLING NUMBERS ON STEWART ISLAND AND THE TWO DEER-FREE OFFSHORE ISLANDS

White-tailed deer have been present on Stewart Island for more than 100 years but never colonised Bench Island, and were absent from Ulva Island for over 30 years prior to permanent plot establishment. We would therefore expect to see differences in forest composition at the time the permanent plots were first established, reflecting the long-term presence (Stewart Island) or absence (Bench and Ulva islands) of white-tailed deer. Figure 3 shows the mean number of seedlings and saplings per plot by ungulate preference categories (see Appendix 1) for plots on Bench and Ulva islands combined, east Stewart Island, and main Stewart Island. Species classed as preferred occurred at significantly lower abundance on east and main Stewart Island when the plots were first established, relative to the two offshore islands. The 95% confidence intervals for the means of other preference classes on Stewart Island and the offshore islands overlapped, although there was a strong ranking of species by preference class in east Stewart Island and to a lesser extent main Stewart Island: avoided species were more abundant than not-selected species, which were more abundant than preferred species. The relative scarcity of preferred seedlings and saplings in main and east Stewart Island at the beginning of the surveys most likely reflects the long-term presence of deer browsing in the forest understorey. The remainder of this report examines changes in forest composition through time from these initial starting points.

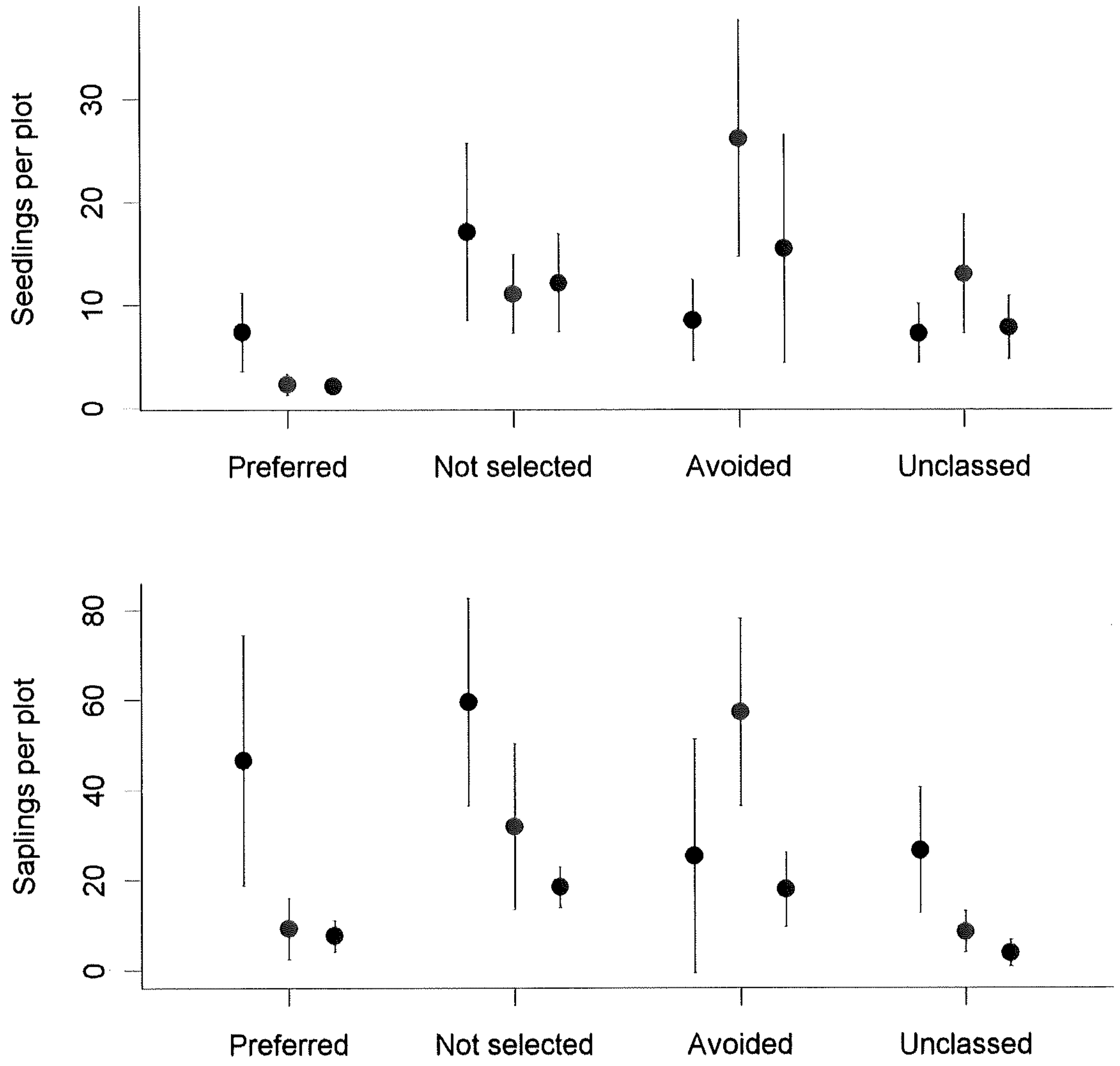

Figure 3. Mean number of seedlings (top panel) and saplings (bottom panel) per plot (with 95% confidence intervals) by ungulate preference class (see Appendix 1), for plots on Bench and Ulva islands (black circles), east Stewart Island (red circles) and main Stewart Island (blue circles). Only data from the first measurement of each permanent plot (excluding exclosure plots) were included in this analysis.

4.3 TEMPORAL CHANGES IN WOODY VEGETATION ON STEWART ISLAND AND THE TWO DEER-FREE OFFSHORE ISLANDS

4.3.1 Overall trends

We examined trends through time in the total number of woody seedlings and saplings per plot, and in the total basal area of trees per plot. We did this separately for plots on main and east Stewart Island, and for plots on Bench and Ulva islands combined, excluding the exclosure plots. The total number of woody seedlings and saplings per plot and the total basal area of trees per plot were calculated for each year in which each plot was measured. Numbers of seedlings and saplings were then log-transformed. We fitted hierarchical regression models with numbers of seedlings, number of saplings and plot total basal area as response variables, and with time of measurement (in years since 1979) as a fixed effect. To account for the repeat measurement of plots and the spatial clumping of plots within surveys, we included a plot term nested within a survey term as random effects, allowing both the intercept and the slope of the time effect to vary by plot. We report the overall slope terms, which estimate the average annual change in the numbers of seedlings and saplings and plot total basal area through time. Numbers of seedlings and saplings were log-transformed for analysis so we report the back-transformed slope estimates, which describe the annual average rate of change in numbers as a proportion of the previous year. We used the standard error (SE) of the regression coefficients to calculate approximate 95% confidence intervals as ±2*SE. We fitted the hierarchical regression models using the lme4 package in R, specifying a normal error distribution. Details of the models fitted are in Appendix 3.

4.3.2 Results

For plots on Bench and Ulva islands, and main Stewart Island, the total numbers of woody seedlings and saplings per plot have remained relatively constant through time (Fig. 4), with the slope estimates for these trends close to one (reflecting no change in numbers of seedlings or saplings) and 95% confidence intervals overlapping one. In contrast, the total number of woody seedlings and saplings increased through time in plots on east Stewart Island, with the 95% confidence intervals exceeding one. The slope estimates for seedlings and saplings (1.10 and 1.14, respectively) imply an average increase in the number of seedlings per year of 10%, and for saplings 14%.

Total plot basal area remained relatively constant through time, showing just a slight increase in plots on main Stewart Island (Fig. 4).

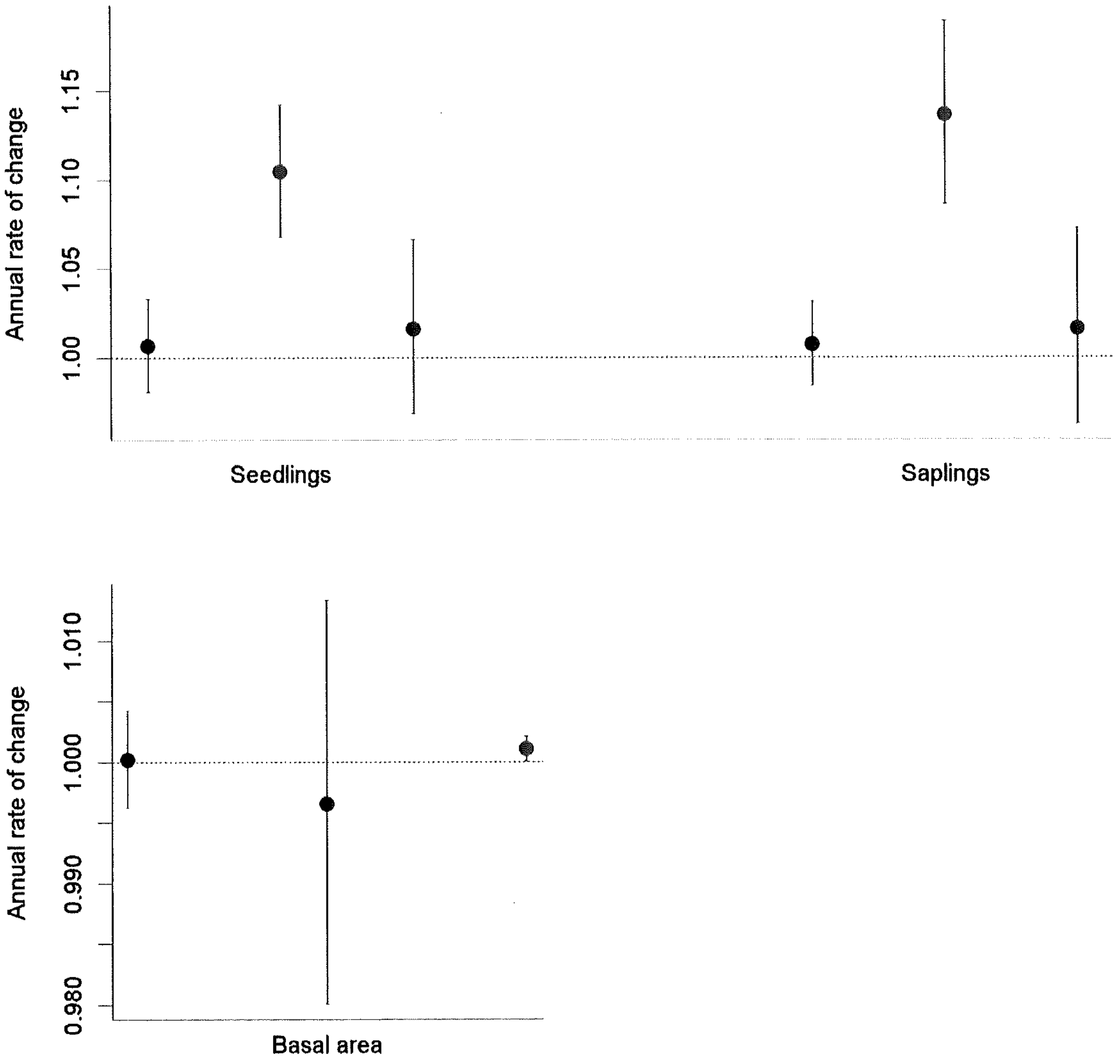

Figure 4. Estimates of the average annual rate of change (as a proportion of the previous year) in the numbers of seedlings and saplings per plot (top panel), and in total basal area per plot (bottom panel), for plots on Bench and Ulva islands (black circles), east Stewart Island (red circles) and main Stewart Island (blue circles), and 95% confidence intervals around those estimates.

4.3.3 Species-level analyses

We examined trends in the numbers of woody seedlings and saplings and in tree basal area through time for each species, performing analyses separately for plots on main and east Stewart Island, and for plots on Bench and Ulva islands combined, excluding all exclosure plots. Our data were the numbers of seedlings and saplings and basal area of each species in each plot for each year in which plots were measured. We again fitted hierarchical regression models with numbers of seedlings, number of saplings, and basal area as response variables, and with time of measurement (in years since 1979) as a fixed effect. To account for the repeat measurement of plots and the spatial clumping of plots within surveys, we included a plot term nested within a survey term as random effects, allowing both the intercept and the slope of the time effect to vary by plot. In addition, we included a species term as a random effect, allowing both the intercept and the slope of the time effect to vary by species. Including a random effect for time across species allows us to model the average trend in the numbers of seedlings and saplings, and in basal area for each species through time, having accounted for survey and plot effects.

We fitted the hierarchical regression models using the lme4 package in R (details of the models fitted are in Appendix 3). For numbers of seedlings and numbers of saplings we specified a quasi-poisson distribution and log-link function, which is appropriate for count data taking account of over-dispersion. Basal area was log-transformed after adding 0.001 (to allow for species that had zero basal area on plots in some years they were measured) and we specified a normal distribution for this model. We are interested in the overall trends through time for each species, so we report the coefficients of the random slope through time effects for each species. Models for numbers of seedlings and saplings used a log-link function and basal area was log-transformed, so the random slope coefficients were back-transformed and thus describe the annual average rate of change in numbers of seedlings or saplings or basal area as a proportion of the previous year. We estimated the standard error (SE) of the random effect coefficients using the 'se.coef' function in the 'arm' package, and report approximate 95% confidence intervals as ±2*SE.

4.3.4 Results

Seedling numbers

Figure 5 summarises trends in the numbers of woody seedlings through time for each species. For plots on main Stewart Island, and Bench and Ulva islands, the mean number of seedlings per plot for each species has remained relatively constant across measurements, with none of the species showing significant increases or declines through time. In contrast, for plots on east Stewart Island, seedlings of all species increased in abundance through time, most significantly so.

Estimated rates of change in seedling numbers were weakly correlated among the three regions (east and main Stewart Island, and Bench and Ulva islands; Table 2), with none being significantly related.

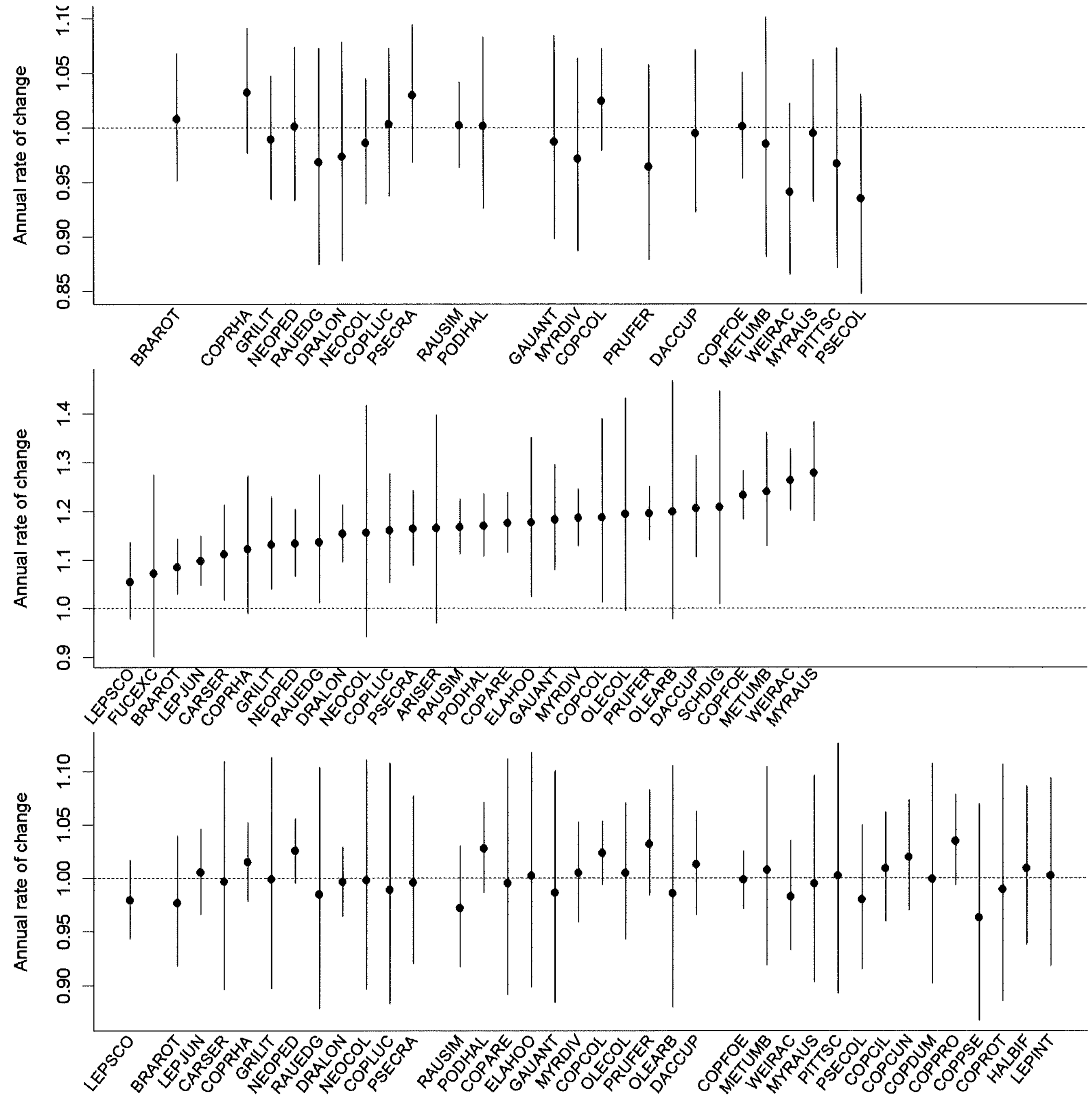

Figure 5. Estimates of the mean annual rate of change in seedling numbers (as a proportion of the previous year) for species in plots on Bench and Ulva islands (top panel), east Stewart Island (middle panel), and main Stewart Island (bottom panel), and 95% confidence intervals around those estimates (grey lines). Species are ranked in order from lowest to highest annual rate of change on east Stewart Island. Species whose 95% confidence intervals do not overlap one are shown in blue, where seedling numbers have increased significantly, or red, where seedling numbers have declined significantly through time.

TABLE 2. PEARSON CORRELATIONS AMONG SPECIES-LEVEL ESTIMATES OF ANNUAL RATES OF CHANGE FOR SEEDLINGS, SAPLINGS AND BASAL AREA, ON BENCH AND ULVA ISLANDS (ISLANDS), SOUTH-EAST STEWART ISLAND (SOUTH-EAST) AND NORTH STEWART ISLAND (NORTH). SIGNIFICANT CORRELATIONS ARE SHOWN IN BOLD WITH $*P < 0.05$

		Islands		East			Main		
		Sap.	BA	Seed.	Sap.	BA	Seed.	Sap.	BA
Islands	Seedling	0.46*	0.27	−0.37	0.33	0.07	0.26	−0.12	−0.51*
	Sapling		0.44	−0.30	−0.04	0.40	0.09	−0.49*	−0.39
	BA			−0.30	0.18	0.18	0.40	0.00	0.08
East	Seedling				0.34	−0.09	0.13	−0.03	0.33
	Sapling					−0.11	0.34	−0.10	0.02
	BA						0.02	−0.27	−0.01
Main	Seedling							0.41*	0.20
	Sapling								0.24

Sapling numbers

Figure 6 summarises trends in the numbers of woody sapling through time for each species. Again, for plots on main Stewart Island, and Bench and Ulva islands, the mean number of saplings per plot for each species has remained relatively constant across measurements, with none of the species showing significant increases or declines through time. In contrast, for plots on east Stewart Island, saplings of all species increased in abundance through time, most significantly so.

Rates of seedling and sapling increase on east Stewart Island were positively but not significantly correlated ($r = 0.34$; Table 2), whereas seedling and sapling changes were more strongly positively correlated on main Stewart Island, and on Bench and Ulva islands. Rates of sapling change on main Stewart Island were significantly negatively correlated with rates of sapling change on the two offshore islands.

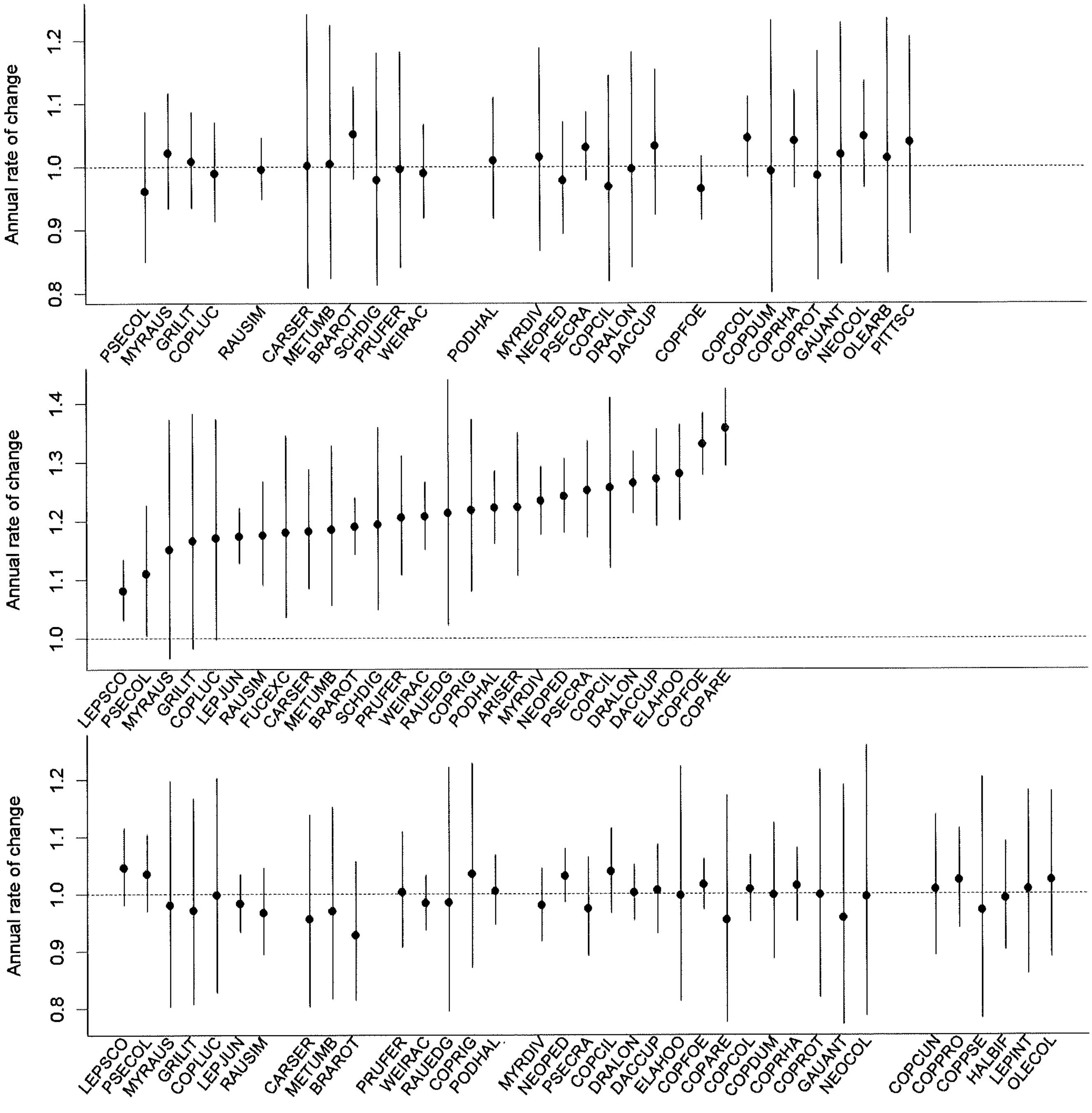

Figure 6. Estimates of the mean annual rate of change in sapling numbers (as a proportion of the previous year) for species in plots on Bench and Ulva islands (top panel), east Stewart Island (middle panel), and main Stewart Island (bottom panel), and 95% confidence intervals around those estimates (grey lines). Species are ranked in order from lowest to highest annual rate of change on east Stewart Island. Species whose 95% confidence intervals do not overlap one are shown in blue, where seedling numbers have increased significantly, or red, where seedling numbers have declined significantly through time.

Basal area

Figure 7 summarises trends in basal area through time for each species in plots on Bench and Ulva islands, and for each species in plots on east and main Stewart Island. On Bench and Ulva islands most species increased in basal area, and for six species (*Pseudopanax colensoi*, *Pseudopanax crassifolius*, *Coprosma lucida*, *Prumnopytis ferruginea*, *Dacrydium cupressinum* and *Brachyglottis rotundifolia*) the 95% confidence intervals around the estimated rate of change in basal area exceeded one.

On east Stewart Island only *Brachyglottis rotundifolia* showed a significant increase in basal area through time, while two species, *Fuchsia excortica* and *Schefflera digitata,* declined significantly.

In contrast, almost all species declined in basal area on main Stewart Island, six species significantly so. The species showing the largest declines tended to be small trees, including several species of *Coprosma*, *Brachyglottis rotundifolia*, *Myrsine divaricata*, *Raukaua simplex* and *Griselinia littoralis.*

In contrast, most species on Stewart Island declined in basal area through time, and for 13 species the 95% confidence intervals around the estimated rate of change were less than one. This result appears to be at odds with the finding that total basal area at the plot level increased slightly, though not significantly, through time on Stewart Island (Fig. 2). While most species on Stewart Island declined in basal area, many of these were small trees and their losses were offset by the tendency for large trees, including *Dacrydium cupressinum*, *Metrodideros umbellata* and *Weinmannia racemosa,* to have increased in basal area.

Changes in basal area in the three regions were poorly correlated, but change in basal area on main Stewart Island was significantly negatively correlated with change in seedling abundance on Bench and Ulva islands (Table 2).

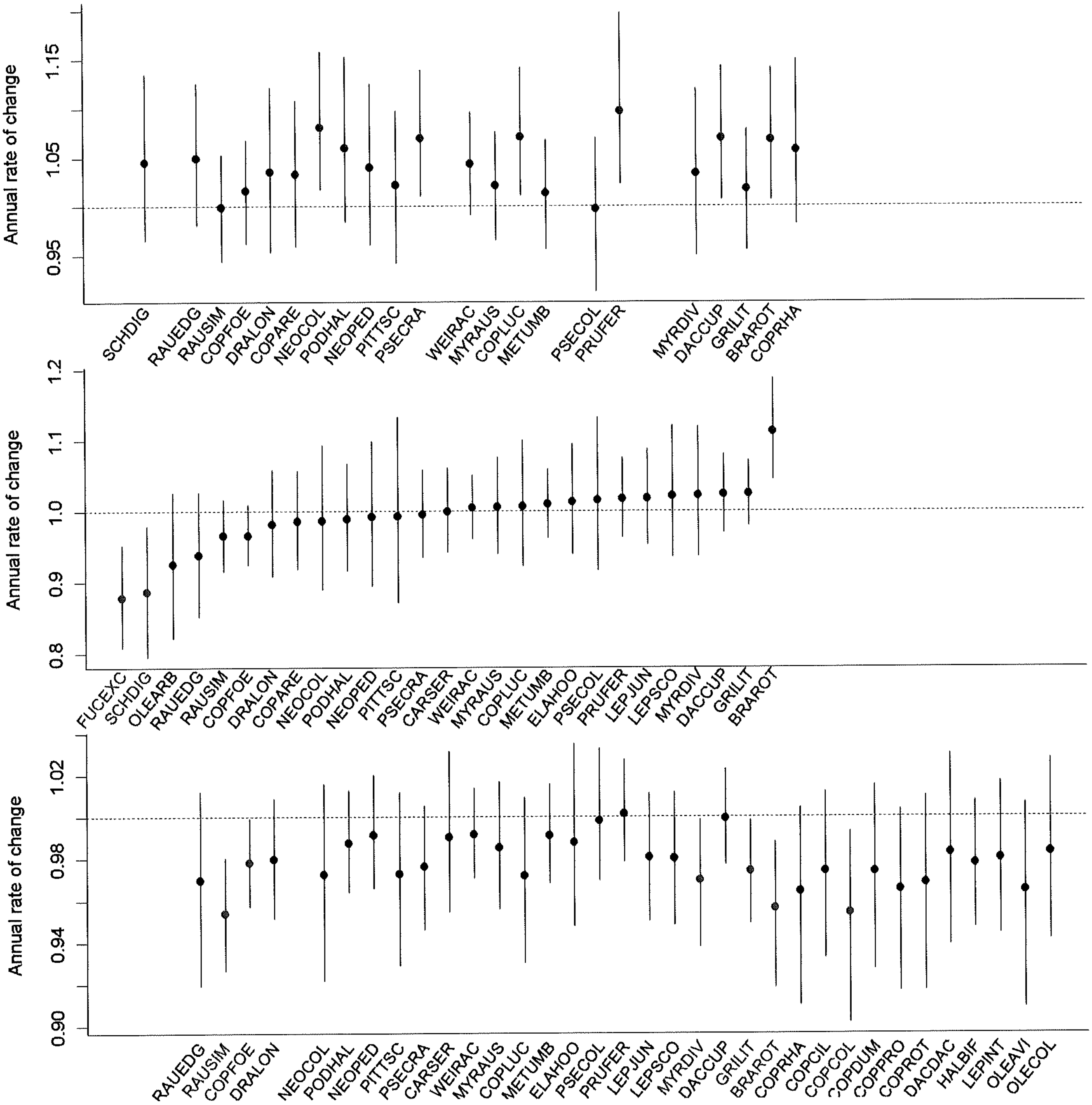

Figure 7. Estimates of the annual average rate of change in basal area (as a proportion of the previous year) for species in plots on Bench and Ulva islands (top panel), east Stewart Island (middle panel), and main Stewart Island (bottom panel), and 95% confidence intervals around those estimates (grey lines). Species are ranked in order from lowest to highest annual rate of change on east Stewart Island. Species whose 95% confidence intervals do not overlap one are shown in blue, where seedling numbers have increased significantly, or red, where seedling numbers have declined significantly through time.

Mortality and recruitment rates

We used the data from consecutive measurements of plots to estimate average annual mortality and recruitment rates for each species over the study period. We identified all plots that had been measured consecutively in the same years (e.g. all plots that had been measured in 1979 and then again in 1985). For each species in this group of plots we identified the initial number of trees alive at the first measurement, the final number of trees alive at the second measurement, the number of trees that survived between the first and second measurement, the number of trees that recruited between the first and second measurement, and the number of years between measurements. It was possible to determine the number of trees that had survived or recruited because individual trees were tagged and their fate followed through time. We assumed that trees had died if they were recorded at one measurement but were absent from the second and subsequent measurements. We repeated this process for all consecutive measurements of plots that had occurred in different combinations of years, and thus had different lengths of time between measurements.

For estimating mortality rates, our data comprise four columns: the species, the initial number of trees of that species present at the first measurement, the number of trees of that species that survived between the first and second measurement, and the number of years between the first and second measurement, with this repeated for each set of plots that were measured consecutively in the same years. We modelled the number of trees of each species that survived between measurements as following a binomial distribution:

$S \sim \text{Binomial}(p_s, I)$,

where S is the number of survivors, I is the initial number of trees and p_s is the probability of survival over the period for a tree of species s. This probability of survival will depend on the number of years between plot measurements; all else being equal, the longer the interval, the less likely it is that a tree will survive for that length of time. To allow for this we can equate the probability of survival between measurements of unequal length to an annual rate of mortality:

$p_s = (1 - m_s)^{\Delta t}$,

where m_s is the annual rate of mortality for species s and Δt is the number of years between consecutive plot measurements. To allow us to deal with small sample sizes for some species, we used a hierarchical approach to model the annual rate of mortality, treating those estimates as if they were drawn from a normal distribution on the logit scale:

$\text{logit}(m_s) \sim \text{Normal}(\mu , \sigma^2)$,

where μ is the overall mean annual mortality rate across all species and σ^2 is the variance in those rates. We fitted this hierarchical model in a Bayesian framework using OpenBugs called from R.

Our recruitment model had the same general formulation except that we modelled the number of trees that recruited between measurements as following a binomial distribution:

$R \sim \text{Binomial}(p_s, F)$,

where R is the number of new recruits, F is the final number of trees, and p_s in this case is the probability of recruitment over the period for a tree of species s.

4.3.5 Results

Figure 8 plots estimated mortality versus recruitment rates for species in each of the three regions. For tree species on main Stewart Island, and on Bench and Ulva islands, mortality and recruitment rates were significantly positively correlated (Bench and Ulva islands: $r = 0.56$, df = 20, $P = 0.006$; main Stewart Island: $r = 0.71$, df = 32, $P < 0.0001$). In these regions, those species with low rates of both mortality and recruitment were long-lived species, including *Dacrydium cupressinum*, *Metrosideros umbellata* and *Dacrycarpus dacrydioides*, while those with high rates were shorter lived species such as *Myrsine divaricata* and species in the genus *Coprosma*. In contrast, on east Stewart Island mortality and recruitment rates of tree species were not significantly related ($r = -0.15$, df = 25, $P = 0.44$).

On Bench and Ulva islands, most species had recruitment rates that exceeded mortality rates, significantly so for several species (Fig. 9). On east Stewart Island, there was a group of species where mortality rate exceeded recruitment rate, significantly so for *Fuchsia excorticata*, *Myrsine australis* and *Raukaua simplex*, and a group of species where recruitment rate exceeded mortality rate, significantly so for *Leptecophylla juniperina*, *Leptospermum scoparium*, *Brachyglottis rotundifolia* and *Coprosma areolata*. On main Stewart Island, mortality rate exceeded recruitment rate in all but five species, and was significantly greater for *Raukaua simplex*, *Myrsine divaricata* and *Brachyglottis rotundifolia*.

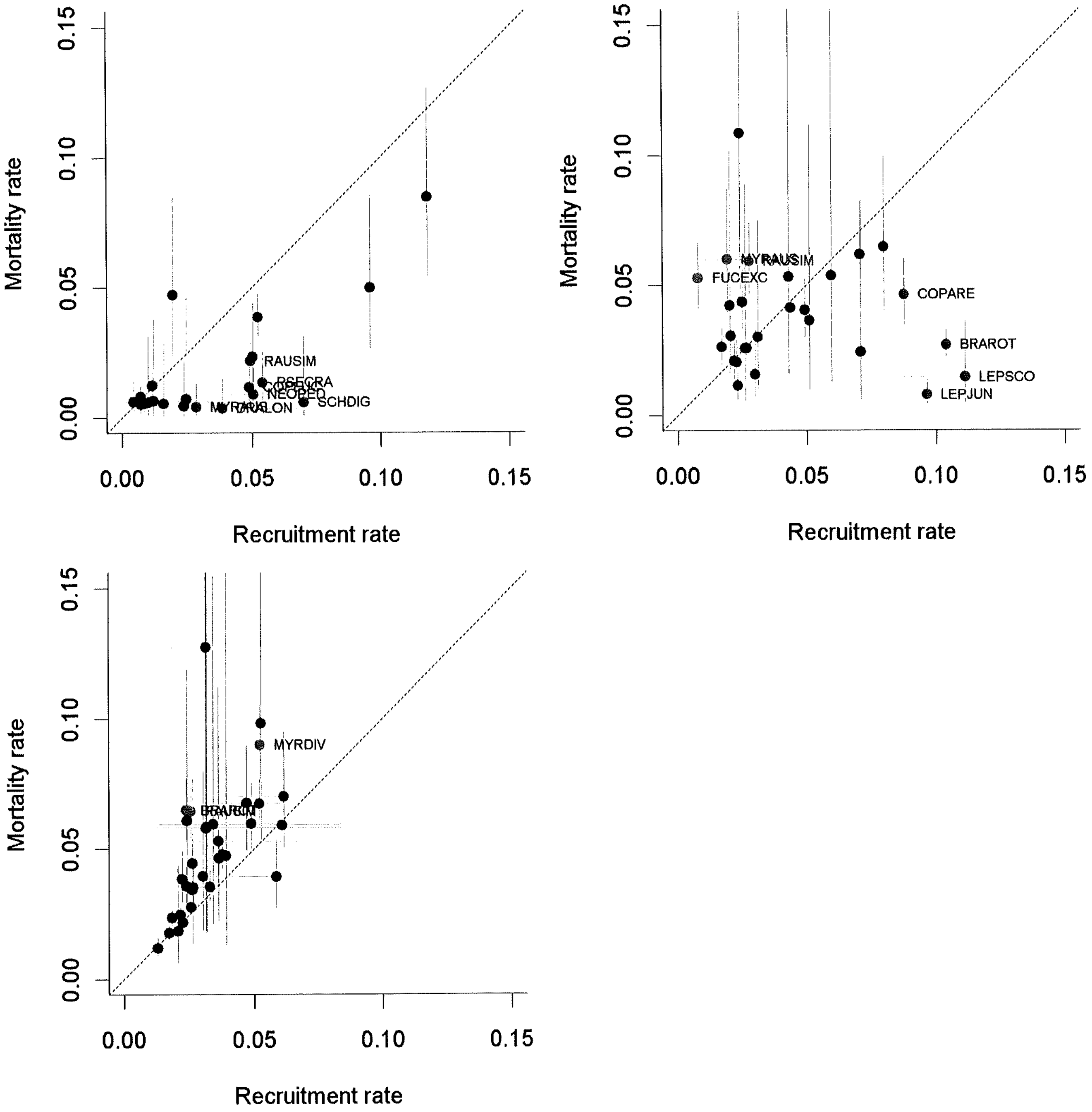

Figure 8. Estimated mortality and recruitment rates for trees in plots on Bench and Ulva islands (top left panel), east Stewart Island (top right panel) and main Stewart Island (bottom right panel), and 95% confidence intervals (grey lines) around those estimates. The dotted line has slope one and shows where mortality equals recruitment rate. All species are shown but only those species whose 95% confidence intervals for mortality and recruitment do not overlap are labelled (i.e. species where recruitment rate is significantly higher or lower than mortality rate). Species where mortality rate significantly exceeds recruitment rate are shown as red circles, and where recruitment rate significantly exceeds mortality rate are shown as blue circles.

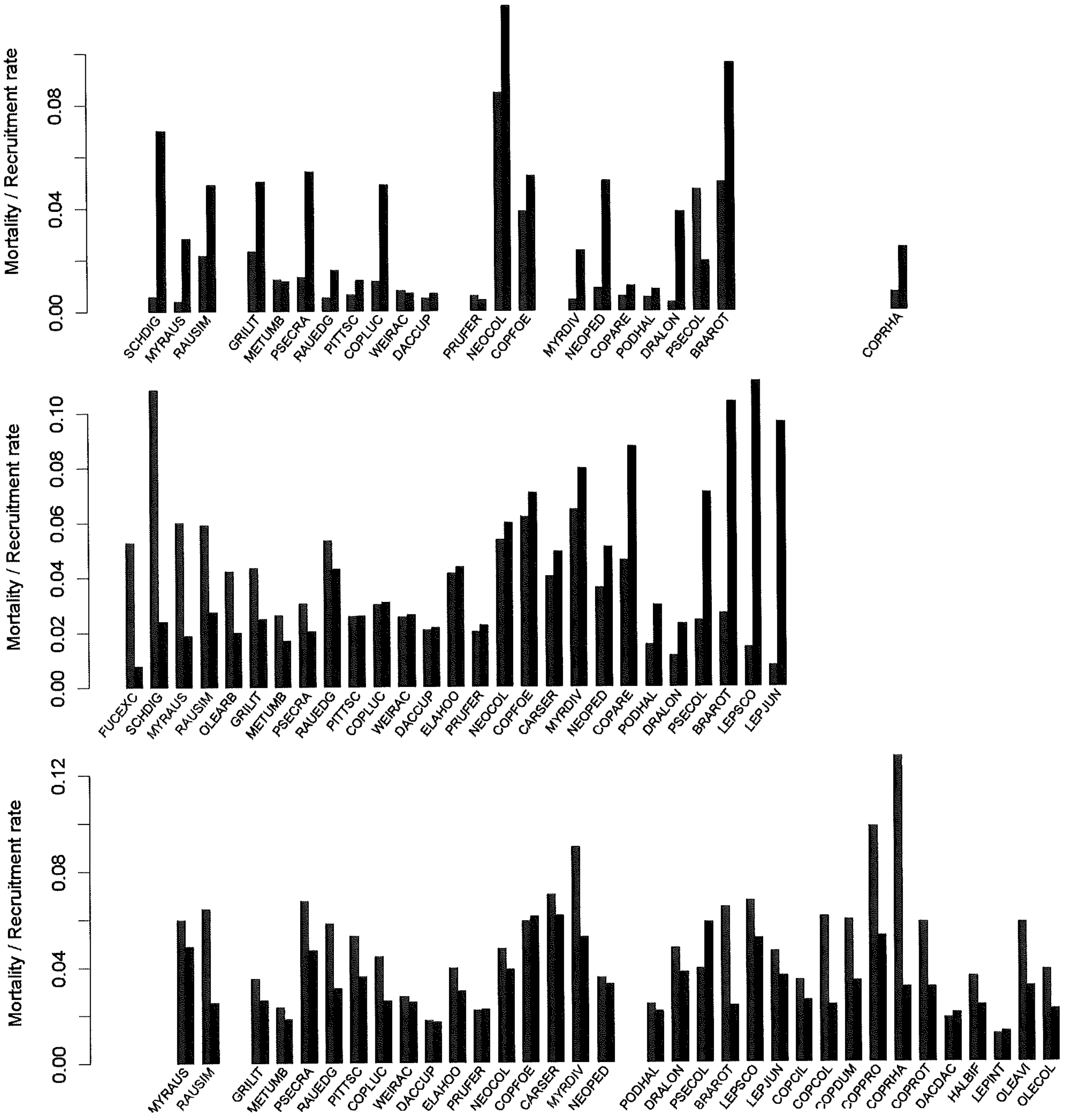

Figure 9. Estimated mortality rates (red bars) and recruitment rates (blue bars) for tree species in plots on Bench and Ulva islands (top panel), east Stewart Island (middle panel) and main Stewart Island (bottom panel). Species are ranked in order of their mortality to recruitment ratio in east Stewart Island. Species whose 95% confidence intervals for mortality and recruitment do not overlap (i.e. species with significant differences in their mortality and recruitment rates) have their names coloured either red (mortality exceeds recruitment) or blue (recruitment exceeds mortality).

4.4 EXCLOSURE PLOT ANALYSIS

4.4.1 Methods

We analysed data from seven paired deer exclosure plots on Stewart Island, excluding paired exclosure plot number three which was inconsistently labelled in the data. Six of the exclosure plots were first measured in 1979 and the seventh in 1980. The total number of seedlings recorded in plots at each measurement are shown in Table 3, and the total number of saplings in Table 4.

TABLE 3. THE TOTAL NUMBER OF SEEDLINGS RECORDED IN PAIRED DEER EXCLOSURE (EXCL) AND CONTROL (CONT) PLOTS ON STEWART ISLAND IN THE YEARS THEY WERE MEASURED. NM INDICATES A PLOT WAS NOT MEASURED IN THAT YEAR.

Plot		1979	1980	1982	1984	1999	2007
1.1	Excl	0	0	0	1	1	1
1.2	Cont	0	0	0	1	3	5
1.3	Excl	0	9	8	21	21	19
1.4	Cont	2	2	0	0	4	0
1.5	Excl	13	12	34	25	48	32
1.6	Cont	9	13	2	6	3	2
2.1	Excl	4	7	6	4	7	9
2.2	Cont	2	3	3	19	0	NM
2.3	Excl	1	1	3	9	20	16
2.4	Cont	7	0	1	5	28	11
2.5	Excl	0	0	17	33	47	43
2.6	Cont	1	0	19	24	25	39
4.1	Excl	NM	13	4	19	13	29
4.2	Cont	NM	7	4	13	61	39

TABLE 4. THE TOTAL NUMBER OF SAPLINGS RECORDED IN PAIRED DEER EXCLOSURE (EXCL) AND CONTROL (CONT) PLOTS ON STEWART ISLAND IN THE YEARS THEY WERE MEASURED. NM INDICATES A PLOT WAS NOT MEASURED IN THAT YEAR.

Plot		1979	1984	1999	2007
1.1	Excl	0	0	23	93
1.2	Cont	0	0	31	51
1.3	Excl	0	3	97	512
1.4	Cont	0	0	2	92
1.5	Excl	2	5	406	275
1.6	Cont	0	4	35	33
2.1	Excl	0	25	7	14
2.2	Cont	0	0	0	NM
2.3	Excl	0	9	183	197
2.4	Cont	0	2	294	282
2.5	Excl	0	11	188	220
2.6	Cont	0	5	9	17
4.1	Excl	NM	0	226	149
4.2	Cont	NM	0	180	226

Most plots contained seedlings, albeit in low numbers, at the first measurement (Table 3). To compare changes in seedling numbers through time between the exclosure and control plots we used as data the numbers of seedlings of each species in each plot for each year in which plots were measured. We fitted a hierarchical regression model with numbers of seedlings as the response variable, and with time of measurement (in years since 1979), treatment (exclosure or control) and their interaction as fixed effects. To account for the repeat measurement and pairing of plots, we included a paired-plot term as a random effect. In addition, we included a species term as a random effect, allowing both the intercept and the slope of the time effect to vary by treatment and species. Including a random effect for the time-by-treatment interaction across species allowed us to model the difference in the average trend in the numbers of seedlings between the exclosure and control plots across species. We report this difference, with positive values (on the log scale) indicating species whose seedling numbers increased more in the control relative to the exclosure plots through time, and negative values indicating species whose seedling numbers increased more in the exclosure relative to the control plots through time.

Saplings were absent in all but one plot at the first measurement but had increased dramatically in several plots by the final measurement (Table 4). We therefore used only the data at the final measurement (2007) to examine differences in sapling numbers between the exclosure and control plots. Our data were the numbers of saplings of each species in the paired plots and we fitted a hierarchical regression model with treatment (exclosure or control) as a fixed effect and paired plot as a random effect. In addition, we included a species term as a random effect, allowing both the intercept and the treatment effect to vary by species. This allowed us to model the difference in the average number of saplings in the exclosure versus the control plots across species. We report this difference, with positive values (on the log scale) indicating species with more saplings in the control relative to the exclosure plots, and negative values indicating species with more saplings in the exclosure relative to the control plots in 2007.

In both cases we fitted the hierarchical regression models using the lme4 package in R (details of the models fitted are in Appendix 3) specifying a quasiPoisson distribution and log-link function, which is appropriate for count data taking account of overdispersion.

4.4.2 Results

Seedling numbers in most plots increased through time (Table 3), with final seedling numbers higher in exclosure versus control plots in five of the seven pairs, although only slightly so in some pairs (e.g. plots 2.5 and 2.6). The hierarchical regression model indicated that overall there were fewer seedlings in the control versus exclosure plots, with the 95% confidence intervals just differing from 0 (overall parameter estimate for difference in slope through time for the control versus exclosure plots = −0.017, 95% confidence intervals −0.033 to 0).

Sapling numbers also increased through time in all plots (Table 4), again with five of the seven pairs having more saplings in exclosure versus control plots in 2007. Despite this, the numbers of saplings in plots were highly variable, and while the hierarchical regression model indicated that, on average, there were slightly fewer saplings in control versus exclosure plots, the confidence intervals around this estimate were wide and overlapped zero (overall parameter estimate for difference in numbers of saplings in 2007 for the control versus exclosure plots = −0.42, 95% confidence intervals −3.18 to 2.34).

Figure 10 summarises differences among species in the numbers of seedlings and saplings in the exclosure relative to the control plots. Eleven species tended to have more seedlings in exclosure relative to control plots (i.e. negative values in Fig. 10), significantly so for four species, with five species significantly more abundant as seedlings in control relative to exclosure plots.

Confidence intervals around the estimates for differences in sapling numbers between the exclosure and control plots tended to be much wider than for seedlings, with only *Raukaua simplex* showing strong evidence of being more abundant in exclosures relative to controls and *Coprosma propinqua* more abundant in controls than exclosures. The wide confidence intervals around the parameter estimates for saplings reflect the wide variability in sapling numbers among plots, with species often absent as saplings from some plots and abundant in others.

We compared the performance of species in exclosure relative to control plots by ungulate preference categories from Forsyth et al. (2002; see Appendix 1). For seedlings, preferred species performed, on average, significantly better in exclosure plots relative to controls (Fig. 11), suggesting that deer exclusion favoured seedling regeneration of deer-preferred species. Not-selected and avoided species showed no clear trend, on average. Similarly, for saplings, there was no strong tendency for species in different preference classes to differ in their response to deer exclusion, perhaps due to the wide variability in sapling responses.

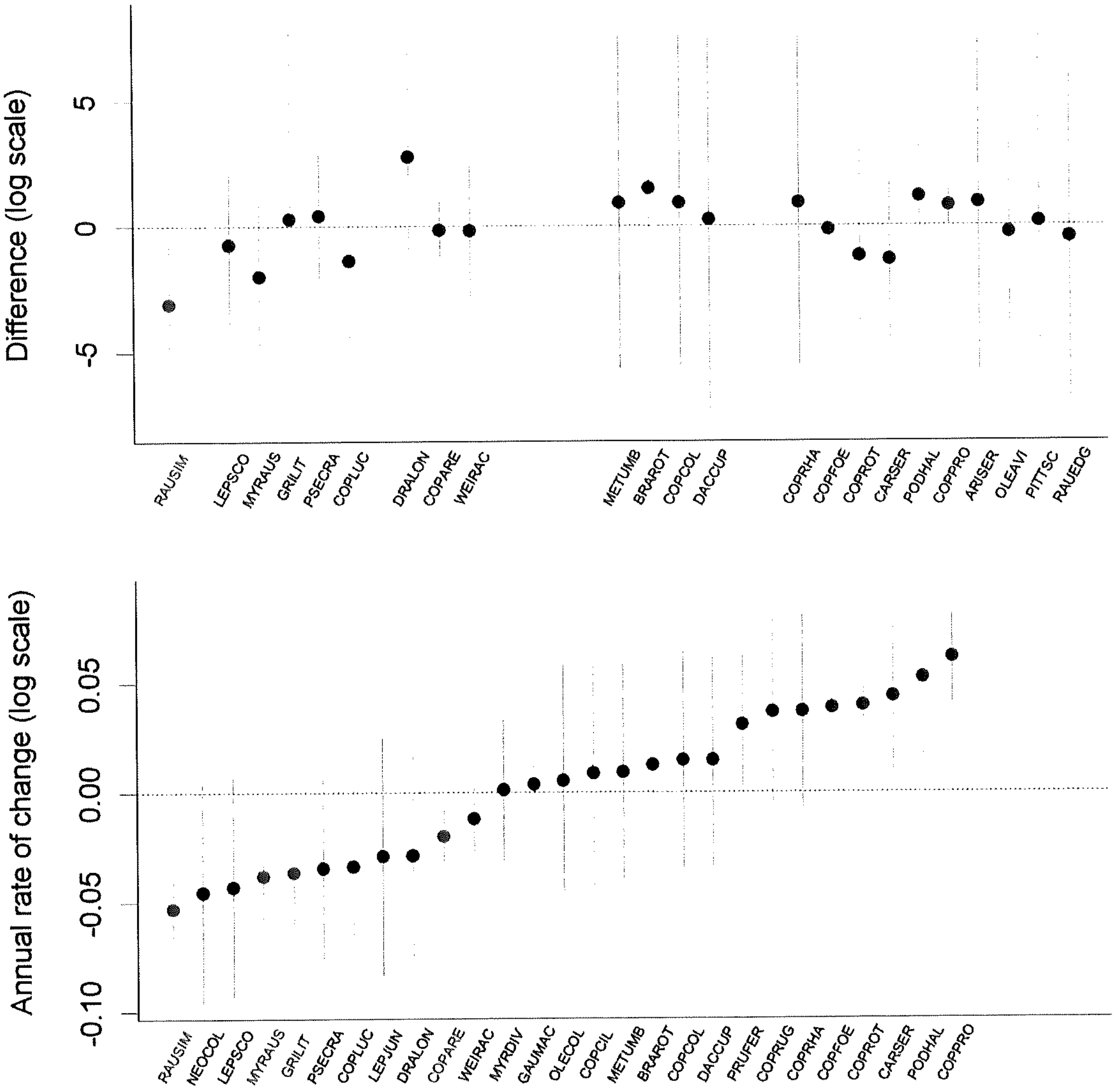

Figure 10. Estimates of the difference in the annual rate of change in seedling numbers between exclosure and control plots (bottom panel) and estimates of the difference in numbers of saplings in exclosure and control plots in 2007 (top panel), and 95% confidence intervals around those estimates (grey lines). Positive values (here on the log scale) indicate species that performed better in the control relative to the exclosure plots, while negative values indicate species that performed better in the exclosure relative to the control plots, in terms of numbers of seedlings or saplings. Species are ranked in order of performance in exclosure versus control plots for seedlings. Species whose 95% confidence intervals do not overlap zero (i.e. no difference between exclosure and control plots) are shown in blue where they performed better in control plots relative to exclosures, or red where they performed better in exclosure plots relative to controls.

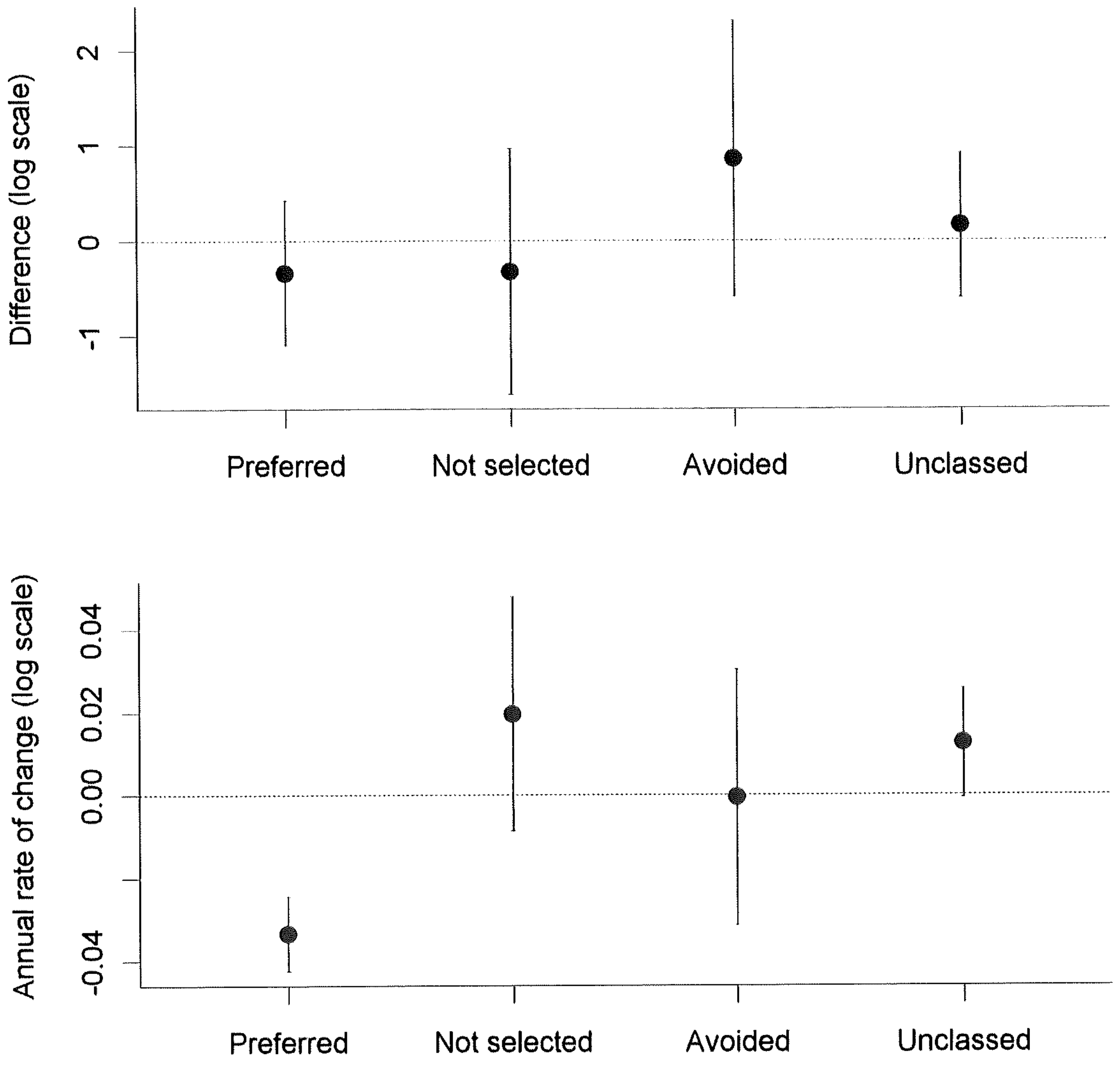

Figure 11. Estimates of the difference in the annual rate of change in seedling numbers between exclosure and control plots (bottom panel) and estimates of the difference in numbers of saplings in exclosure and control plots in 2007 (top panel) by ungulate preference classes (see Appendix 1), and 95% confidence intervals around those estimates.

4.5 LINKING CHANGES IN LONG-TERM PERMANENT PLOTS ON STEWART ISLAND TO UNGULATE PREFERENCE CLASSES AND RESPONSE TO DEER EXCLUSION

The ungulate preference classes (Appendix 1) and our analysis of exclosure versus control plots on Stewart Island provide us with two measures of deer impact on species that are independent of the temporal trends in the permanent plot data. Here we relate these measures of deer impact to changes in seedling and sapling numbers, tree basal area, and the ratio of tree mortality to recruitment in the Stewart Island plots.

4.5.1 Results

Figures 12 and 13 show the mean annual rates of change in seedling numbers, sapling numbers and tree basal area, along with the ratio of mortality to recruitment for species by ungulate preference classes. On east Stewart Island, seedlings and saplings in all preference classes have on average increased in number through time, but with no clear difference in the rate of increase among preference classes. On Bench and Ulva islands, and on main Stewart Island, seedling and sapling numbers have remained relatively constant through time, with some tendency on main Stewart Island for preferred species to have declined on average while avoided species have increased.

For trends in basal area and the ratio of mortality to recruitment, there was no clear pattern by preference class for species on Bench and Ulva islands, or main Stewart Island. However, for species on east Stewart Island change in basal area and the ratio of mortality to recruitment appeared linked to preference class, with preferred species declining on average in basal area and having mortality-to-recruitment ratios that significantly exceeded one, avoided species tending to increase in basal area and having mortality-to-recruitment ratios significantly less than one, with not-selected species intermediate between these (Fig. 13).

Table 5 shows the correlations of species trends in seedling and sapling abundance, basal area, and the ratio of mortality to recruitment with response to deer exclusion from the exclosure plot analysis. There are no significant correlations on Bench and Ulva islands. On main Stewart Island there are significant positive correlations between change in seedling abundance through time and performance in the exclosure plots. In this region, those species whose seedlings tended to increase in abundance through time were those that performed well in control plots, while those that declined through time were favoured by deer exclusion.

On east Stewart Island, the ratio of mortality to recruitment for tree species was negatively correlated with response to deer exclusion, significantly so for the sapling response; those species whose saplings were more abundant in the absence of deer tended to be those species in which tree mortality exceeded recruitment rate.

TABLE 5. PEARSON CORRELATION COEFFICIENTS BETWEEN SEEDLING AND SAPLING PERFORMANCE IN EXCLOSURES VERSUS CONTROLS (SEE FIG. 10) AND ESTIMATES OF RATE OF CHANGE IN SEEDLING AND SAPLING NUMBERS AND BASAL AREA, AND THE RATIO OF MORTALITY TO RECRUITMENT, FOR PLOTS ON BENCH AND ULVA ISLANDS (ISLANDS), EAST STEWART ISLAND (EAST) AND MAIN STEWART ISLAND (MAIN). SIGNIFICANT CORRELATIONS ARE SHOWN IN BOLD WITH $*P < 0.05$, $** P < 0.01$.

		Seedlings	Saplings	Basal Area	Mortality/ Recruitment
Islands	Seedling exclosure	0.12	−0.13	0.25	0.41
	Sapling exclosure	0.04	0.36	0.36	0.08
East	Seedling exclosure	0.11	0.34	0.12	−0.30
	Sapling exclosure	−0.13	0.35	0.29	-0.54^{*}
Main	Seedling exclosure	0.62^{**}	0.21	0.11	0.13
	Sapling exclosure	0.49^{*}	0.10	0.05	0.06

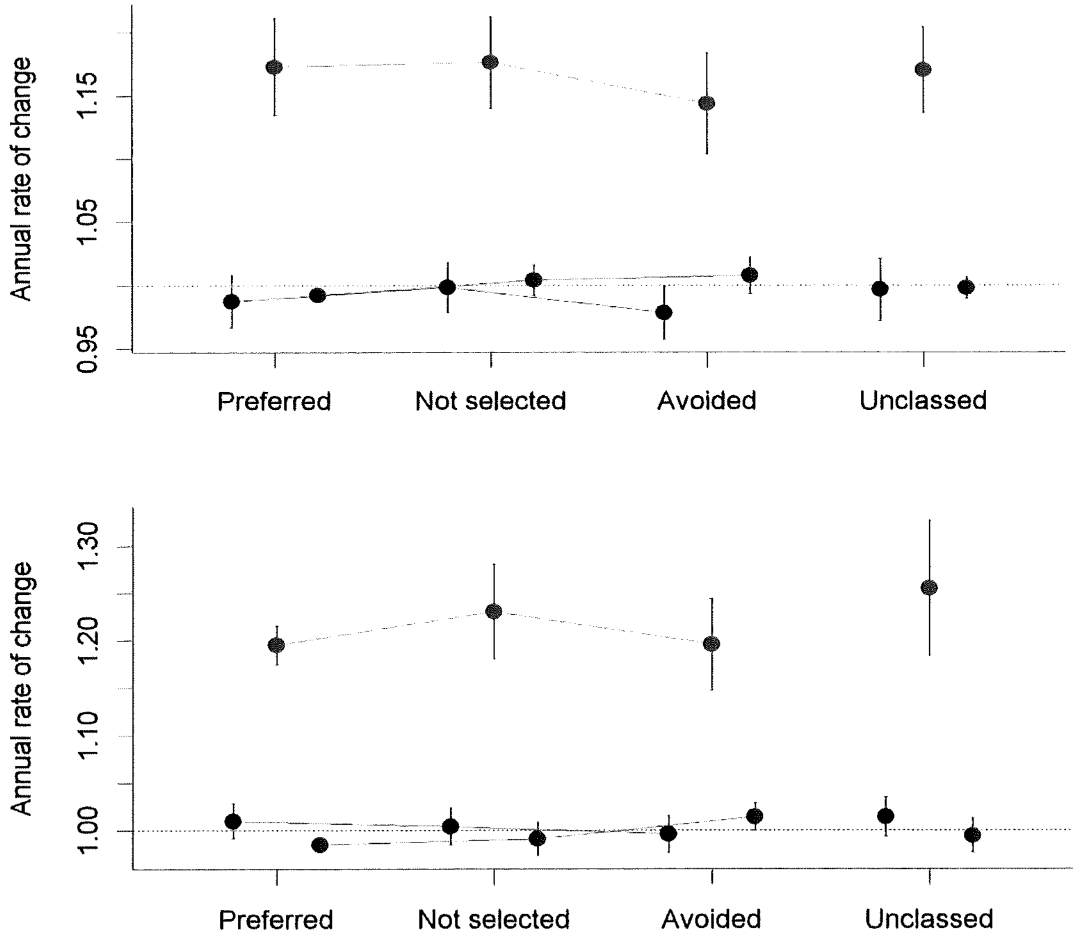

Figure 12. Mean annual rate of change in seedling numbers (top panel) and sapling numbers (bottom panel; both with 95% confidence intervals) for species by ungulate preference classes (see Appendix 1)), for plots on Bench and Ulva islands (black circles), east Stewart Island (red circles) and main Stewart Island (blue circles). Figures 5 and 6 show the individual species estimates from which the means were derived.

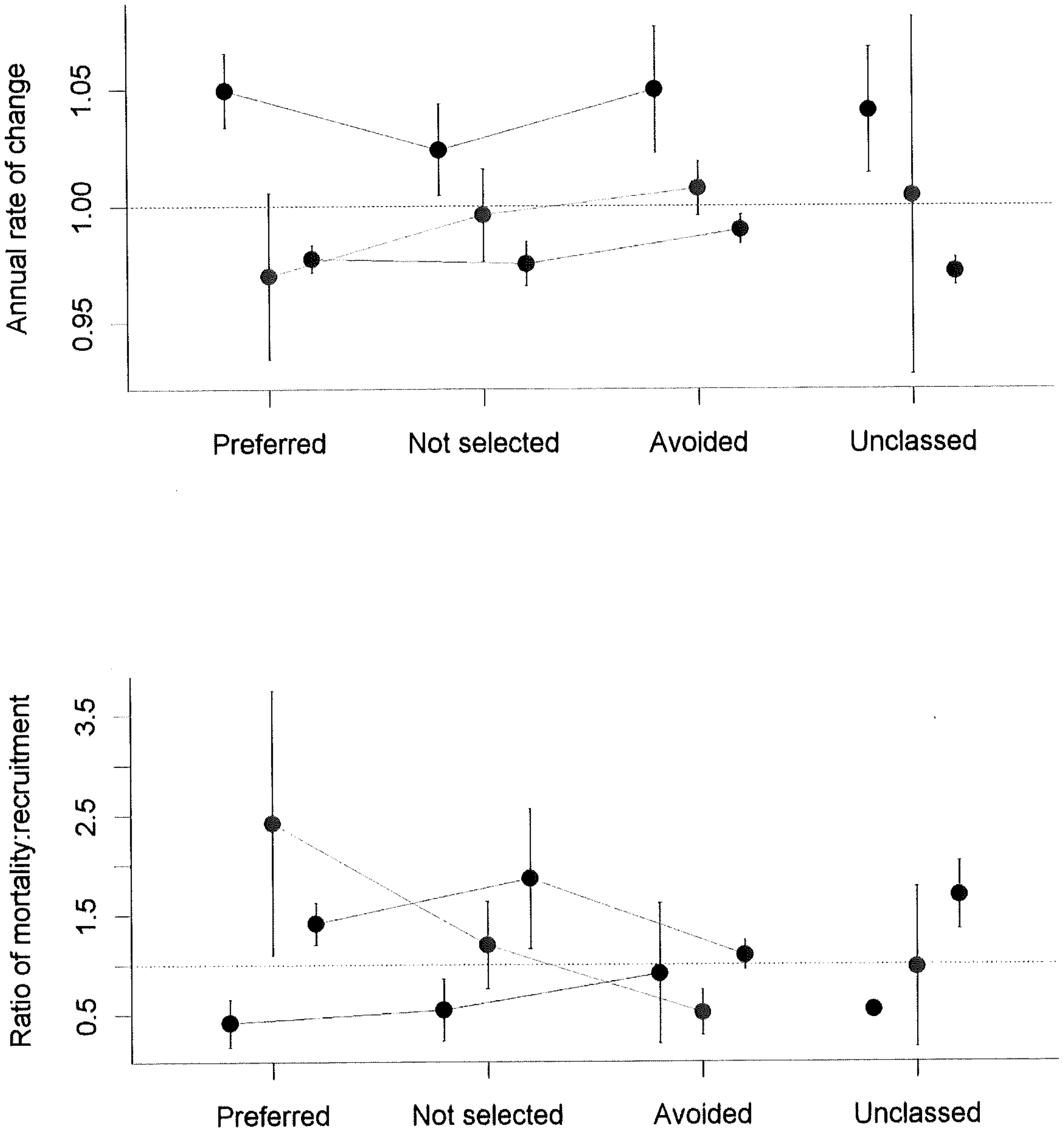

Figure 13. Mean annual rate of change in basal area (top panel) and the ratio of morality to recruitment rate (bottom panel; both with 95% confidence intervals) for species by ungulate preference classes (see Appendix 1), for plots on Bench and Ulva islands (black circles), east Stewart Island (red circles) and main Stewart Island (blue circles). Figures 6 and 7 show the individual species estimates from which the means were derived.

5 Discussion

On Bench and Ulva islands there has been relatively little change in the structure and composition of the woody vegetation in the permanent plots over time. There were no significant differences in the abundances of seedlings and saplings by deer preference classes when plots were first established on the islands, and seedling and sapling numbers of all species have stayed about the same over time. Tree recruitment rates exceed mortality rates for most species, with some species having increased significantly in basal area. Among species, none of the changes are related to deer preference categories or response to experimental deer exclusion, as expected given that deer are absent from these islands and change must result from other processes.

On main Stewart Island (Port Pegasus and Stewart Island North surveys) and particularly on east Stewart Island (Port Adventure and Chew Tobacco Bay surveys) there have been more-marked changes in the woody vegetation over time. In both regions, relative to Bench and Ulva islands, there were significantly fewer seedlings and sapling of deer-preferred species when the plots were first established, reflecting the long history of understorey browsing by white-tailed deer on Stewart Island (Nugent & Challies 1988; Veblen & Stewart 1980). On main Stewart Island, seedling and sapling numbers have remained relatively constant through time, with no species showing significant increases or declines. Nevertheless, trends in seedling numbers through time on main Stewart Island were significantly correlated with seedling and sapling performance in the experimental exclosure plots. Those species whose seedlings tended to increase in abundance through time were those that do well in the presence of deer, while those species whose seedlings declined were favoured by deer exclusion. Thus, while seedling numbers have not changed significantly through time on main Stewart Island, there is evidence that deer are having an impact on seedlings by suppressing populations of deer-preferred species. There is no indication that deer have caused significant shifts in the sapling tier over the study duration. In the tree tier, most species on main Stewart Island have mortality rates that exceed recruitment rates, and several have declined significantly in basal area. Several of the species that have declined in abundance are highly palatable to white-tailed deer (including *Raukaua simplex* and *Brachyglottis rotundifolia*) but, overall, the extent to which mortality rate exceeds recruitment rate, and the extent to which species have declined in basal area, was not significantly correlated with deer preference or response to experimental deer exclusion. Deer may have contributed to declines of some species but other processes may also be driving these shifts. In particular, the largest declines in basal area appear to be among early-successional trees and shrubs (e.g. *Coprosma* and *Olearia* species), consistent with changes that might be expected following pervasive disturbance some time in the past (Bellingham & Allan 2003).

The most marked changes occurred in plots on east Stewart Island. Here, forest composition differed from plots on the rest of the Island, with lower conifer basal area and often a canopy or subcanopy of hardwood species typical of more fertile sites. While mortality and recruitment rates were significantly positively correlated across species on main Stewart Island, and on Bench and Ulva islands, the two were not significantly correlated on east Stewart Island, suggesting that several species were markedly out of equilibrium. In these forests, tree species with high mortality rates relative to recruitment rates were those preferred by ungulates and whose saplings had responded to experimental deer exclusion, while those with high recruitment relative to mortality rates tended to be species avoided by deer. This suggest that, in this forest type, the presence of white-tailed deer has influenced tree population dynamics, with browsing in the understorey causing a shift in tree composition toward less-deer-palatable species. In addition, several species showing high mortality rates and a decline in basal area are considered highly palatable to possums (e.g. *Fuchsia excortica*, *Schefflera digitata*), which may also have contributed to these changes. Despite this, two of the major canopy dominants on Stewart Island, *Weinmannia racemosa* and *Metrosideros umbellata*, show no significant change in these forests over time.

While there is evidence that deer, and probably possums, have affected populations of some tree species on east Stewart Island, seedlings and saplings of all species have increased in abundance over the last 30 years, at an average rate of 10% per year for seedlings, and 12% per year for saplings. The rate at which seedlings and saplings have increased in abundance shows no clear relationship to deer preference. The overall increase implies substantial recovery of woody understorey vegetation over the last 30 years, potentially due to decreased deer numbers resulting from a lowered carrying capacity due to depletion of preferred species (Nugent & Challies 1988).

There are at least two related explanations for the different dynamics of woody vegetation in plots on east Stewart Island relative to main Stewart Island. First, plots on east Stewart Island are in coastal areas, which support higher densities of white-tailed deer (Nugent 2005), and in vegetation with a greater proportion of deer-palatable hardwood species. In contrast, many of the sites on main Stewart Island are inland locations, where white-tailed deer densities are low, and, even in coastal areas, the vegetation comprises a greater proportion of less-palatable conifer and hardwood species (Appendix 2). Consequently, the coastal areas around east Stewart Island may have supported higher deer densities resulting in greater impacts, evident as shifts in tree species composition, and more substantial recovery once deer populations were reduced. Second, vegetation recovery following a reduction in deer densities may have occurred more rapidly because sites on east Stewart Island appear to be of higher fertility. Notably, the exclosure plots tend to be located in this vegetation type, where we would expect to see particularly strong responses to deer exclusion. These may not provide a clear picture of the likely response of other vegetation types to deer exclusion.

Overall, our results show that in north Stewart Island and around Port Pegasus, the composition of the tree tier has shifted over the last 30 years, with most species declining in abundance, while the same species have not declined on Bench and Ulva islands. We could not link these changes to measures of deer impact, suggesting there may be other drivers. Changes in seedling populations could be linked to deer preference, suggesting that deer are having some impact on seedling dynamics, although not sufficient to cause significant declines in the numbers of seedlings of deer-preferred species. This may be because the forests sampled in these areas do not typically support high enough deer densities to cause more substantial impact.

In contrast, there is evidence that white-tailed deer, and probably possums, have impacted tree populations on more fertile coastal sites around Port Adventure and Chew Tobacco Bay. These sites show a shift in tree species composition towards less deer (and possum) palatable species, most likely because these forests historically would have supported high deer densities. They also show significant recovery of understorey woody vegetation over the last 30 years, probably in response to lower deer densities.

Our results suggest that the impacts of white-tailed deer vary across Stewart Island, most likely as a consequence of variation in deer densities and their interaction with forest composition, which in turn is influenced by site characteristics such as fertility. The response of vegetation to deer control will therefore be spatially variable. The greatest impacts of white-tailed deer appear to be in apparently more fertile coastal sites with a high proportion of deer-preferred species. The vegetation at these sites should benefit the most from reductions in deer densities.

6 Recommendations

1. The current set of exclosure plots are not representative of forest types across Stewart Island. We recommend establishing exclosure plots in other forest types to get a more representative idea of vegetation responses to deer exclusion.

7 Acknowledgements

We thank George Ledgard for discussion and staff of the various Stewart Island Vegetation Surveys who collected the data (1979–2008). Hazel Broadbent extracted the data from the NVS database. Susan Wiser, Jenny Hurst and Anna Marburg provided codes to update plant names and Peter Bellingham provided insightful comments on an earlier draft .

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Appendix 1 Woody species included in the analysis

The first column are the six-letter codes used for species; the second column are the ungulate preference classes taken from Forsyth et al. (2002) (p = preferred, ns = not selected, a = avoided, blank = unclassified); the third column are the current scientific names used in the text; and the fourth column are the equivalent names in Wilson (1987b).

Code	Pref. class	Scientific name	Wilson (1987b) name
ARISER	p	*Aristotelia serrata*	*Aristotelia serrata*
BRAROT		*Brachyglottis rotundifolia*	*Senecio reinodlii*
CARSER	ns	*Carpodetus serratus*	*Carpodetus serratus*
COPARE		*Coprosma areolata*	*Coprosma areolata*
COPCIL		*Coprosma ciliata*	*Coprosma ciliata*
COPCOL		*Coprosma colensoi*	*Coprosma colensoi*
COPCUN		*Coprosma cuneata*	*Coprosma cuneata*
COPDUM		*Coprosma sp. p 'dumosa'*	*Coprosma sp. p*
COPFOE	ns	*Coprosma foetidissima*	*Coprosma foetidissima*
COPLUC	p	*Coprosma lucida*	*Coprosma lucida*
COPPRO	ns	*Coprosma propinqua*	*Coprosma propinqua*
COPPSE		*Coprosma pseudocuneata*	*Coprosma pseudocuneata*
COPRHA	ns	*Coprosma rhamnoides*	*Coprosma rhamnoides*
COPRIG		*Coprosma rigida*	*Coprosma rigida*
COPROT		*Coprosma rotundifolia*	*Coprosma rotundifolia*
COPRUG		*Coprosma rugosa*	*Coprosma rugosa*
DACCUP	a	*Dacrydium cupressinum*	*Dacrydium cupressinum*
DACDAC		*Dacrycarpus dacrydioides*	*Dacrycarpus dacrydioides*
DRALON	a	*Dracophyllum longifolium*	*Dracophyllum longifolium*
ELAHOO	ns	*Elaeocarpus hookerianus*	*Elaeocarpus hookerianus*
FUCEXC	p	*Fuchsia excorticata*	*Fuchsia excorticata*
GAUANT		*Gaultheria antipoda*	*Gaultheria antipoda*
GAUMAC		*Gaultheria macrostigma*	*Pernettya macrostigma*
GRILIT	p	*Griselinia littoralis*	*Griselinia littoralis*
HALBIF		*Halocarpus biformis*	*Dacrydium biforme*
LEPINT		*Lepidothamnus intermedius*	*Dacrydium intermedium*
LEPJUN	a	*Leptecophylla juniperina*	*Cyathodes juniperina*
LEPSCO	a	*Leptospermum scoparium*	*Leptospermum scoparium*
METUMB	ns	*Metrosideros umbellata*	*Metrosideros umbellata*
MYRAUS	p	*Myrsine australis*	*Myrsine australis*
MYRDIV	ns	*Myrsine divaricata*	*Myrsine divaricata*
NEOCOL	p	*Pseudopanax colensoi*	*Pseudopanax colensoi var. fiordensis*
NEOPED	a	*Neomyrtus pedunculata*	*Neomyrtus pedunculata*
OLEARB		*Olearia arborescens*	*Olearia arborescens*
OLEAVI		*Olearia avicenniifolia*	*Olearia avicenniifolia*
OLECOL		*Olearia colensoi*	*Olearia colensoi var. argentea*
PENCOR	ns	*Pennantia corymbosa*	*Pennantia corymbosa*
PITTSC		*Pittosporum tenuifolium subsp. colensoi*	*Pittosporum tenuifolium subsp. colensoi*
PODHAL	a	*Podocarpus hallii*	*Podocarpus hallii*
PRUFER	a	*Prumnopitys ferruginea*	*Podocarpus ferrugineus*
PSECOL	a	*Pseudowintera colorata*	*Pseudowintera colorata*
PSECRA	p	*Pseudopanax crassifolius*	*Pseudopanax crassifolius*
RAUANO		*Raukaua anomalus*	*Pseudopanax anomalus*
RAUEDG	p	*Raukaua edgerleyi*	*Pseudopanax edgerleyi*
RAUSIM	ns	*Raukaua simplex*	*Pseudopanax simplex*
SCHDIG	p	*Schefflera digitata*	*Schefflera digitata*
WEIRAC	p	*Weinmannia racemosa*	*Weinmannia racemosa*

Appendix 2. Table of species (rows) by plots (columns), with the values indicating the total basal area of each species in each plot at the first measurement (.= not present as a tree in the plot, 1 = basal area >0-0.1 m^{2}ha^{-1}, 2 = >0.1-1, 3 = >1-10, 4 = >10). The species and plots are ordered by their scores from the non-metric multidimensional scaling ordination (Figure 2), with the plots labelled and coloured by survey (N = Stewart Island north, P = Port Pegasus, C = Chew Tobacco, A = Port Adventure, E = exclosure, U = Ulva Island, B = Bench Island)

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      NNNNNNPPPANUPPNANNNNNNCNUAANPPCNNNNPUNNPPAUPNNNPNNPCPPCUAPPNCNNNNNNNUNNCEPBCNAPPBCNENCNNNNNNEANUCUNCCNACNNACENABNAACBNCAAAAEBCNCECEAACECCACENACEAACAEAEC
ACCCACACCCAAA
LEPSCO444444333.3.....3.3..433..2....3........2.........3...2.....................3.................................................3.........................
.............
COPDUM.1.............................1.........................................1..............................................................................
.............
LEPINT......444...4...3......3.....3...2.3....3..2...33.2........2...................2........................................................................
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HALBIF.....2232.....4.3.32...4...2.3...3.2.3.....2....3.2..........3.3.2..........3.......2.........2.........................................................
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LEPJUN.....12.121...2.31211.32..32....32.................2..2....3.....1....2.....2.......2......................1............................................
.............
PODHAL.....3434344224.3.333..3432433...2..34433.44.4.34.2..3.3.422..32232.433.....2.24..4....1322...24.4...43.........1.............2.............1...........
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DRALON1..213322.2.232.3....333.223....12..2...2.1....33.214.33..34.....2..........321...........2..23....2.1.............3..1.......3.........................
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DACCUP....344433344443444.3.34444444444444444444344444444444444434444444444443343433 44.4444.4444434..4424.43..44.344.13.4..3........2.........................
.............
PRUFER.....2333334313.3434..314343234.33434344344333433333.3333432433.4334433..314.332.4143.23.3343..4.33.333.........4.3..3...4..............................
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NEOPED.2...1.12..2..1..1222...2..1.2...2.22.213.22.....32....3.2.3..2.223.223..2....23..1.2.13.1.......2..2........1.......1..................................
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COPCIL................................1.....1..........1..............1..............1........................................................................
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DACDAC..............................................................3.........................................................................................
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MYRDIV.2.....121.1......1.211....1.1........2.2.......121....2.1.3..1..1..22...........1.12.....2...1......2...1.2....2.......................................
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OLECOL....................3...............................3.........................................4.........................................................
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COPPRO...............................2.................1...............1......................1.....................................2.........................
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ELAHOO.1...2...................................3............3..............3..........................4.................3.....................................
.............
PSECRA.....1..21.2...2.221...12.2.2...1.2.2....22......2.12..21...3..2...21.....2.........1..2...2...3.1...12....2...13....2.....1.1222.......................
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METUMB......43234343334....334344343341333.44.424444434344..43443434434.44244343424344.4.44.43444.4..3.434.4.34.4.4444344.44434444333..34....3....3.3.23....
....2........
COPFOE.....11.11211332232222322..1123.222222222323333232132233323312233332223333332.1223.31.3222222.2332332222.32222333.323322.32323.33..223.2......2........2
.3...........
RAUSIM........11.21322221122.2.212..2.21..221.1.22223222222.322.3....222.231233.2.2...23.3..1.21222.1211.2.23...322..31.2.32..332232.22...22.......2.....1....
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COPLUC...........1........................2..11.1.........2..11...........2.....2...2..2.1..........23..2.........1........1.......2..........2.1.............
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COPCOL.................................................1............1.1........................1....................................1.........................
.............
RAUEDG...........................1........2...............................................................2..........1............1..........2................
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WEIRAC....3333333333.333334333334433.433434433344333344433444333443444444444444343344.444434444443.34344444344444444444343444444444.4444434444.4443.2........
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PSECOL..............................11....1..1.........1............1.12.......3...212.1.1.11.1........2..2.......1..............................3...........
.............
NEOCOL...................................................................................................2.......................2...........................
.............
COPRHA.......................1........................................1............................................................2.........................
.............
OLEAVI.............................................................................................................................2.........................
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BRAROT............3..2...2321.......3............22.2....3.32..2..2............3.3.........2...1..43..1.2...3........23.3..233.....3........2.....3...33..3..
.............
PITTSC..........1.......................................................2..............................3..........3.2.....2..................................
.3...3.......
GRILIT.......1.2............2.1...12..2.22.132.2212231...3122.322.3.33222...222223.332...2.2.3.323.333.3..3223333423.3334433332.4.4333..334333.2443..43434334
344..33333...
COPROT..............................1............................................................1....................................2....2....2........2.2.
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MYRAUS..........2...122.2..2........3..2.2.1..22.3..1.......21...2...12..1.....1....21...2..1.12......33......2...3.21....2...22.3.322......22..33....23..2.3
.3.2.2..1333.
SCHDIG...................................................................................................................1.....................3.....2.......
2......2.....
CARSER.................................................................................2...3.....3...3.3..........3..3....3....3......33.3.3.3.33..2....3.3.3
333.3434.23..
FUCEXC...................................................................................................................................3...344........3.2..
......44..333
COPARE..............................................................................................................1....2.....2......2..3.1...22..233..2...2
.34333..3.2..
OLEARB......................................................................................................................................................2
.3...........
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Appendix 3 Specification of the hierarchical models fitted using the lmer function in R

Overall trends

Data are the total numbers of seedlings and saplings per plot and total plot basal area (in m^2 ha^{-1}) for each year in which each plot was measured.
Time is a continuous variable expressing the year in which a plot was measured as number of years since 1979 (the first year any plot was measured).

lmer(log(total number of seedlings per plot) ~ time + (time|survey/plot))

lmer(log(total number of saplings per plot) ~ time + (time|survey/plot))

lmer(total plot basal area ~ time + (time|survey/plot))

Species-level analyses

Data are the numbers of seedlings and saplings of each species per plot and basal area of each species per plot (in m^2 ha^{-1}) for each year in which each plot was measured.
Time is a continuous variable expressing the year in which a plot was measured as number of years since 1979 (the first year any plot was measured).

glmer(number of seedlings ~ time + (time|survey/plot) + (time|species), family=quasipoisson)

glmer(number of saplings ~ time + (time|survey/plot) + (time|species), family=quasipoisson)

lmer(log(basal area + 0.001) ~ time + (time|survey/plot) + (time|species))

Exclosure plot analyses

Seedlings: data are the numbers of seedlings of each species in each plot for each year in which plots were measured. Time is a continuous variable expressing the year in which a paired plot was measured as number of years since 1979, and excl specifies the treatment (coded as 0 for an exclosure plot and 1 for a control plot). Plot is a variable coding for each plot pair (i.e. each paired exclosure and control plot have the same value).

glmer(number of seedlings ~ time*excl + (1|plot) + (time*excl|species), family=quasipoisson)

Saplings: data are the numbers of saplings of each species in each plot in 2007. Excl specifies the treatment (coded as 0 for an exclosure plot and 1 for a control plot). Plot is a variable coding for each plot pair (i.e. each paired exclosure and control plot have the same value).

glmer(number of saplings in 2007 ~ excl + (1|plot) + (excl|species), family=quasipoisson)