Tree species richness and turnover throughout New Zealand forests

Bellingham, P.J.[1]*, Stewart, G.H.[2] & Allen, R.B.[1]

[1]*Landcare Research, P.O. Box 69, Lincoln, New Zealand;*
[2]*Soil, Plant & Ecological Sciences Division, Lincoln University, P.O. Box 84, Lincoln, New Zealand;*
Corresponding author; Fax +64 3 325 2418; E-mail bellinghamp@landcare.cri.nz

Abstract. Patterns of mortality, recruitment, and forest turnover were investigated using permanent plot data from temperate forests in 14 localities throughout New Zealand. Tree mortality and recruitment rates were calculated from tagged trees ≥ 10 cm diameter at 1.4 m on individual 400 m² plots, and turnover rates were calculated as the mean of mortality and recruitment rates. Turnover rates (1.4% per year) were very similar to those recorded for tropical forests (i.e. 1.5% per year). As was shown in tropical forests, we also found significant relationships between forest turnover and species richness. In New Zealand forests there was also a decrease in species richness and turnover rates with increasing latitude. Although species richness is well known to decline with latitude, our study provides support for a possible link between seasonality and disturbance with tree turnover and species diversity. While tree mortality and recruitment rates were approximately in balance at some localities, in others there were imbalances between mortality and recruitment rates.

Keywords: Browsing mammal; Disturbance; Latitude; Mortality; Recruitment; Temperate forest.

Nomenclature: Allan (1961); King (1990).

Introduction

In tropical rain forests, diversity (as measured by species richness) was found by Phillips et al. (1994) to be positively correlated with tree turnover rates, i.e. the average of tree mortality and recruitment rates. They considered that forests with higher turnover, and higher diversity, were those subject to more frequent fine-scale disturbance. It is unknown whether the relationship between species richness and turnover rates found by Phillips et al. (1994) applies in less species-rich temperate forests. If there is a positive relationship between turnover rates and species richness in temperate forests, we might also expect a negative correlation between turnover rates and latitude, since there is generally a decrease in species richness of forests with increasing latitude (e.g. Currie & Paquin 1987). Correlations of geographic patterns in turnover and species richness with those environmental variables that change with latitude do not provide a mechanistic explanation for observed patterns (Huston 1999). Recently, Givnish (1999) proposed that tree turnover should decrease with increas-

ing latitude due to increasing seasonality; this produces conditions less favourable to abundance of natural plant enemies, i.e. insects and fungi which, at low latitudes, cause more frequent tree death. If such geographic, or environmental, patterns in turnover exist, they may represent a mechanistic link to species diversity patterns resulting from disturbance.

Tree mortality and recruitment are also influenced by many forms of disturbance, both natural and human-induced (Pickett & White 1985). After intensive disturbance, forest development often includes periods of self-thinning, in stands with high stem density and/or basal area, where high mortality rates and low recruitment rates are apparent (Waring & Schlesinger 1985). Disparities between mortality and recruitment rates, as a result of disturbance, can also be pronounced at an individual species level (Harcombe 1987). For example, during succession after disturbance there are often high mortality rates and low recruitment rates of early successional species and the converse for late successional species (Veblen 1992).

In this paper, we investigate whether there are relationships between forest turnover rates and tree species richness in New Zealand's temperate rain forests. We also test whether forest turnover, or tree species richness are related to latitude. These relationships are tested using tree census data from permanent plots sampling 14 localities throughout New Zealand. Forests at some localities included in this study are subject to 'dieback' events (*sensu* Mueller-Dombois et al. 1983) resulting from natural or human-induced disturbance (e.g. Grant 1963; Pekelharing & Reynolds 1983; Ogden et al. 1993). In these forests, we examine whether there are imbalances between mortality and recruitment rates, and compare the resulting turnover rates with those of forests without 'dieback' elsewhere. Although turnover rates among all species allow comparisons among compositionally and structurally different forests, individual species responses are needed to determine coexistence mechanisms and successional changes (Kohyama 1993; Condit et al. 1995). Because many New Zealand tree species are widespread (Meurk 1995), we are also able to test whether there are imbalances in mortality *vs.* recruitment for individual species at different localities.
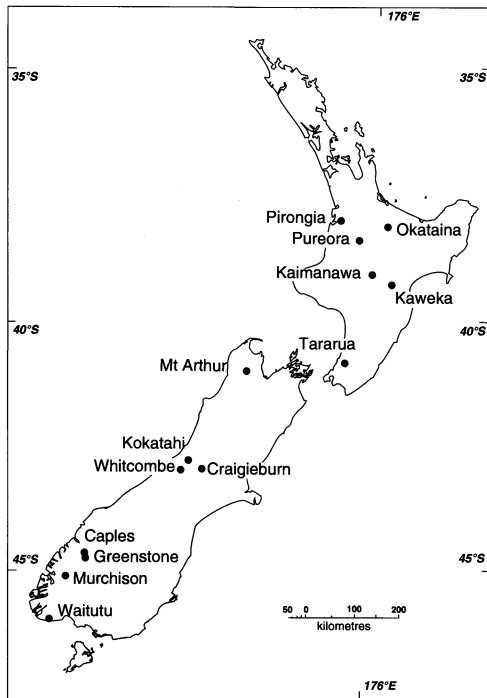
Fig. 1. 14 localities in New Zealand with long-term (≥ 8 yr) census data from permanent forest plots.

Methods

We determined forest turnover rates on plots from 14 localities covering more than 8° latitude (Fig. 1) and a range of underlying lithology, soils, and forest types (Table 1). Broad forest types were defined for each locality according to the basal area dominance, across all plots, in a locality of: conifers; angiosperm trees other than *Nothofagus* ('hardwoods'); and *Nothofagus* species, which often dominate stands (Ogden et al. 1996). All localities have at least 8 years of census data (maximum = 27 yr), sampled with various numbers of permanent 20 m × 20 m plots located along compass lines (see Allen 1993). The origin of each line, in each locality, was located along a stream course in a restricted random fashion. Plots were then located at 200 m intervals along these compass lines, except in Kokatahi and Whitcombe where plots were located at regular altitudinal intervals, thus at each locality the plots can be used to portray the average dynamics of the forests. Within each plot, all stems ≥ 10 cm diameter at 1.4 m height (dbh) were tagged at measurement height at the earliest census, mortality of tagged stems noted at later censuses, and ingrowth stems (i.e., stems that grew to become ≥ 10 cm dbh) were tagged at later censuses.

Summaries of numbers of stems for each plot at each census were derived from Hall (1994). We calculated a mortality rate for all species combined in each plot as an

annual percentage of the initial stems using a logarithmic model (McCune & Cottam 1985; Sheil et al. 1995), and calculated a recruitment rate above the minimum size (10 cm dbh) for each plot as an annual percentage according to a similar logarithmic model (modified from McCune and Cottam 1985). Turnover rates per plot were defined as the mean of mortality and recruitment rates (after Phillips & Gentry 1994). Species richness was calculated for each plot as the number of species ≥ 10 cm dbh/400 m², after Phillips et al. (1994). We also computed a Shannon-Wiener index for each plot using stems ≥ 10 cm dbh (H', a frequently used measure of species diversity as well as dominance; e.g. Magurran 1988; Tilman et al. 1996). Stem density and basal area (all of stems ≥ 10 cm dbh at the most recent census) were calculated for each plot as surrogates for stand development following disturbance (Harper 1977). We examined relationships between the three demographic rates (i.e. mortality, recruitment and turnover rates), latitude, species richness and diversity, as well as stem density and basal area as variables for each plot using generalised linear models (GLMs, Crawley 1993), with variables nested within localities. We also related the mean of the demographic rates per locality with the mean altitude and mean annual rainfall of the localities using Spearman's rank correlations. Demographic rates were compared between localities for four widespread common tree species, i.e. *Nothofagus menziesii* and *Nothofagus solandri* var. *cliffortioides* (both Fagaceae), *Podocarpus hallii* (Podocarpaceae), and *Weinmannia racemosa* (Cunoniaceae). Demographic rates were also compared for each species with the mean proportion each comprised of total stem density and total basal area. For individual species analyses, the total number of stems of each species was aggregated across all plots at a locality, and demographic rates computed across all plots.

All percentage data were arcsine square-root transformed for analysis. Generalised linear models were conducted in S-Plus version 4.0 (Anon. 1997). Spearman's rank correlations (r_s) and ANOVA tests were conducted using SYSTAT version 7.0 (Wilkinson 1997).

Results

All species combined

Across all plots, there were significant negative relationships of latitude with tree mortality, recruitment and turnover rates (GLMs, $F_{14, 659}$ = 1.84, 1.89 and 2.39 respectively, all $P<0.05$, Fig. 2). Mortality, recruitment and turnover rates were also significantly different between the 14 localities (GLMs, $F_{13, 673}$ = 9.82, 22.25 and 16.33 respectively, all $P<0.01$, Table 2).

Table 1. Site details of forests in various localities in New Zealand.

Locality	Forest type	Latitude, Longitude	Lithology	Soils*	Elevation mean (m), (range)	Rainfall (mm)†
Pirongia	Hardwood	37°59'S, 175°02'E	Basalt	Dystrochrepts	470 (200-760)	1600
Okataina	Hardwood-conifer	38°08'S, 176°27'E	Recent volcanic tephras	Udorthents	480 (320-800)	2060
Pureora	Hardwood-conifer	38°23'S, 175°35'E	Ignimbrite	Vitric hapludands	530 (350-850)	1770
Kaimanawa	Mixed *Nothofagus*-hardwood	39°03'S, 175°58'E	Greywacke overlain with volcanic ash	Vitric hapludands and vitrandric dystrochrepts	860 (240-1210)	1530
Kaweka	*Nothofagus* (mono-dominant)	39°15'S, 176°25'E	Greywacke	Vitrandric dystrochrepts	1180 (920-1400)	1580
Tararua	Mixed *Nothofagus*-hardwood	41°00'S, 175°13'E	Greywacke/Argillite	Dystrochrepts	720 (530-1080)	2750
Mt. Arthur	Mixed *Nothofagus*	41°11'S, 172°38'E	Limestone	Endoaquepts	1160 (1080-1270)	2400
Kokatahi	Hardwood-conifer	42°57'S, 171°12'E	Schist	Humaquepts and endoaquepts	590 (320-780)	6000-8000
Whitcombe	Hardwood-conifer	43°05'S, 171°01'E	Schist	Humaquepts and endoaquepts	560 (250-850)	8090
Craigieburn	*Nothofagus* (mono-dominant)	43°10'S, 171°35'E	Greywacke/Argillite	Dystrochrepts	1050 (640-1420)	1400-2500
Caples	Mixed *Nothofagus* - conifer	44°52'S, 168°13'E	Greywacke/Argillite/ Siltstones	Dystrochrepts	680 (290-1140)	2300
Greenstone	Mixed *Nothofagus*	44°57'S, 168°15'E	Greywacke/Argillite/ Siltstones	Dystrochrepts	750 (290-1140)	2300
Murchison	Mixed *Nothofagus* - hardwood	45°18'S, 167°38'E	Gneiss and granite	Dystrochrepts	690 (210-1090)	2400-4500
Waitutu	Mixed *Nothofagus*-hardwood-conifer	46°12'S, 167°04'E	Sedimentaries and alluvium (glacial outwash and marine)	Haplorthods and dystrochrepts	260(3-890)	1160

* Soil classifications follow US Department of Agriculture (Anon. 1998).

† Rainfall estimates are from the nearest rainfall station (Anon. 1973) for all localities except Kokatahi (estimated from Griffiths & McSaveney 1983), Whitcombe (data from Griffiths & McSaveney 1983), Craigieburn (data from Harcombe et al. 1998) and Murchison (data from two rainfall stations in the study area, W.G. Lee, pers. comm.).

Both species richness and species diversity (Shannon-Wiener H') declined with latitude (GLMs, $F_{14, 659}$ = 5.75 and 4.67 respectively, both $P < 0.01$), and were highly significantly different between localities (GLMs, $F_{13, 673}$ = 133.55 and 149.96 respectively, both $P < 0.001$, Table 2). Species richness and diversity declined with increasing mean altitude of localities ($r_S = -0.81$ and -0.78 respectively, both $P < 0.002$), but were not significantly correlated with mean rainfall of localities ($r_S = 0.02$ and 0.01 respectively, both $P > 0.1$).

Across all localities, there were positive relationships between tree mortality, recruitment and turnover rates and species richness (GLMs, $F_{14, 659}$ = 2.30, 2.01 and 2.05 respectively, all $P < 0.025$, Fig. 3), and species diversity (H') (GLMs, $F_{14, 659}$ = 2.60, 2.32 and 2.56 respectively, all $P < 0.01$, Fig. 4).

Across all plots, tree mortality, recruitment and turnover rates of all species combined were highest when total stem density was lowest (Table 2, GLMs, $F_{14, 659}$ = 3.09, 1.97 and 2.59 respectively, all $P < 0.025$). Similarly, tree mortality, recruitment and turnover rates of all species combined declined with increasing plot basal area (Table 2, GLMs, $F_{14, 659}$ = 5.38, 3.41 and 6.95 respectively, all $P < 0.01$). Species richness increased

with increasing stem density and plot basal area (GLMs, $F_{14, 659}$ = 5.45 and 2.39 respectively, both $P < 0.01$). Likewise, species diversity (H') increased with increasing stem density and plot basal area (GLMs, $F_{14, 659}$ = 4.52 and 2.25 respectively, both $P < 0.025$).

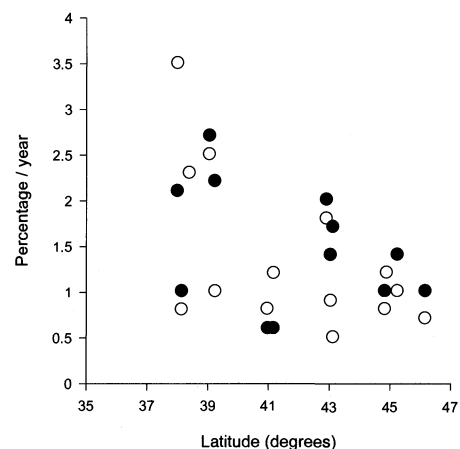In most localities, mortality and recruitment rates

Fig. 2. Mean mortality rates (●) and recruitment rates (O) of tree stems ≥ 10 cm dbh in permanent forest plots in 14 localities in New Zealand *vs* latitude.
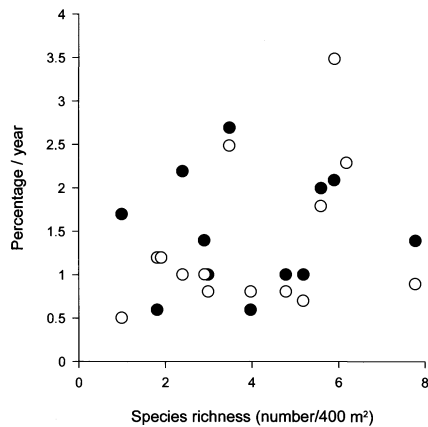
Fig. 3. Mean mortality rates (●) and recruitment rates (○) of tree stems ≥ 10 cm dbh *vs* mean species richness (number of species ≥ 10 cm dbh) in permanent forest plots in 14 localities in New Zealand.
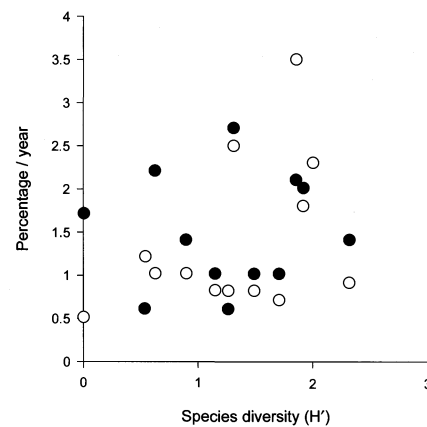
Fig. 4. Mean mortality rates (●) and recruitment rates (○) of tree stems ≥ 10 cm dbh *vs* mean species diversity (Shannon-Wiener H', calculated on stems ≥ 10 cm dbh per species) in permanent forest plots in 14 localities in New Zealand.

were similar, i.e. <0.5%/yr difference between the two rates (Table 2). The greatest differences between mortality and recruitment rates were in Craigieburn (high altitude mono-dominant *Nothofagus solandri* var. *cliffortioides* forests), where mortality rates exceeded recruitment rates by 1.1%/yr, and in Pirongia (hardwood forests), where recruitment rates exceeded mortality rates by 1.3%/yr. There was no consistent pattern of discrepancies (i.e. positive or negative differences between mortality and recruitment rates) that related to species richness or diversity, latitude, altitude or rainfall of localities, or mean plot stem density or basal area (r_S all <0.38, all P>0.1).

Individual species

Across all localities present, the mean recruitment rates of the conifer *Podocarpus hallii* ($\bar{x}$ = 0.4±0.2%/yr) were significantly lower than those of the three angiosperm species (*Nothofagus solandri* var. *cliffort-ioides*: 0.9±0.1%/yr; *Nothofagus menziesii*: 1.1±0.19%/yr; *Weinmannia racemosa*: 1.4 ± 0.28%/yr; Table 3, ANOVA, P=0.01). Mortality and turnover rates were not different among the four species (Table 3, ANOVA, P > 0.05). Mortality rates of *W. racemosa* exceeded recruitment rates by 4.8%/yr in Pureora, but in Pirongia and Kaimanawa recruitment rates of *W. racemosa* ex-

Table 2. Species diversity and richness as well as mortality, recruitment and turnover rates of trees ≥ 10 cm dbh in forests at various localities in New Zealand.

Locality	No. of plots and total area (ha)	Trees/ 400 m²	Basal area (m²/ 400m²)	Diversity index (H')	Species richness (species/ 400 m²)	Time (years)	Inventory period	Mortality rate (%/yr)	Recruit-ment rate (%/yr)	Turn-over rate (%/yr)
Pirongia	20 (0.80)	29.1	1.55	1.87	5.9	8	1979-1987	2.1	3.5	2.8
Okataina	36 (1.44)	46.3	1.92	1.50	4.8	8.7	1983-1992	1.0	0.8	0.9
Pureora	28 (1.12)	27.1	1.47	2.02	6.2	18.7	1975-1993	2.3	2.3	2.3
Kaimanawa	40 (1.60)	16.0	2.68	1.32	3.5	8.6	1979-1988	2.7	2.5	2.6
Kaweka	30 (1.20)	31.0	1.56	0.63	2.4	13.9	1981-1995	2.2	1.0	1.6
Tararua	10 (0.40)	45.8	2.66	1.26	4.0	20.8	1975-1996	0.6	0.8	0.7
Mt Arthur	34 (1.36)	47.3	2.00	0.54	1.8	8.7	1978-1987	0.6	1.2	0.9
Kokatahi	22 (0.88)	35.6	1.96	1.93	5.6	23.2	1972-1995	2.0	1.8	1.9
Whitcombe	23 (0.92)	44.6	2.81	2.33	7.8	26.8	1972-1999	1.4	0.9	1.1
Craigieburn	250 (10.00)	41.8	1.83	0.01	1.0	19.2	1974-1994	1.7	0.5	1.1
Caples	20 (0.80)	20.7	2.03	1.15	3.0	21	1976-1997	1.0	0.8	0.9
Greenstone	29 (1.16)	27.0	2.57	0.55	1.9	13	1976-1989	1.2	1.2	1.2
Murchison	38 (1.52)	29.5	2.57	0.90	2.9	22.6	1976-1998	1.4	1.0	1.2
Waitutu	107 (4.28)	32.0	3.03	1.72	5.2	19.1	1978-1997	1.0	0.7	0.9

Table 3. Demographic rates of trees ≥ 10 cm dbh of four species in forests at various localities in New Zealand. P = mean percentage each species forms of total stems per plot; M = mortality rate (%/yr); R = recruitment rate (%/yr); T = turnover rate (mean of mortality and recruitment rate, %/yr).

Locality	Nothofagus menziesii				Nothofagus solandri var. cliffortioides				Podocarpus hallii				Weinmannia racemosa			
	P	M	R	T	P	M	R	T	P	M	R	T	P	M	R	T
Pirongia													38.2	1.4	2.8	2.1
Okataina													32.0	0.8	0.3	0.5
Pureora													6.5	6.6	1.8	4.2
Kaimanawa	55.7	2.0	2.1	2.1									10.1	1.6	2.7	2.1
Kaweka					79.5	2.0	1.0	1.5	4.6	2.8	0.9	1.8				
Tararua	27.8	0.3	0.7	0.5					2.0	0.0	0.9	0.4	52.8	0.5	0.9	0.7
Mt Arthur	46.8	0.3	1.2	0.8	51.4	1.1	1.4	1.2								
Kokatahi									2.8	3.1	0.0	1.5	24.2	1.0	0.9	1.0
Whitcombe									9.2	1.4	0.2	0.8	27.9	0.6	0.8	0.7
Craigieburn					99.9	1.4	0.5	0.9								
Caples	39.3	1.1	0.7	0.9	27.1	0.7	0.9	0.8	5.5	0.4	0.0	0.2				
Greenstone	47.1	1.1	1.1	1.1	33.8	1.4	1.3	1.3								
Murchison	27.6	1.5	1.1	1.3	44.7	1.1	0.8	1.0					9.2	1.2	1.3	1.3
Waitutu	22.1	0.7	0.6	0.6	14.8	1.2	0.6	0.9	3.4	0.5	0.5	0.5	35.8	0.7	0.8	0.7

ceeded mortality rates by 1.4%/yr and 1.1%/yr (Table 3). For the other six localities in which *W. racemosa* was common, recruitment and mortality rates were similar. Mortality and recruitment rates of *N. menziesii* were generally similar at most localities, with the greatest discrepancy at Mt Arthur where recruitment rates exceeded mortality rates by 0.9%/yr (Table 3). While recruitment rates of *N. solandri* var. *cliffortioides* were similar to, or slightly exceeded, its mortality rates in most localities (Table 3), mortality rates of this species greatly exceeded recruitment rates in two montane forests where it was mono-dominant (by 1.1%/yr in Craigieburn and 1.0%/yr in Kaweka). Mortality rates of *P. hallii*, a minor component of six forests, were higher than recruitment rates in four localities (Table 3). Most notably, 3.1%/yr mortality of this conifer in Kokatahi over 23 yr contrasts with nil recruitment over the same period (Table 3), with a less extreme contrast between 0.4%/yr mortality and nil recruitment over 21 yr in Caples, and a disparity between 2.8%/yr mortality and 0.9%/yr recruitment over 14 yr in Kaweka.

Mortality and recruitment rates of *W. racemosa* were greatest when total stem density was lowest ($r_S = -0.85$ and -0.87 respectively, both $P<0.01$). Mortality rates of *N. menziesii* were also greatest at least total stem density ($r_S = -0.86$, $P < 0.05$), although its recruitment rates were not significantly correlated with total stem density. Mortality and recruitment rates of *N. solandri* var. *cliffortioides* and *P. hallii* were not significantly correlated with total stem density ($r_S = 0.14$ and -0.07 for *N. solandri* var. *cliffortioides* and -0.14 and 0.29 for *P. hallii*, all $P > 0.1$). For three species (*N. menziesii*, *N. solandri* var. *cliffortioides* and *P. hallii*) there were no significant correlations between demographic rates and the proportion each species formed of total stems in

each locality (Spearman's correlations, all $P>0.1$). In the case of *W. racemosa*, there was a weak correlation between mortality rate and the proportion of stems it comprised in a stand ($r_S=-0.67$, $P<0.1$). Mortality and recruitment rates of the four species were not significantly correlated with mean plot basal area in each locality, or with the proportion that each species comprised of the basal area of plots.

Discussion

The relationship between turnover and species richness found by Phillips et al. (1994) in tropical forests was also apparent in our analyses of data from throughout New Zealand's temperate forests. Within New Zealand, it has long been noted that there is a decline in tree species richness with latitude (Cockayne 1928; Wardle 1991). Productivity is considered by many to decrease with increasing latitude (e.g. Adams & Woodward 1989), so the additional relationship we found between turnover rates and latitude may in part be related to increasing productivity with decreasing latitude (Givnish 1999), and in our study this trend was evident within some localities and thus may operate a fine scale. However, others (e.g. Huston 1999) consider that productivity increases with increasing latitude. If this is the case, other explanations for decreasing turnover with latitude are needed. One possible explanation for higher turnover rates in New Zealand forests at lower latitudes may be more frequent disturbance. For example, cyclones of tropical origins affect forests at low latitudes more frequently than those at high latitude (Shaw 1983). Such disturbances may cause more frequent mortality of canopy trees in forests at low lati-

tudes, hence more rapid turnover. The relationship we show between declining tree turnover with increasing latitude (Fig. 2) gives support to the types of mechanisms proposed by Givnish (1999). His explanation for these phenomena are that at high latitudes, conditions are less favourable for pathogens and insects that accelerate rates of tree death, thus mortality rates are lower and hence there is a lower tree species diversity. Lower species diversity in some New Zealand forests is also likely where they have been isolated for millions of years and subjected to repeated local extinctions during glacial periods (McGlone 1988, 1996). An ability to also incorporate these landscape stability processes, as well as turnover, may allow us to explain national-scale diversity patterns more comprehensively (McGlone 1985; Huston 1999).

Contemporary disturbance influences on New Zealand's forests (e.g. drought, cyclones, vulcanism, and earthquakes) are likely to have enduring effects on forest dynamics (Wardle 1991). For example, natural 'diebacks' in high altitude mono-dominant *Nothofagus solandri* var. *cliffortioides* forests have occurred in two of the study localities (Wardle 1983, Ogden et al. 1993). Mortality rates exceeded recruitment rates in these forests by 1.1%/yr in Craigieburn, and by 0.9%/yr in Kaweka; such imbalances between mortality and recruitment rates in forests, and among individual tree species, are often indicative of adjustments to past major disturbances (Nakashizuka 1991). In the case of the two mono-dominant *N. solandri* var. *cliffortioides* forests, we attribute observed imbalances in mortality and recruitment rates to past disturbance (wind and snow storms and pathogens at Craigieburn, Harcombe et al 1988; drought and pathogens at Kaweka, Hosking & Hutcheson 1988). Following widespread death of canopy trees there is a lag between mortality and recruitment (Ogden et al. 1993; Harcombe et al. 1998), thus we expect in the future, recruitment rates will exceed mortality rates in these two localities. The range of mortality, recruitment and turnover rates among the 14 New Zealand forests were not different from those at low latitudes in 65 tropical rain forests (Phillips 1996; mortality: $\bar{x}$ = 1.5%/yr New Zealand, 1.5%/yr tropics; recruitment: 1.4%/yr, 1.6%/yr; turnover: 1.4%/yr, 1.6%/yr; unpaired t-tests, all $P > 0.2$). While no attempt was made to remove forests that are subject to major disturbances from the New Zealand dataset, this was attempted in the case of the tropical forest data sets used in Phillips's (1996) analysis.

New Zealand forests are also widely influenced by the impacts of browsing mammals introduced last century (Wardle 1991). Amongst the most widespread introduced animals are brushtail possums (*Trichosurus vulpecula*), marsupials native to Australia, introduced to

New Zealand in 1858 (Cowan 1990). Brushtail possums selectively browse foliage of certain canopy tree species and have caused tree death in some species (e.g. Meads 1976). Of the four individual species we examined in this study, *Weinmannia racemosa* and *Podocarpus hallii* are both common in brushtail possum diets (Fitzgerald 1976; Coleman et al. 1985; Rogers & Leathwick 1997), and the local mortality of these two species has been attributed to their browsing (e.g. Rose et al. 1992). In contrast, *Nothofagus* species, including the two species considered in this study, are scarcely represented in the diet of brushtail possums (Wardle 1984; Owen & Norton 1995). We found no evidence that forests where tree species palatable to brushtail possums predominate, and where brushtail possums have been present for several decades, have consistently higher mortality than forests dominated by the unpalatable *Nothofagus* species.

Compensatory recruitment of *Weinmannia racemosa* offset its mortality in all localities in our study except Pureora (Table 3). High turnover of *W. racemosa* was evident in stands of low total stem density. In the Orongorongo forests studied by Campbell (1990), where there was high mortality of *W. racemosa*, it was a minor component of the forests. For the nine localities in our study where *W. racemosa* was common there was a weak negative relationship between its mortality rates and the proportion of total stems contributed by this species. Further data from other localities are required to determine whether there is a relationship between mortality rates of this species and its abundance. While turnover rates across all species are approximately in balance in forests dominated by trees browsed by introduced mammals, those of individual palatable species may not be in balance. For example, whereas mortality and recruitment rates of *W. racemosa* were similar in most localities in our study, this was often not the case for *Podocarpus hallii*, especially in Kokatahi where high mortality (3.1%/yr) and no recruitment over 23 years suggests that it may become locally extinct as a canopy species (cf. Wardle 1978).

During successional change in New Zealand forests where *Nothofagus menziesii* co-occurs with *N. solandri* var. *cliffortioides*, Wardle (1983) hypothesised *N. menziesii* would progressively dominate stands as they aged. This expectation would be fulfilled at a locality scale where *N. menziesii* recruitment rates exceed its mortality and where *N. solandri* var. *cliffortioides* mortality rates exceed its recruitment. In this study, there were three localities where *N. menziesii* and *N. solandri* var. *cliffortioides* each contributed similar proportions of individuals, and in combination >70% of stems (Mt Arthur, Caples and Greenstone, Table 3). At one locality, Mt Arthur, *N. menziesii* recruitment rates markedly

exceeded mortality rates, but we did not find the other requirement of *N. solandri* var. *cliffortioides* mortality rates exceeding recruitment. Therefore we found no evidence from long-term census data of gradual replacement of *N. solandri* var. *cliffortioides* by *N. menziesii* in mixed stands at a locality scale, and it is more likely to be a process that operates at a finer (plot) scale.

The network of spatially extensive small permanent forest plots in New Zealand (ca. 6500 nationally, mostly established in the 1970s) gives opportunities for understanding long-term changes in forests, both nationally and regionally, in relation to successional trends, within-species competitive interactions (Osawa & Allen 1993) and effects of introduced herbivores (Stewart & Burrows 1989). The potential is being expanded and realised with the reporting requirements of international agreements (e.g. Convention on Biological Diversity). For example, New Zealand's plot network has been used recently to develop a 1990 estimate of carbon stored in indigenous forests, a requirement of the Framework Convention on Climate Change (Hall et al. 1998). Phillips & Gentry (1994) showed increasing turnover rates in tropical rain forests with time, and they believed this was a likely consequence of increased atmospheric CO_2. New Zealand's national network of permanent plots, in combination with similar networks of plots in other countries, will be able to help evaluation of whether such a phenomenon is true, and, if so, whether it is widespread.

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