

## Carbon and plant diversity gain during 200 years of woody succession in lowland New Zealand

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**Abstract:** Natural regeneration of new forests has significant potential to mitigate greenhouse gas emissions, but how strong is the potential biodiversity co-benefit? We quantified carbon accumulation and biodiversity gain during secondary succession of two New Zealand lowland forests. The rate of carbon sequestration was the same for the kanuka–red beech succession as for the coastal broadleaved succession (c. 2.3 Mg C ha<sup>-1</sup> year<sup>-1</sup>) over the first 50 years of succession. Mean above-ground carbon stocks were 148 ± 13 Mg C ha<sup>-1</sup> for kanuka–red beech forests and 145 ± 19 Mg C ha<sup>-1</sup> for tall coastal broadleaved forests after at least 50 years of succession. Biodiversity gain was investigated through the quantification of ‘ecological integrity’, which comprises dominance by indigenous species, occupancy of indigenous species or a group of species fulfilling a particular ecological role, and gain in representation of lowland forests within each ecological region. All components of ecological integrity increased with carbon accumulation for both successions. In addition, above-ground carbon stocks were correlated with the Shannon and Simpson diversity indices and species richness for both successions, suggesting that conventional metrics of diversity also show biodiversity gain with above-ground carbon during succession of recently non-forested lands to secondary forest.

**Keywords:** biodiversity; ecological integrity; secondary succession; sequestration

### Introduction

Growing international interest in measurement and optimisation of the co-benefits of carbon sequestration projects (e.g. Klooster & Maser 2000; Ferretti & de Bitez 2006) has been mirrored within New Zealand. This is especially true within the Department of Conservation (DOC) as the primary agency charged with restoring and maintaining biodiversity. Land managed for biodiversity can contribute significantly to mitigation of New Zealand’s greenhouse gas emissions through afforestation/reforestation of ‘currently’ non-forested lands as well as through management of existing forests to promote higher standing stocks of carbon. Increasing the carbon storage within existing forests is difficult because of complex feedbacks (Wardle et al. 2007; Peltzer et al. 2010; Holdaway et al. 2012), compared with the large, rapid and measurable carbon gains that can be made through afforestation/reforestation of currently non-forested lands (e.g. Knapp et al. 2008; Pinno & Wilson 2011). Afforestation could promote net gains of at least 100 Mg of total carbon stock per hectare (Hall 2001), even with a one-off loss of carbon from the soils of grassland ecosystems that can occur during the process of land use change leading to forest (Guo & Gifford 2002). In a survey of restoration practitioners we found indigenous afforestation/reforestation establishment costs to be \$750 to >\$50,000 per hectare, when planting is used. Given that current gross annual returns for carbon sequestration in indigenous forests range from \$40 to \$325 per hectare, natural succession is the most economically viable establishment method for new indigenous forests.

New forests could be promoted through natural successions that favour either species with high initial rates of carbon

sequestration or species that can store a lot of carbon over a long period of time (Hall 2001). Carbon is not expected to accumulate linearly in successions (Peet 1981); across biomes, sequestration rate is generally greatest before maximum biomass is achieved (Marin-Spiotta et al. 2007; Peri et al. 2010). However, patterns of carbon sequestration in regenerating forests of New Zealand are largely unknown. One group of authors has examined recovery of carbon stocks in an indigenous forest during single-species stand development following natural disturbance (Davis et al. 2003). Additionally, the sequestration rate of seral mānuka (*Leptospermum scoparium*) has been recorded at up to 2.5 Mg C ha<sup>-1</sup> year<sup>-1</sup>, (Trotter et al. 2005), yet the rate of accumulation during succession to other species has not been measured. To date, change in carbon stocks during succession has simply been estimated through the use of an ecosystem-process-based model, LINKNZ (Hall 2001). LINKNZ was developed to simulate forest development under New Zealand conditions and is a generalisation of the LINKAGES model designed for the mainly deciduous temperate eastern forests of North America (Post & Pastor 1996). In this study, we measure carbon stocks and estimate sequestration rates during secondary succession of two lowland forests. These measurements are compared with the carbon accumulation predicted by LINKNZ, which uses a process-based stochastic approach to simulate ecosystem behaviour from individual species (Hall & Hollinger 2000).

‘Ecological integrity’ has now been embraced by DOC as its primary biodiversity outcome (DOC 2011). Ecological integrity has been defined as ‘the full potential of indigenous biotic and abiotic factors, and natural processes, functioning in sustainable communities, habitats, and landscapes’ by

Lee et al. (2005). These authors suggest ecological integrity has components of long-term indigenous dominance (high influence of indigenous species on ecosystem processes compared with exotic species), occupancy by all appropriate biota, and full representation of ecosystems. The presence of groups of species fulfilling a particular ecosystem role is now thought more important for ecosystem functioning than the presence or absence of any single plant species (Diaz & Cabido 2001). Therefore 'occupancy' of all biota should include occurrence of key functional types as well as species' occurrence. Functional plant types include groups of plant species 'sharing similar roles in (or effects on) ecosystems and biomes' (Cornelissen et al. 2003). In this study we investigate the relative abundance of plant species that provide resources for birds – a key role in New Zealand's indigenous forests. We ask, is there evidence for an increase in ecological integrity with above-ground carbon stocks?

This study examined relationships between carbon stocks, ecological integrity, and species richness during two lowland successions to tall forest species. The successions were: kānuka (*Kunzea ericoides*, Myrtaceae) to red beech (*Nothofagus fusca*, Nothofagaceae) forest, and tauhinu (*Ozothamnus leptophyllus*, Compositae) to coastal broadleaved forest. These successions were selected because they sit near the upper end of the potential rate of both carbon gain and attainment of tall forest stature. Kānuka–red beech is thought to be a relatively widespread lowland successional pathway (Sullivan et al. 2007), with kānuka currently occupying at least 400 000 ha of New Zealand (Wiser et al. 2011). The coastal broadleaved succession is much more localised in its occurrence (we estimate only 25 000 ha of coastal broadleaved forest remain nationally) but is a vegetation type now chronically under-represented in national terms; any increase representing an improvement. Kānuka is relatively long lived (>100 years) whereas tauhinu has a relatively low initial biomass and quickly (<20 years) cedes dominance to a range of broadleaved shrub species. Grime (1973, 1979) originally proposed that plant diversity is maximised at intermediate levels of productivity, whereas a more recent review suggested that maximum diversity occurs on relatively unproductive land (Huston & Marland 2003). However, other evidence suggests that the relationship depends on both the scale (Gillman & Wright 2006) and ecological context (Belote et al. 2011) of the study. We investigated whether ecological integrity or species richness increases with increasing carbon stocks in mesic conditions on fertile soils. Given the urgency that is required for global action for mitigation, we ask whether natural regeneration of indigenous forests can provide rapid gains in both carbon and biodiversity?

## Methods

### Study sites

Change in forest composition and biomass (carbon) during secondary succession was inferred through a space-for-time study of two lowland secondary successions in the eastern South Island. The study was limited to the initial phase of the succession (<240 years) where the conditions required for use of space-for-time substitution were met, namely low diversity of vascular plants, rapid species turnover, and low frequency and severity of disturbance (Walker et al. 2010). Further, we selected single trajectories where the successional pathways have been previously documented (in Wassilieff

1982; Walls & Laffan 1986; Wilson 1994) and the sampled stands contained well-established seedlings and saplings of later-successional species demonstrating their ability to regenerate under senescing individuals of species of the previous stage. Environmental variables (aspect, soil structure, topography, altitude) were closely matched among the sites representing the different successional stages. For all study sites the regenerating forest is legally protected and both wild and domestic animals have been exterminated or heavily controlled to aid rapid achievement of tall forest. Altitude spanned 70–200 m above sea level.

The kānuka–red beech succession was investigated at Hinewai Reserve, near Akaroa on Banks Peninsula (43°50' S, 173°04' E). About 25% of the property is covered by an extensive mosaic of kānuka stands at various stages of regeneration (Wilson 1994). Grazing stock was progressively removed from 1987 and pest herbivores such as possums and goats have been intensively controlled since. Older stands previously protected from grazing are also present and consist of tall forest dominated by red beech, and to a lesser extent Hall's totara (*Podocarpus hallii*). Predicted successional trajectories at Hinewai Reserve have been previously described as involving progression to a beech–podocarp mix as the tallest forest stage (Wilson 1994).

The coastal broadleaved succession was investigated on two adjacent peninsulas in the outer Marlborough Sounds, in order to capture the full range of pre-described stages. The first was Queen Charlotte Wilderness Park on Cape Jackson (41°02' S, 174°16' E) and the second was Cape Lambert Scenic Reserve (41°0' S, 174°12' E) on Cape Lambert. A detailed description of this succession has been published in Mason et al. (2011).

In each type of succession 32–35 plots were selected to represent the entire successional trajectory from woody species that invade exotic pasture through to tall (>12 m) canopy trees. Plot locations were determined by stratified random sampling, i.e. random locations within strata representing hypothesised successional stages and well-stocked stands. These pre-defined strata or successional stages were determined from the literature (Wassilieff 1982; Walls & Laffan 1986; Wilson 1994). We attempted to capture the longest lived (centuries rather than decades) cohort of the succession at the study site.

### Carbon measurements

Stem density and tree size were measured at all plots to enable calculation of the above-ground volume of live plants. For the kānuka–red beech succession, stand basal area was quantified by species, using angle-count sampling (Bitterlich 1984). Diameter at breast height (dbh, 1.35 m) was measured for all stems included in the angle count to enable calculation of point densities for all species present (Beers & Miller 1964). These stem densities, diameters, and measurements of tree height were all used to calculate biomass for all plots in this succession. Permanent sample plots (20 × 20 m; Hurst & Allen 2007) were established for all sampled stands of the coastal broadleaved succession (Mason et al. 2011). Within these plots, tree, shrub volume or both were measured using either forest methodology (suitable for trees ≥ 2.5 cm dbh) or that for continuous shrub cover (Payton et al. 2004), depending on whether plots were covered predominantly in trees or continuous shrubland. Counts of stems from these plots were also used to calculate stem densities in this succession.

## Carbon calculations and analysis

### Successional age

For the coastal broadleaved succession, maximum stand age was determined by landowner records for the youngest ( $\leq 10$  years) tauhinu stands and increment coring of the largest individual trees within a plot. Full details are published in Mason et al. (2011).

For the kānuka–red beech succession we constructed an age–dbh relationship (Payton et al. 1984; Kelly & Bowler 2005) for early-successional stands ( $< 50$  years) by harvesting 40 discs of different sized kānuka trees from land adjacent to the study site to avoid destructive harvest in the reserve. Harvested trees had the same diameter distribution, topography and soil type as the kānuka trees in the successional plots. This relationship was then applied to the individual trees comprising the 95th percentile of diameter in a stand in order to estimate the maximum successional age. For the later successional stands, the five largest red beech trees were cored per stand. The ages of scattered Hall’s totara trees within stands were estimated from published studies of the relationship between diameter and age (Wells 1972; Bergin 2000). Maximum plot age was also determined using individuals comprising the 95th percentile of diameter, whether beech or Hall’s totara.

### Carbon stocks and sequestration

Above-ground biomass (AGB) of individual trees was calculated using an allometric formula previously designed for use across a range of New Zealand forest species (Coomes et al. 2002) and also used by the LINKNZ model:

$$AGB = \rho (DBH^2 h)^b (1 - cDBH) + dDBH^e + fDBH^g,$$

where the constant  $\rho$  indicates wood density ( $\text{kg m}^{-3}$ ) and  $h$  indicates plant height (m). This allometric function explicitly includes trunk, branch and foliage mass. Wood density varies by species and location so whole-stem wood density (oven-dry mass/‘green’ volume) was measured for kānuka ( $642 \text{ kg m}^{-3}$ ) and published values used for other species (Beets et al. 2008; Russo et al. 2010). Where species-specific values were unavailable, congeneric values were used, or in their absence, the mean of all published values in Beets et al. (2008). Values for the other constants used are consistent across species (derived from destructive harvest) and were as follows:  $a = 0.0000598$ ;  $b = 0.946$ ;  $c = 0.0019$ ;  $d = 0.03$ ;  $e = 2.33$ ;  $f = 0.0406$ ;  $g = 1.53$  (Coomes et al. 2002). Litter and coarse woody debris components have not been included in above-ground biomass of the current study as previous quantification shows only a very small contribution to shrubland carbon stocks ( $< 3\%$  for coarse woody debris; Coomes et al. 2002), their contribution becoming more significant only once tall forest is attained (sensu Ross et al. 2009).

Above-ground biomass (AGB) on plots with continuous cover shrub was calculated after Coomes et al. (2002):

$$AGB = \sum(sd \times V),$$

where  $sd$  = shrub density ( $\text{kg m}^{-3}$ ) and  $V$  = shrub volume ( $\text{m}^3$ ) for a given species within a plot. Shrub density values were taken from Peltzer & Payton (2006).

Biomass was summed for all individual stems in a plot, and added to estimates of continuous cover where both types of vegetation were present on a given plot. The summed carbon stocks were then converted to carbon stock per hectare, expressed on a horizontal area basis. Carbon was assumed to comprise 50% of live biomass, as is standard in forest carbon

measurement (Schlesinger 1991).

Differences in carbon stocks and rates of carbon sequestration between entire successions were evaluated using carbon sequestration curves fitted to the summed plot data from each succession, using non-linear least squares regression in R (version 2.11.1, R Development Core Team, <http://www.r-project.org/>). Akaike’s Information Criteria (AIC) (Burnham & Anderson 2002) were used to determine the shape of the curve that best fitted the data. Linear, log, power, hyperbolic and quadratic functions were all investigated. The influence of a variable on the fitted relationship was tested through removing single terms from the full fitted model, independent of order. Because the majority of data points were concentrated in the initial (linear) part of the sequestration curve ( $< 50$  years), further linear regression was performed on these data to investigate differences between early-successional sequestration rates, using non-transformed data. Average sequestration rates for the first 50 years were estimated as the slopes of the lines fitted to these data.

### Measurements and analyses of ecological integrity and species richness

In this study, ecological integrity has been measured as change in indigenous dominance, comparison of woody species occupancy with potential woody species occupancy, change in representation of one key plant functional group during succession, and the current representation of each of the lowland forest types compared with its potential representation within its ecological region.

We quantified indigenous dominance through measurement of change in the indigenous proportion of both biomass and ground-cover species richness during succession. Biomass was quantified for each plot as described above and then separated into indigenous and adventive species. The indigenous proportion of biomass was regressed against above-ground carbon, using generalised linear modelling following arcsin transformation (Crawley 2007), for the kānuka–red beech succession only (as indigenous species represented 100% of the biomass throughout the coastal broadleaved succession). We then examined the ratio of indigenous-to-exotic plant richness in plot ground cover (species  $< 30$  cm height) within  $20 \times 20$  m plots. The plots spanned the entirety of the coastal broadleaved succession but the kānuka–red beech succession was subsampled through the use of seven plots evenly spread through the stand ages. All species (including non-woody vascular plants) in all plots were identified and scored for abundance using a standard cover-abundance scale (Mueller-Dombois & Ellenberg 1974). The proportion of indigenous species contributing to ground cover was regressed against above-ground carbon, using generalised linear modelling in R, with a binomial error distribution.

Occupancy by all potential indigenous woody species was quantified for both successions in two ways. First, we examined the proportion of actual versus potential indigenous species present during succession. Potential presences of woody species for stand ages were derived using the LINKNZ model. Differences between actual and potential species occupancy for each of the c. 30 successional stands per succession were examined using Jaccard similarity. Because Jaccard similarity coefficients are bounded by zero and one, arcsin transformation was necessary. After arcsin transformation the Jaccard similarity coefficients were regressed against above-ground carbon, using generalised linear modelling. We also examined the occupancy of one plant functional group that provides

resources for birds (Lee et al. 2005) through examination of the proportion of biomass represented by species of this functional group. These species are particularly important for biodiversity conservation within New Zealand, because of their close evolutionary relationship with frugivorous birds (Lord 2004). Species present were assessed as to whether they provided fleshy fruits, flowers, buds, nectar or foliage for consumption or substrate for insectivores to forage on (collated from Clout et al. 1986; Clout & Hay 1989; Best & Bellingham 1991; O'Donnell & Dilks 1994; Williams & Karl 1996; Mills & Mark 1997; Murphy & Kelly 2001; Lord 2004; Wotton & Ladley 2008). The proportion of biomass represented by trees providing resources for birds was regressed against above-ground carbon, using non-linear least squares regression, following arcsin transformation. Linear, logarithmic and quadratic fits were all investigated through the use of AIC.

Environmental representation was examined for both successions as the proportion of actual versus potential lowland forest in their respective ecological regions. Actual area of lowland forest was taken as 'lowland podocarp-broadleaved', 'lowland podocarp-broadleaved-beech' or 'broadleaved' forest classes (F2, F4, F8) from the vegetative cover maps of Newsome (1987) whereas the area of potential 'lowland forest' was quantified as those areas predicted by Hall and McGlone (2006) to support 'temperate' forest classes of podocarp, broadleaved and beech mixtures (rather than 'cool').

### Species richness

Woody species richness and the Shannon and Simpson abundance-weighted species richness indices (Hill 1973) were calculated for each plot within each succession. Woody species richness, and the Shannon and Simpson diversity indices were all examined for correlations with above-ground carbon, using a Spearman's correlation test.

### Model predictions

The ecosystem process model LINKNZ (Hall & Hollinger 2000) predicted species successional sequences and associated above-ground carbon stocks for each of the two successions. This tool was selected because it predicts forest cover in the absence of human disturbance instead of relying on current forest distributions (Hall & McGlone 2006). LINKNZ has been used previously to estimate carbon accumulation during forest succession (Hall 2001), predict potential forest cover for all of New Zealand (Hall & McGlone 2006), and evaluate the impacts of forest management on long-term biomass accumulation (Meurk & Hall 2006; Davies-Colley et al. 2009). All sample plots were assumed to be receptive to seedling establishment of all species available to the model subject to current site conditions. Measured values of above-ground carbon were compared with those predicted by LINKNZ, using correlations generated by generalised least squares regression in R allowing for autocorrelation with time.

## Results

### Carbon

Field-based estimates of above-ground carbon stocks for the kānuka–red beech succession were only moderately well correlated with those predicted by LINKNZ ( $r^2 = 0.53$ ; Fig. 1a), but those for the coastal broadleaved succession were well-correlated with those predicted by the model ( $r^2 = 0.91$ ; Fig. 1b).

The relationship constructed for kānuka age as a function of diameter at breast height was:

$$A = 1.1625DBH + 6.56,$$

where  $A$  = stand age (years) and  $DBH$  = dbh (cm). This relationship had a coefficient of determination ( $r^2$ ) of 0.91 (data not shown).

Despite investigation of a range of linear and non-linear fits between maximum successional age and carbon, a natural log-log fit was the most parsimonious. The relationship between stand age and above-ground carbon stock ( $AGC$ ,  $Mg\ C\ ha^{-1}$ ) for the kānuka–red beech succession can be expressed as:

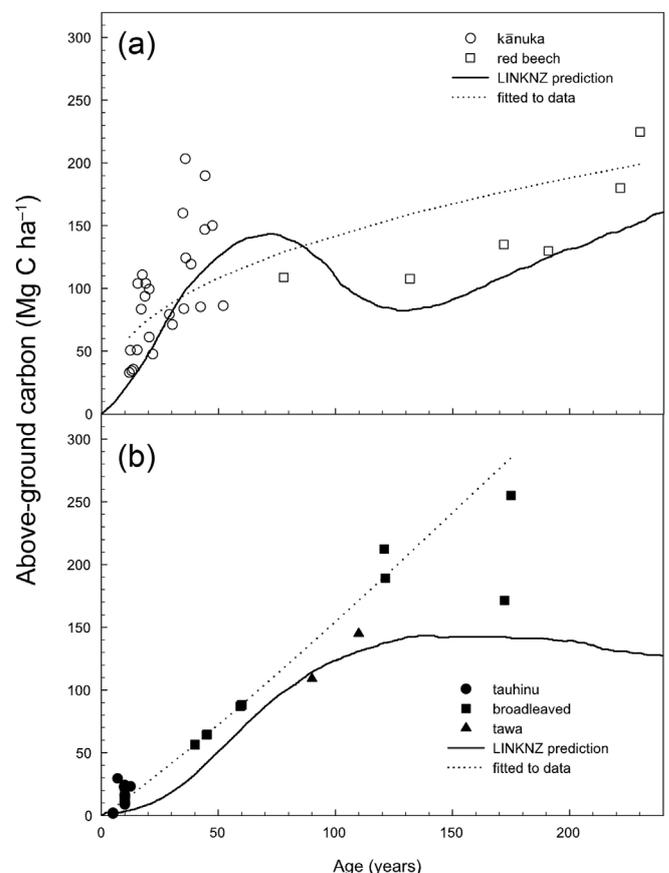
$$\text{Log}(AGC) = 0.40\text{log}A + 3.1,$$

where  $A$  = age (years). For the broadleaved coastal succession the relationship between stand age and above-ground carbon stock can be expressed as:

$$\text{Log}(AGC) = 1.10\text{log}A - 0.01.$$

The coefficient of determination for the fitted relationship was 0.85.

Carbon stocks at 12 years of age were greater in the kānuka–red beech succession, but the rate of carbon gain (sequestration) was at least double in the broadleaved



**Figure 1.** Above-ground carbon stocks ( $Mg\ C\ ha^{-1}$ ) predicted by the LINKNZ ecosystem process model during the first 240 years of (a) kānuka–red beech succession and (b) coastal broadleaved succession. Stocks estimated from field measurement are shown as points. Symbols change to represent the dominant canopy species at each stage. Also shown are the relationships fitted by regression to field measurements.

succession when comparing sequestration rate across the entire succession (Fig. 1). A significant positive interaction between type of succession and successional age on above-ground carbon was observed ( $F = 33.9$ ;  $P < 0.05$ ).

When only the initial linear part of the sequestration curve was considered (age < 50 years), sequestration rates were the same at both sites ( $2.3 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ ), but initial stocks of carbon (i.e. carbon stock at the time the stands became fully stocked and were first measured) were significantly higher ( $F = 27.8$ ;  $P < 0.05$ ) for the youngest stands measured in kānuka than comparable tauhinu stands. These fitted relationships can be expressed as:

$$AGC = 2.29A + 36.4,$$

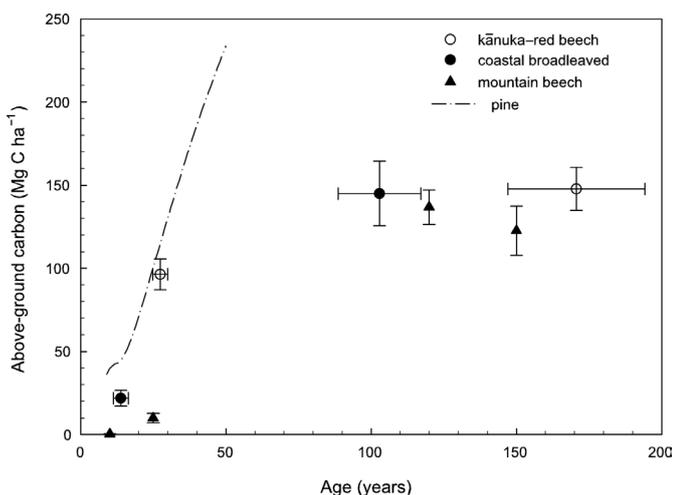
for the kānuka–red beech succession and

$$AGC = 2.29A - 9.74$$

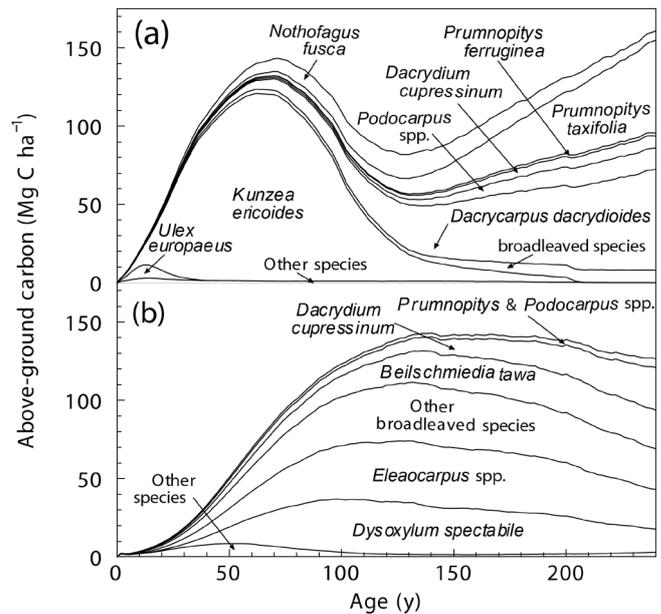
for the coastal broadleaved succession ( $r^2 = 0.77$ ).

Mean values for carbon stocks in plots dominated by the shrubland species (age < 50 years) compared with older forest plots are shown in Fig. 2, which also compares sequestration with other species. The mean value for shrubland stocks across both successions was  $61.5 \pm 7.7 \text{ Mg C ha}^{-1}$ . The mean value for forest stocks across both successions was  $146 \pm 14 \text{ Mg C ha}^{-1}$ .

Measured species' contributions to carbon along both successional trajectories were similar to those predicted by LINKNZ. For the kānuka–red beech succession early-stage carbon is largely composed of kānuka stems in both modelled and measured stands although measured stands comprised a greater broadleaved component (*Pseudowintera colorata*; *Aristotelia serrata*; *Schefflera digitata*) of carbon than was predicted by LINKNZ at c. 40 years (compare Table 1 with



**Figure 2.** Mean values of above-ground carbon stock ( $\text{Mg C ha}^{-1}$ ) for the shrubland and ‘older forest’ stages of two South Island lowland forest successions. Shrubby plots were aged < 50 years, whereas ‘older forest’ plots are those aged > 50 years. Error bars represent one standard error of the mean. In addition, data are shown from a montane stand-development sequence (mountain beech) with the predicted sequestration curve for planted pine in Canterbury–Westland. The lowland forest successions comprise seral vegetation from secondary successions invading exotic pasture, whereas stand development in mountain beech follows windthrow of the previous generation (mountain beech data from Davis et al. (2003)). Pine data come from MAF (2009) and assume the crop is first rotation but not harvested.



**Figure 3.** Species' contributions to total above-ground carbon stocks during lowland succession predicted by LINKNZ for (a) kānuka–red beech succession and (b) coastal broadleaved succession.

‘Other species’ in Fig. 3a). For the coastal broadleaved succession *Eleoacarpus dentatus* was predicted by LINKNZ to comprise a greater proportion of the carbon than was observed, and also the podocarps are not yet (c. 170 years of succession) represented in situ beyond occasional seedlings in the forest (Table 2, Fig. 3b). Here, tauhinu-dominated shrublands most frequently co-occurred with kānuka, mānuka, *Pteridium esculentum* and *Pseudopanax arboreus*. The most frequently occurring broadleaved species, in order of decreasing density, were *Dysosyllum spectabile*, *Hedycarya arborea*, *Pseudopanax arboreus*, *Melicytus ramiflorus* and *Macropiper excelsa* (kawakawa). Stem densities increase until about 45–50 years of the coastal broadleaved succession, but are maximised within the initial 15 years of the kānuka–red beech succession (Tables 1 & 2).

### Ecological integrity

Indigenous dominance of biomass did not change with above-ground carbon ( $P > 0.05$ ) for the two successions studied here. We find a single cohort of an exotic woody species representing 15% of total biomass early in the kānuka–red beech succession (c. 20 years) that is subsequently eliminated (Table 1, Fig. 4a). In the coastal broadleaved succession, there were no woody exotic species (Table 2). Indigenous dominance of ground cover plants did increase with above-ground carbon ( $P < 0.05$ ) for both successions (Fig. 4a).

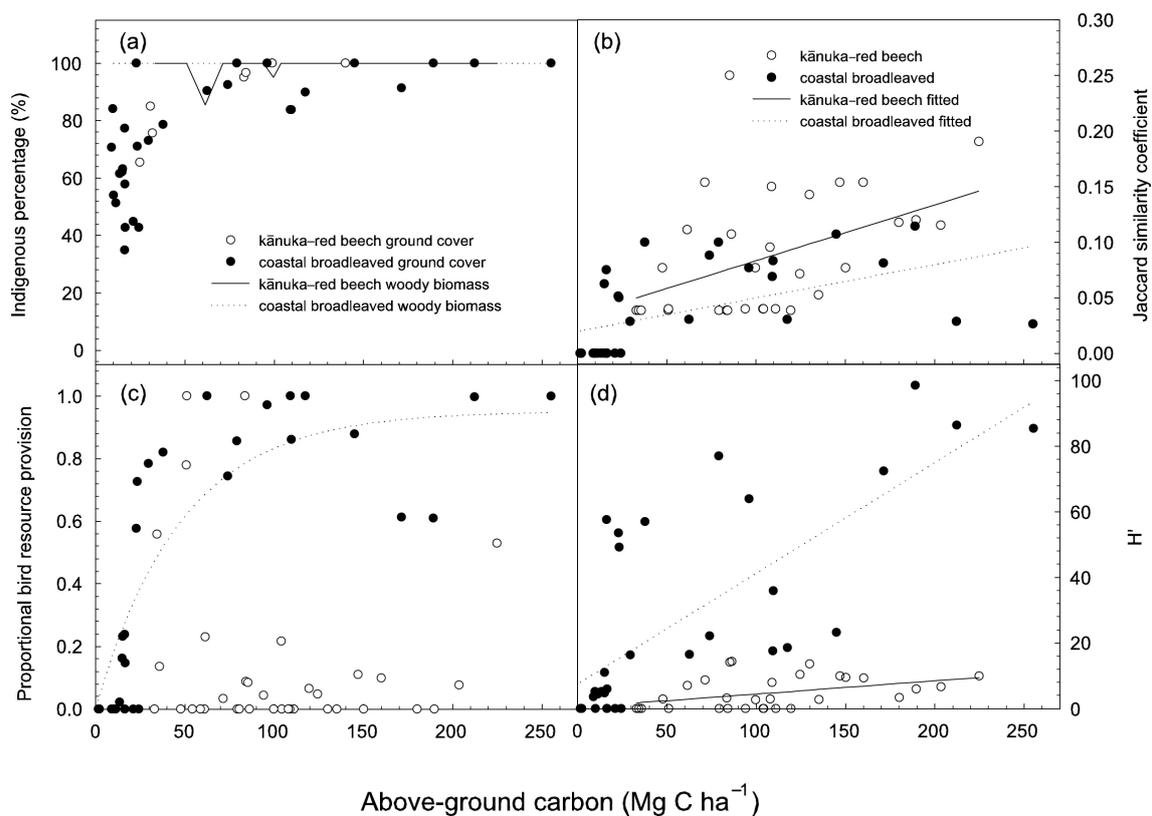
Indigenous species occupancy appears to increase with above-ground carbon for both successions (Fig. 4b), i.e. the vegetation nears the predicted potential composition as carbon increases. This was inferred from the increase in Jaccard similarity between measured and predicted species composition with above-ground carbon for both successions ( $P < 0.05$ ) although the relationship was slightly stronger in the coastal broadleaved succession ( $r^2 = 0.26$ ) than the kānuka–red beech succession ( $r^2 = 0.21$ ).

**Table 1.** Mean density (stems ha<sup>-1</sup>) ± 1 SE of all trees measured in stands within a kānuka–red beech succession. A single standard error for the cohort is given.

Species	Successional age (years)				
	12–15	15–19	20–30	30–52	42–221
<i>Aristotelia serratus</i>				1669 ± 1049	
<i>Carpodetus serratus</i>					72 ± 72
<i>Coprosma colensoi</i>				212 ± 150	
<i>Coprosma rotundifolia</i>				1394 ± 986	
<i>Cyathea smithii</i>				16 ± 11	
<i>Fuchsia excorticata</i>				349 ± 290	34 ± 34
<i>Kunzea ericoides</i>	68 522 ± 10 494	31 824 ± 3048	12 840 ± 2936	4169 ± 1639	258 ± 127
<i>Meliccytus ramiflorus</i>				1557 ± 1056	
<i>Nothofagus fusca</i>					1689 ± 1165
<i>Nothofagus solandri</i>					17 ± 17
<i>Pittosporum eugeniooides</i>			41 ± 41	1117 ± 865	
<i>Pittosporum tenuifolium</i>		413 ± 413			
<i>Podocarpus hallii</i>					297 ± 295
<i>Pseudopanax arboreus</i>				475 ± 239	
<i>Pseudopanax colensoi</i>			86 ± 86	140 ± 99	4354 ± 4354
<i>Pseudowintera colorata</i>				2648 ± 1502	
<i>Schefflera digitata</i>			1732 ± 1732	2771 ± 1933	
<i>Ulex europaeus</i>			2631 ± 1722		
Total	68 522	32 237	17 330	15 083	6705

**Table 2.** Mean density (stems ha<sup>-1</sup>) ± 1 SE of all trees measured in stands within a coastal broadleaved forest succession.

Species	Successional age (years)			
	5–13	40–45	59–74	90–172
<i>Aristotelia serratus</i>				35 ± 77
<i>Brachyglottis repanda</i>				238 ± 143
<i>Beilschmiedia tawa</i>			25 ± 55	
<i>Coprosma grandifolia</i>			68 ± 152	
<i>Coprosma lucida</i>		29 ± 51	25 ± 55	12 ± 26
<i>Coprosma robusta</i>	16 ± 52	10 ± 17		
<i>Cordyline australis</i>	22 ± 75	48 ± 44	28 ± 27	
<i>Corynocarpus laevigatus</i>		0	136 ± 194	10 ± 23
<i>Cyathea dealbata</i>		10 ± 17	12 ± 28	
<i>Cyathea medullaris</i>			56 ± 124	
<i>Dysoxylum spectabile</i>		1251 ± 851	1861 ± 908	552 ± 124
<i>Elaeocarpus dentatus</i>		0	5 ± 11	
<i>Griselinia littoralis</i>		0	66 ± 148	
<i>Hebe parviflora</i>	13 ± 44	88 ± 153		
<i>Hebe stricta</i>	3 ± 9			
<i>Hedycarya arborea</i>		1405 ± 622	788 ± 545	196 ± 46
<i>Kunzea ericoides</i>	143 ± 138	0	10 ± 23	
<i>Laurelia novae-zelandiae</i>		0		34 ± 21
<i>Leptospermum scoparium</i>	34 ± 34	45 ± 28		
<i>Leucopogon fasciculatus</i>		98 ± 170		6 ± 13
<i>Macropiper excelsum</i>		0	84 ± 46	346 ± 275
<i>Meliccytus ramiflorus</i>		795 ± 552	353 ± 202	252 ± 126
<i>Metrosideros diffusa</i>		0	6 ± 13	6 ± 13
<i>Metrosideros fulgens</i>			62 ± 138	73 ± 76
<i>Metrosideros perforata</i>				18 ± 40
<i>Myoporum laetum</i>	5 ± 17			
<i>Myrsine australis</i>	5 ± 17	214 ± 85	57 ± 78	
<i>Olearia paniculata</i>	25 ± 83	239 ± 158		
<i>Olearia rani</i>		0	102 ± 133	29 ± 29
<i>Ozothamnus leptophyllus</i>	1276 ± 1276			
<i>Pennantia corymbosa</i>	47 ± 82	8 ± 14	11 ± 10	23 ± 27
<i>Prumnopitys ferruginea</i>		0	5 ± 11	
<i>Pseudopanax arboreus</i>		2456 ± 1882	204 ± 456	
<i>Pseudopanax crassifolius</i>				12 ± 26
<i>Rhopalostylis sapida</i>		0	5 ± 11	34 ± 18
Totals	1587	6697	3968	1876



**Figure 4.** Ecological integrity and species diversity as a function of above-ground carbon stock for two lowland forest successions. (a) Indigenous dominance is shown both as the proportion of woody biomass occupied by indigenous species and as the proportion of ground cover species that are indigenous. (b) Indigenous species occupancy is represented by the similarity between predicted (potential) and observed species' occurrences, using Jaccard similarity coefficients. (c) Functional group occupancy is represented by the proportion of plot biomass occupied by species that provide resources for birds. Resources provided are either fruit, flowers, buds, nectar or substrate for insectivore foraging. (d) Species diversity is represented by Shannon Diversity Index ( $H'$ ). Fitted lines in (b)–(d) represent the general trends of untransformed data, where a statistically significant correlation existed.

We find no evidence for an increase in occupancy of plant functional groups that provide resources for birds with increasing carbon in the k anuka–red beech succession ( $r^2 = 0.05$ ,  $P > 0.05$ , Fig. 4c). For the coastal broadleaved succession, however, the proportion of total biomass comprising species that provide resources for birds was significantly correlated with above-ground carbon ( $r^2 = 0.72$ ;  $P < 0.05$ ) suggesting that the occupancy of this functional group is increased in this instance. A non-linear relationship between bird resource provision and above-ground carbon was best supported.

With respect to environmental representation, the amount of lowland k anuka–beech forest ('lowland podocarp-broadleaved-beech' forest in Newsome (1987)) present in 1987 was sufficiently small to avoid being mapped altogether for the Banks Peninsula Ecological Region, despite indications that 80% of the area (82 000 ha) could support combinations of these species (area derived from Hall & McGlone (2006)). The gradual progression of this particular succession to later successional species will result in 1–2% achievement of potential representation of lowland forest in this ecological region, which is likely to be two orders of magnitude greater than current representation. Within the Sounds-Wellington Ecological Region, Newsome (1987) mapped 37 700 ha of 'lowland podocarp-broadleaved-beech' and 1300 ha of 'broadleaved forest'. In contrast, Hall and McGlone (2006) indicate that up to 95% of this area (202 000

ha) could support lowland forests. The progression of the coastal broadleaved succession would represent a 2% increase in representation of lowland forest in the ecological region and an 84% increase in representation of lowland forest in the Cook Strait Ecological District.

### Species richness

Above-ground live carbon stocks were positively correlated ( $P < 0.05$ ) with the Shannon Diversity Index ( $H'$ ) in both successions (Fig. 4d). In addition, above-ground carbon was also correlated with woody species richness and the Simpson Index of Diversity for both successions ( $P < 0.05$ , data not shown).

## Discussion

Our data suggest that gains in above-ground carbon, ecological integrity and woody species richness occur concurrently during secondary succession from shrub species to tall forest trees.

### Shrubland carbon

We found more above-ground carbon ( $61.5 \pm 7.7 \text{ Mg C ha}^{-1}$  across both successions) than most previous shrubland studies. For example, Beets et al. (2009) report a mean above-ground

stock value of  $34 \text{ Mg C ha}^{-1}$  across many types of New Zealand shrubland. An earlier study measuring carbon stocks across a South Island transect reported  $21 \text{ Mg C ha}^{-1}$  for shrubland (Coomes et al. 2002 – data corrected here to remove below-ground biomass), although Schönerberger (1984) recorded  $67 \text{ Mg C ha}^{-1}$  of above-ground carbon in beech–shrubby plots. Our high value is likely attributable to the very high rate of biomass gain of kānuka, which was at low altitude on fertile soil and rapidly succeeding to taller forest. International evidence also suggests that site conditions play a highly significant role in shrubland carbon sequestration (Manrique et al. 2011) to the extent that rainfall can even determine whether shrubland reversion within pasture results in a net sink or source of carbon (Knapp et al. 2008). We note also that Banks Peninsula kānuka is one of the bigger forms, notable for its large stature and rapid rates of growth (de Lange 2007). In addition, only fully stocked stands were included in the present study so some individuals in the youngest cohort may actually be older than 12–15 years if they were present as scattered invaders of grassland prior to the rest of the stand but do not have the greatest diameters. This might partially explain the much higher carbon stocks of the kānuka–red beech succession once fully stocked (12 years of succession), compared with the tauhinu-dominated broadleaved succession at the same age. Another contributor will be the higher wood densities of kānuka.

When data were restricted to early-successional (<50 years) stands, sequestration rates did not differ between successions. The combined sequestration rate was c.  $2.3 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ . This value is very close to the mean  $2.25 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  reported by Trotter et al. (2005) for mānuka–kānuka shrublands over 40 years (corrected here to remove the contribution of litter and deadwood pools). We note, however, that the use of maximum successional age will not represent mean age for a given stand – sequestration rates in this study are, therefore, conservative.

Kānuka carbon stocks approach those modelled for the first 20 years of carbon accumulation for planted *Pinus radiata* (pine) stands in the corresponding region (MAF 2009), after correction for below-ground carbon (sensu Beets et al. 2007) (Fig. 2). Although non-harvested pine maintains a higher rate of sequestration after 20 years, most planted stands are harvested between 25 and 28 years. The pattern of carbon sequestration for the two successions is consistent with other sites around New Zealand modelled by LINKNZ where maximum sequestration rates were predicted to occur in the first 50 years of the succession (Hall 2001; Meurk & Hall 2006). While stem densities of kānuka appeared to self-thin during succession, we found no evidence of a concurrent loss of biomass at stand scale – instead, carbon stock dropped during the transition from kānuka to red beech. The measured dip in carbon stocks associated with the transition from kānuka to red beech occurred slightly earlier (50–70 years) than predicted by LINKNZ (70–100 years).

### Carbon in later successional stages

Measured mean values of above-ground carbon stocks in the red beech stage (70–235 years) of the kānuka–red beech succession ( $147.7 \pm 12.9 \text{ Mg C ha}^{-1}$ ) were similar to previous studies of beech carbon accumulation. For example, Patagonian *Nothofagus antarctica* has been recorded as containing  $126 \text{ Mg C ha}^{-1}$  for above-ground components under optimal growth conditions (Peri et al. 2010). Within New Zealand, Hall et al. (2001) estimated that above-ground carbon stocks would be

$135 \text{ Mg C ha}^{-1}$  for beech forest at a national scale, assuming that 20% of the total live carbon is below-ground. Davis et al. (2003) estimated up to  $136 \text{ Mg C ha}^{-1}$  of carbon in above-ground stemwood of mountain beech (Fig. 2). The top value for beech in the current study was  $225 \text{ Mg C ha}^{-1}$ , which is substantially greater than the estimate given for pole stands in Davis et al. (2003). However, the difference can be explained by the mesic conditions of the study site and the greater potential biomass of red beech compared with mountain beech (Wardle 1984; Hurst et al. 2007). In addition, Davis et al. (2003) measured only stemwood; foliage and branch mass were not included in their estimates, which makes a difference of c. 40% (Beets 1980). The single existing study that used harvesting and weighing of trees, rather than relying on allometric relationships (Hart et al. 2003), measured  $166 \text{ Mg C ha}^{-1}$  of carbon in total above-ground biomass of *Nothofagus truncata* (hard beech). Hard beech can reach similar biomass to red beech but the study site reported by Hart et al. (2003) was considerably higher, colder and less fertile than the site in the current study.

For later successional forest in the coastal broadleaved succession we measured an average above-ground carbon stock of  $145 \pm 19 \text{ Mg C ha}^{-1}$  in comparison with  $130 \text{ Mg C ha}^{-1}$  after below-ground correction of Hall et al. (2001). Our figure may represent the upper end of potential carbon stocks for this forest type as a result of extensive wild animal control, but it is more likely that the Hall et al. (2001) figure reflects the national paucity of data from lowland broadleaved forests. The shape of the fitted sequestration curve does not suggest a decrease in sequestration rate during this succession. However, only four data points influence the fitted curve beyond 100 years. Although a log-log fit was the most parsimonious for the data, more data from older (>100 years) stands would be required to accurately predict sequestration at this later stage. Given the over-mature state of the *Dysoxylum spectabile* in the oldest broadleaved stands we predict an imminent decline in above-ground live stocks in the absence of an emergent podocarp and/or *Metrosideros* tier (as expected by Wassilieff (1982) and Walls & Laffan (1986)). LINKNZ predicts podocarps to establish early in succession but reach the canopy after only 100–150 years.

For Northern Hemisphere forests, albeit across a wide climatic range, biomass is generally maximised at around 200 years and then declines to an asymptote at 350 years (Peet 1981). LINKNZ predictions predominantly support a peak in biomass later in succession than suggested by Peet (1981), consistent with the longevity of New Zealand conifer species (Hall & Hollinger 2000). A study of net primary and ecosystem productivity across tropical, temperate and boreal vegetation biomes suggests maximum productivity occurs between 30 and 120 years, although living biomass continues to increase beyond 200 years for temperate forests (Pregitzer & Euskirchen 2004). This apparent decoupling between maximum ecosystem productivity (including heterotrophic respiration) and attainment of maximum biomass underscores the importance of future work examining how carbon shifts between live biomass, soil and coarse woody debris pools during succession (sensu Thuille & Schulze 2006; Risch et al. 2008; Pinno & Wilson 2011).

### Carbon, ecological integrity and species diversity

With the exception of representation of plant functional types that provide services for birds in the kānuka–red beech succession, we find evidence for an increase in all components

of ecological integrity with carbon gain. For both successions, indigenous dominance of shade-tolerant ground cover increased with above-ground carbon. Although conventional successional theory predicts increasing species richness during succession (Odum 1960; Spellerberg 1991) it is encouraging to observe that the increase favours indigenous species. The increase in indigenous dominance of ground cover with above-ground carbon suggests that the ecological integrity of the future forest will be maintained given the representation of future canopy seedlings in the current ground cover. Indigenous dominance of biomass did not increase with above-ground carbon because indigenous species contain almost all of the biomass from very early in succession.

Indigenous species occupancy increased with above-ground carbon in both successions. Because LINKNZ permits all species to establish at a given site as long as suitable environmental conditions exist, the total pool of predicted species was always larger than that observed. The increase in similarity is therefore suggestive of an increase in the number of woody species present with increasing above-ground carbon.

For the coastal broadleaved succession we find an increase in occupancy of the functional group of plants that provides resources for birds. As the above-ground carbon increases, there is greater biomass representation of species that produce fleshy fruits and buds and flowers/nectar for birds to eat (particularly *Dysoxylum spectabile*, *Hedycarya arborea*, *Rhopalostylis sapida*) as well as substrate for insects. This is consistent with other studies showing strong shifts in plant functional traits during forest succession (e.g. Vile et al. 2006) and functional relationships between woody plant complexity and bird diversity (e.g. Kissling et al. 2008). Interestingly, the latter relationship was more strongly influenced by vegetation complexity than trophic interaction, a factor not considered in our study, but worthy of future investigation. We note that in other instances, direct resource-consumer interactions are strongly correlated (Kissling et al. 2007; Menéndez et al. 2007), suggesting differing functional relationships in different situations. The slight decrease in representation of bird-provisioning trees near the end of the successional range captured can be explained by the dominating presence of two large *Laurelia novae-zelandiae* trees, not included within the list of species that provide particular resources to birds. Inclusion of information on size-class distribution would be one way of incorporating some of the other resources that trees provide for birds (e.g. perching and nesting sites). Hatanaka et al. (2011) suggest that such inclusion would allow carbon projects to be ranked for their ability to provide ecological 'complexity' or provision of a variety of habitats.

Environmental representation cannot be compared quantitatively with above-ground carbon. However, given that carbon is increasing as the succession proceeds, it is reasonable to assume that an increased area of lowland forest through natural succession will also enhance environmental representation, given appropriate long-term legal protection. The context for biodiversity change has been emphasised by other authors studying potential trade-offs between carbon and biodiversity. For example, conversion of agricultural land to forest for the purpose of increasing carbon sequestration has been shown to decrease bird densities because farmland generally supports higher densities of farmland birds than the densities of forest species supported by forests (Matthews et al. 2002). The authors suggest that the positioning of afforestation to increase connections between existing remnants may achieve the greatest increase in species numbers – a suggestion also

likely to confer benefit to indigenous lowland plant diversity within New Zealand.

Woody species richness, and Shannon and Simpson diversity indices were correlated with carbon in both successions, suggesting that species richness plus species occurrence weighted by abundance can be gained in tandem with carbon stocks. This is not the same, however, as maximising rate of sequestration as this clearly occurs in the first 30 years of the kānuka–red beech succession, whereas the major species gains occur after this time. Other authors have also observed maximum plant biodiversity at intermediate levels of productivity (summarised by Huston & Marland 2003) suggesting that both values are unlikely to be maximised at the same point on either spatial or temporal scales although a general increase co-occurs across both ecosystem properties.

Our data suggest that gains in above-ground carbon, ecological integrity and woody species richness occur concurrently during secondary forest succession, but that the strength of the correlation depends on site and floristic composition. Management for gain in above-ground carbon therefore appears consistent with gain in biodiversity in these instances where the pasture-invading species are indigenous, and the successions are not otherwise hampered by their pastoral legacy. Standish et al. (2009) cite many instances where repeated burning and intense grazing have prevented New Zealand natural successions proceeding to forest. Future studies should investigate whether the results are repeatable with an exotic woody species as the pasture invader. We recommend that new indigenous forest successions are managed for rapid succession through to tall forest through prevention of fire or other anthropogenic disturbance that would effectively renew the succession and release the stored carbon back to the atmosphere. In addition, long-term legal protection is essential to ensure that successions progress to tall forest. These measures will aid both gain and maintenance of carbon and ecological integrity.

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