

Options for enhancing forest biodiversity across New Zealand's managed landscapes based on ecosystem modelling and spatial design

Colin D. Meurk* and Graeme M. J. Hall

Landcare Research, P.O. Box 69, Lincoln 8152, New Zealand

*Author for correspondence (E-mail: meurkc@landcareresearch.co.nz)

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Abstract: In most regions of the world removal of environmental stress facilitates regeneration of native plants and habitats. However, in many of New Zealand's modified landscapes, exotic species are likely to respond first to any reduction in stress because these fast-growing species are prevalent in local vegetation and dominate seed banks. Given the trend in agriculture towards intensive management on larger units, the indigenous character in New Zealand landscapes is being marginalised and there is the risk that further reduction in visibility of native vegetation may be perpetuated by a growing familiarity and identification with ubiquitous exotic species. Alternative landscapes, based on an understanding of ecosystem processes, need to be explored if biodiversity goals set by international convention and national resource management law are to be achieved. This study provides a set of predictions and pathways, backed by field observations, to underpin a restoration strategy at patch to landscape scales. A forest model, LINKNZ, is employed to simulate species succession under New Zealand conditions. The incorporation of disturbance regimes and species dispersal processes in the model permits a wide range of scenarios to be investigated encompassing indigenous forest development, exotic species interactions with indigenous forest ecosystems, management of mixed introduced-indigenous forests, and landscape dynamics. The results illustrate an approach that identifies potential biosecurity threats and provides additional options for integrating nature and production in New Zealand's rural and urban landscapes.

Keywords: biodiversity; biosecurity; cultural landscapes; forest succession; landscape dynamics; landscape planning; production forests; scenario generation; simulation modelling

Introduction

There is abundant evidence that human settlement often leads to deforestation and decimation of macrofauna (Flannery, 1994). As the last significant temperate landmass to be occupied (*c.* 800 years ago) New Zealand is no exception (McGlone, Anderson and Holdaway, 1994; McGlone, Mildenhall and Pole 1996). One significant factor that differentiates New Zealand from other landmasses is that its biota had been previously isolated from the main thrust of terrestrial, continental evolution for more than 80 million years. This meant that not only were idiosyncratic forms of life present, but significant groups of organisms and growth forms that had been successful elsewhere were absent (e.g. needle conifers, deciduous hardwood trees, nut trees, sward grasses, annual herbs, spring flowers, terrestrial mammals (browsing, herd-grazing and predatory), seed-eating birds, modern reptiles (tortoises, crocodiles, snakes) and frogs, colonial hymenoptera, and conspicuous butterflies) (Dawson, 1988; Meurk, 1995).

New Zealand is recognised as a biodiversity hotspot (Mittermeier *et al.*, 1999), and is phylogenetically significant. For instance, New Zealand retains many ancestral forms of hepatics, ferns, conifers, monocotyledons, onychophorans, microlepidoptera, freshwater fish, frogs, reptiles, passerines, parrots, ratites, rails and bats, largely within forests of late Mesozoic character (Bremer and Janssen, 2004; Gibbs *et al.*, 2004; Wilson, 2004 but see McGlone, 2006). About 80% of terrestrial birds and plants, 90% of freshwater fish, and 100% of frogs, reptiles and bats are endemic. By contrast, the flora and avifauna in the similar-sized British Isles are less than 1% endemic (Wilson, 2004). The isolation and lack of exposure to successful species from elsewhere has increased the risk to New Zealand's endemic biota. The introduction of browsing mammals has been implicated in the increased mortality of several indigenous tree species (Brockie, 1992), and the introduction of dry-fruited and wind-pollinated trees in the lowlands may eventually threaten the viability of New Zealand's frugivorous and honey-eating birds, which are co-

adapted to a high proportion (*c.* 75%) of woody plants that bear fleshy fruits or nectar (Burrows, 1994).

The need to protect and restore the biodiversity of New Zealand has long been recognised (e.g. Hinds and Reid, 1957; J.A. Wardle, 1984; P. Wardle, 1991; Meurk, 1987; Brockie, 1992). However, legislation passed to protect New Zealand's indigenous species, such as the Resource Management Act (1991) and ratification of the Biodiversity Convention, has been widely interpreted and appears to have been unable to prevent attrition of natural habitat and landscape character in some areas. In New Zealand the sustainability of the country's biota raises both ecological and social questions. There are the ecological problems concerned with protecting endemic species against a variety of risks posed by the importation of superior competitors, consumers, and predators. At the same time, most of the indigenous biota that is centred in lowland managed landscapes is of limited extent (Meurk and Buxton, 1990; Wardle, 1991) and most New Zealanders are familiar with landscapes characterised by European and more recently American, Australian and Asian species. It has therefore been suggested that the visibility and utility of indigenous species in urban/rural landscapes ought to be raised if they are to be a sustainable part of these lowland landscapes (Meurk and Swaffield, 2000).

Ecological models offer a framework to evaluate the consistency and understanding of complex processes (Rastetter, 1996). Models can be used to predict transitions and consequences from differing initial conditions, and to investigate the outcomes of various management options (Barlow and Choquenot, 2002).

For this study, an ecosystem process model, LINKNZ, is employed to predict likely long-term responses of New Zealand forests to the impacts of introduced plants and imposition of harvesting. The emphasis on tracking the life-history of individual trees, the stochastic design, and the inclusion of major ecosystem processes, general adaptability, and the ability to simulate long-term dynamics make this class of models suited to investigate several important ecological questions (Shugart, 1984). Such models have a long history of development and have been used to predict the effects of chestnut blight on Appalachian forests (Shugart and West, 1977), impacts of different harvesting regimes on forest productivity in northern hardwood forests of New England (Aber *et al.*, 1982), and the effects of air pollution on regional forest growth (Dale and Gardner, 1987). The models also offer a means to predict changes in species composition, and carbon and nitrogen dynamics, including organic matter accumulation, of the forest ecosystem under varying conditions (Solomon, 1986; Pastor and Post, 1988; Kellomäki and Kolström, 1992).

Several studies have shown that LINKNZ's predictions of species composition, biomass, and density correspond well to independent field data, and that the model could usefully contribute to ecological issues associated with New Zealand forests (Hall and Hollinger, 2000). It has produced acceptable sequences of species replacement in indigenous forest ecosystems at sites distributed along distinct environmental gradients and provided insights into conifer–hardwood and beech forest succession (Hall and Hollinger, 2000). The model has been successfully applied in areas depleted of forest cover in Southland–Otago under both present and inferred past climate conditions (Hall and McGlone, 2001); its predicted species composition and biomass satisfactorily matched recorded pollen percentages for the recent past (700–800 yr BP) and for a period of the early Holocene (7000–8000 yr BP). It has been used to study the impacts of exotic tree species on live tree carbon and stream–wood quality by modelling the transition from a *Pinus radiata* plantation to an indigenous forest ecosystem at a site in Canterbury (Hall, 2001) and a site in the central North Island (Meleason and Hall, 2005).

This study aims to demonstrate the applicability of the LINKNZ forest succession model to different environmental conditions, to investigate interactions between exotic tree species and native forests, and to explore how logging regimes for the extraction of both indigenous and exotic timber could alter composition and biomass. This latter objective attempts to show that gains in biodiversity may not be incompatible with managing a potentially productive resource. Finally, a forest succession model that incorporates species dispersal processes is used to assist with the task of devising workable greenspace configurations to link forest patches across modified or managed landscapes. This required drawing together concepts from successional and spatial modelling, reserve design theory, and greenspace planning to try to accommodate productive and conservation land uses. Implementation of a greenspace plan is needed because a major limit to plant establishment across New Zealand's fragmented landscapes is lack of receptive sites of sufficient quality to attract birds, suppress rank grass, and exclude browsing and predatory mammals. Most light-demanding, early successional native species rely on wind- or gravity-dispersed seed and most unshaded areas are cultivated and grazed or are covered by tall exotic grasses, inhibiting establishment of exotic grasses.

Methods

The forest model

The LINKNZ model simulates, on a yearly cycle, the

establishment, growth, and mortality of all individual trees on a 0.0833-ha plot, and tracks the effects of climate, soil moisture, soil nutrients, and competition on each plant. The stochastic nature of the model requires stand development to be simulated on a number of plots to obtain an adequate description of the mean dynamics for the entire forest. Various studies of plant succession show that growth dynamics of a sufficient number of sample plots of different ages describe the changes in a forest ecosystem (Watt, 1947; Yamamoto, 1992). For this study the model generated 50 successions for each site to smooth out any anomalous events. The emphasis on modelling the growth of individual plants typifies the class of forest-gap models that predict the overall ecosystem dynamics through interactions between plants and available resources. Early models were constructed to reproduce the population dynamics in mixed-species forests of north-eastern North America (Botkin *et al.*, 1972; Shugart and West, 1977) and determined the sample plot area from the average gap created by the fall of a dominant tree in a forest. Like these models, LINKNZ assumes there is a constant supply of propagules for each species and randomly sets the initial diameter of each sapling at breast height (d.b.h.) to vary between 1.27 cm and 1.42 cm. The number of growing seasons, or annual cycles, at each site was set to allow the simulated forest biomass to reach an approximate steady state to accommodate the longevity of several widespread dominant New Zealand tree species (Hinds and Reid, 1957; Wardle, 1991). This required that forest development be simulated for periods covering 800–2000 annual cycles compared to the 250–400 normally considered sufficient for eastern North American species (Pastor and Post, 1985).

Unlike former models, both LINKNZ and its immediate predecessor LINKAGES (Pastor and Post,

1986) explicitly maintain a dynamic soil-moisture balance and a litter decomposition soil nutrient cycle. These models also track details of soil organic matter and nitrogen pools as well as site water balance. Such features were considered necessary for the New Zealand environment given the steep rainfall gradients, disturbed landscapes, and generally infertile soils (Molloy, 1988; Wardle, 1991). Available soil moisture was determined by monthly rainfall and temperature variables together with soil-moisture capacity and wilting point. Available soil nitrogen was initialised for each site and then determined annually by external inputs: losses due to leaching, and dynamics associated with the processes of immobilisation and mineralisation during litter decomposition (Post and Pastor, 1996). Typically, soil organic matter and soil N accumulate on a plot for several centuries until reaching an approximate steady state. By contrast, the estimates of transpiration depend only on the physical environment.

As a simulation progresses, trees establish and grow to create a canopy, which gradually alters the light available to each tree. Changes in the light environment affect growth rates and alter the pattern of species establishment and subsequent composition. As the stand develops, the availability of soil-nitrogen changes, influencing growth rates and species composition, and this in turn changes the amount and quality of litter and its decomposition rate. The variation in these key processes is tracked by the model to reproduce the dynamics of stand development (Aber *et al.*, 1982; Pastor and Post, 1986).

Most forest models are designed for one region and may not include all the variables necessary to successfully model succession in another area (Shugart, 1984). To deal with this LINKNZ incorporates several extensions so it can make acceptable predictions for temperate forests over New Zealand and North America

Table 1a. Location and climatic conditions used for the simulation sites (New Zealand Meteorological Service, 1983).

Site	Altitude (m)	Latitude (°S)	Longitude (°E)	Temperature (MAT, °C)	Precipitation (mm/yr)
Auckland	45	36.46	174.40	14.2 ± 0.90	1268 ± 236
Christchurch	7	43.32	172.38	12.1 ± 0.53	716 ± 165
Queenstown	349	45.02	168.40	10.1 ± 0.58	779 ± 119

Table 1b. Soil parameters set for the simulation sites (New Zealand Soil Bureau, 1957, 1968). Mg = megagrams or tonnes.

Site	Initial soil organic matter (Mg/ha)	Initial soil N (Mg/ha)	Soil moisture field capacity (mm)	Soil moisture wilting-point (mm)
Auckland	74	1.69	383	200
Christchurch	86	4.39	270, 200	100
Queenstown	60	0.80	189	84

(Hall and Hollinger, 2000). For example, the predominantly evergreen species of New Zealand have a higher leaf mass per unit area than the mostly deciduous species of eastern North America and so the light availability equations and canopy-gap decay rates in LINKAGES (Pastor and Post, 1986), based on foliar mass, were reformulated to correct for underestimates. In addition, the poor-growth conditions common to many forest-gap models were changed to match the survival chances of several slow-growing, major New Zealand species. Finally, the effects of disturbance impacts on forest structure associated with the extensive, unstable mountain ranges (Molloy, 1988) were simulated on the higher-elevation sample site by applying whole-stand disturbances at a mean return rate of 1 in 300 years.

The full list of the 76 native species available to the model is presented in Hall and Hollinger (2000). Model parameters obtained from the species' life-history attributes included maximum height, maximum diameter, maximum longevity, limits of annual growing degree-day sums, shade and nutrient tolerances, establishment conditions and rates, and various canopy, foliage, and litter properties.

Study sites

Forest growth is modelled at Auckland, Christchurch, and Queenstown (Table 1a, b). Auckland was chosen because it has a warm, moist climate that supports a relatively high diversity of tree species. The cooler Christchurch site has a low annual rainfall that favours the establishment of more drought-tolerant species, allowing the effects of changes in soil-moisture on species composition to be investigated. Queenstown is located in a mountainous region with relatively seasonal climate and a moderate annual rainfall. The forest composition at Queenstown is simulated at two elevations (349 m a.s.l., 500 m a.s.l.) and the effects of disturbance on forest composition and biomass modelled.

Indigenous forest succession

Successions of indigenous forest were modelled at each site to provide a basis for comparison with impacts of exotic tree species and a proposed harvest regime.

Exotic species impacts

Populations of exotic *Acer pseudoplatanus* (sycamore) and *Pseudotsuga menziesii* (Douglas fir) have established around Queenstown and elsewhere in the high country. The possible long-term impacts of exotic species at Queenstown were examined under two scenarios. Firstly, *P. menziesii* was included in the pool of indigenous species available to the model and a successional sequence was simulated without

invoking a major disturbance regime. Secondly, to investigate the resilience of the New Zealand beech species both *P. menziesii* and *A. pseudoplatanus* were introduced after the indigenous forest had become established for 200 years and a mean 1:300-year, whole-stand disturbance regime was imposed. This scenario was simulated at both elevations.

At the drier Christchurch site, relative competitiveness of indigenous and exotic species was examined under low soil moisture conditions (field capacity 200 mm, wilting point 100 mm) and moderate soil moisture conditions (field capacity 270 mm, wilting point 100 mm). The difference between field capacity and wilting point determined available soil moisture to plants. In both scenarios the dynamics of an exotic forest composed of *Acer pseudoplatanus*, *Pinus contorta*, *Pinus radiata*, and *Pseudotsuga menziesii* were modelled for 500 years and then indigenous species introduced. No major disturbance factors were incorporated.

Production from mixed exotic-indigenous forests

A harvesting regime was imposed to investigate the possibility of incorporating an indigenous component in exotic lowland plantations. The extension of the model to simulate mixed forest development and to mimic transitions from plantation to mixed forest was described in Hall (2001) and Meleson and Hall (2005). Scenarios were modelled at Auckland and Christchurch, starting with a *Pinus radiata* plantation and with a *Pseudotsuga menziesii* plantation, followed by the introduction of indigenous species from either a nearby seed source or by active planting. An initial harvesting regime thinned the plantation by removing 20% of the stems at year 15 for *P. radiata* and year 20 for *P. menziesii*, and indigenous species were introduced at the same time. The mixed forest was harvested by removing 20% of stems with a d.b.h >30 cm every 20 years for the *Pinus*-initiated forest and every 30 years for the *Pseudotsuga*-initiated forest, but always leaving at least 12 stems/ha. These cutting regimes were expected to bias the forest composition in favour of slower-growing indigenous species and against exotic trees.

Dispersal distance effects

A version of the forest simulation model that incorporated species dispersal processes to simulate the effect of distance from a propagule source on forest patch dynamics was applied to landscape restoration. Forest species establishment density was sampled at measured distances from unambiguous, nearest-source populations and the data summarised to develop generalised bird- and wind-dispersed species equations that predicted the probability of plant establishment

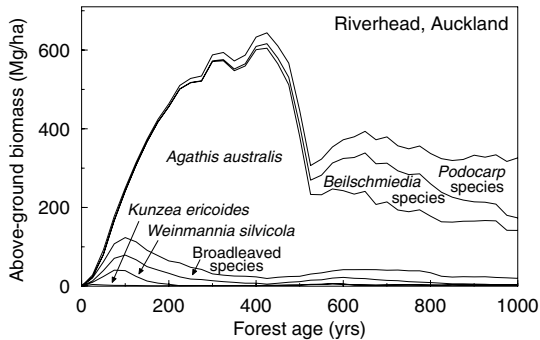


Figure 1. Modelled indigenous forest above-ground biomass at Auckland. The contribution of each species and species group to the total biomass (top line) is cumulative. “Broadleaved species” include *Knightia excelsa*, *Elaeocarpus dentatus*, and *Nothofagus truncata*. “Beilschmiedia species” include *B. tawa* and *B. tarairi*. “Podocarp species” comprise the large trees *Dacrydium cupressinum*, *Prumnopitys ferruginea*, and *P. taxifolia*.

over a given distance from a propagule source. Distances modelled ranged from 20 m to several kilometres and the equations indicated that most successful dispersal events occurred within 100 m of the propagule source.

The effects of dispersal processes on forest dynamics at receptive sites are forecast for Riverhead, Auckland. Although the model has the capability, no allowance was made for sites with multiple propagule sources, or for differential propagule pressure due to variation in the area of the forest source. Therefore estimates of dispersal rates to the receptive patches (based on establishment) are probably conservative.

Results

Indigenous forest succession

Auckland

The forest model predicted the massive conifer species *Agathis australis* would quickly establish and dominate the indigenous forest biomass for c. 500 years before slowly declining for the next 500 years (Fig. 1). An evaluation of the model’s performance showed major species composition matched that observed, the biomass of major species was not dissimilar to harvest-based estimates, and the successional sequence included patterns identified by previous studies (Hall and Hollinger, 2000). The simulation reproduced the early colonisation by several fast-growing, short-lived small trees – *Leptospermum scoparium*, *Kunzea ericoides*, and *Aristotelia serrata*, and the slower-growing but

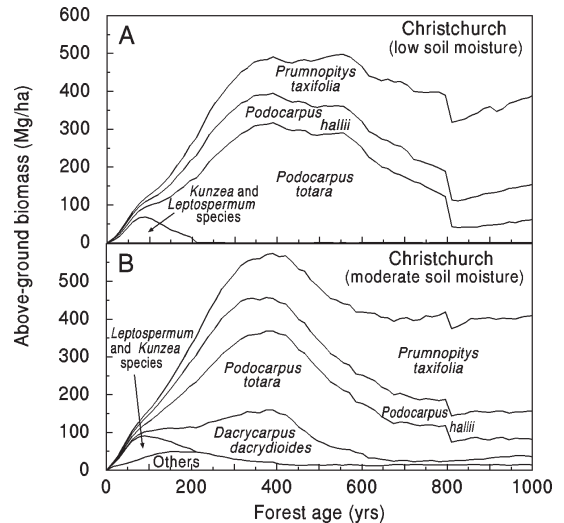


Figure 2. Modelled indigenous forest above-ground biomass for a site near Christchurch under (A) low soil moisture conditions and (B) moderate soil moisture conditions. “*Kunzea* and *Leptospermum*” include the colonising species *K. ericoides* and *L. scoparium*. “Others” include *Griselinia littoralis*, *Pittosporum eugenioides*, *Aristotelia serrata*, *Fuchsia excorticata*, *Elaeocarpus hookerianus*, *Libocedrus bidwillii*, and *Nothofagus fusca*.

more persistent *Phyllocladus trichomanoides*, as described by Ogden (1983). Similarly it predicted the decline in the biomass of these pioneers as taller broadleaved species established: *Weinmannia silvicola*, *Knightia excelsa*, *Elaeocarpus dentatus*, and *Nothofagus truncata*. During this period *Agathis australis* was forecast to account for c. 90% of the total biomass, attaining a peak 585 Mg/ha after 425 years. The model also produced the long-term replacement pattern described by Ogden *et al.* (1987) – the decline in biomass of *Agathis australis* and steadily increasing contribution from the shade-tolerant *Beilschmiedia tawa* and *B. tarairi* and the podocarps *Dacrydium cupressinum*, *Prumnopitys ferruginea*, and *P. taxifolia*.

Species diversity at Auckland was predicted to be relatively high, compared to the cooler and drier Christchurch and Queenstown sites, with >50 tree species established at various times during the simulation.

Christchurch

The simulations for Christchurch predicted that the indigenous forests would be dominated by drought-tolerant conifer species after 100 years (Fig. 2A, B). On a drier soil the forest canopy was expected to be dominated by *Podocarpus totara*, *Podocarpus hallii*,

and *Prumnopitys taxifolia* (Fig. 2A). On soils with a greater moisture capacity the composition was more complex and included the podocarp *Dacrycarpus dacrydioides* (Fig. 2B). On both soils the model predicted the indigenous forests would initially be dominated for 50 years by the widespread colonising species *Kunzea ericoides* and *Leptospermum scoparium*. These small tree species maintained a presence for 200 years, until the podocarp species had established in the canopy and reduced available light at the forest floor below levels necessary to sustain regeneration. Additional simulations (results not shown) predicted that the drier the soil moisture conditions, the longer the early-successional species *Kunzea ericoides* and *Podocarpus totara* would persist. At the time of European settlement much of the well-drained Canterbury Plains were occupied by *Kunzea*, a fire-induced seral state initiated c. 700 years ago by Polynesian colonisers (Molloy, 1969; McGlone *et al.*, 1994).

The moister soil conditions were forecast to influence the pattern of succession by the establishment of additional species. Among these were the broadleaved species *Griselinia littoralis*, *Pittosporum eugenioides*, *Aristotelia serrata*, *Fuchsia excorticata*, *Elaeocarpus hookerianus*, and a small presence of *Libocedrus bidwillii* and *Nothofagus fusca*. After 165 years the mean above-ground biomass of this group reached a peak of c. 47 Mg/ha, or nearly 20% of the forest total. *Griselinia littoralis* was the major contributing species during this period. In the forest canopy *Dacrycarpus dacrydioides* became a significant component of the biomass for c. 500–600 years and retained a presence throughout the simulation period. After 400 years the above-ground forest biomass peaked at a mean 570 Mg/ha, of which *Dacrycarpus* contributed 25% and *Podocarpus totara* 36%. By the end of the simulation period *P. taxifolia* was dominant.

The modelled forest composition corresponded well to that of the few forest stands remaining around Christchurch including a remnant forest preserved at Riccarton Bush with a large component of mature *Dacrycarpus dacrydioides* (Wardle, 1991; Molloy, 1995). A comparison of the simulation against harvest- and plot-data recorded in similar forests indicated that the modelled species biomass estimates were acceptably close (Hall, 2001).

Queenstown

At the lower-elevation Queenstown site (349 m a.s.l.), the model predicted a mixed beech–podocarp forest would develop in the absence of whole-stand disturbance impacts (Fig. 3A). After year 400, canopy composition was stable with the shade-tolerant species *Nothofagus menziesii* and *Podocarpus hallii* accounting for c. 60–70% of the total biomass. Prior to this, the

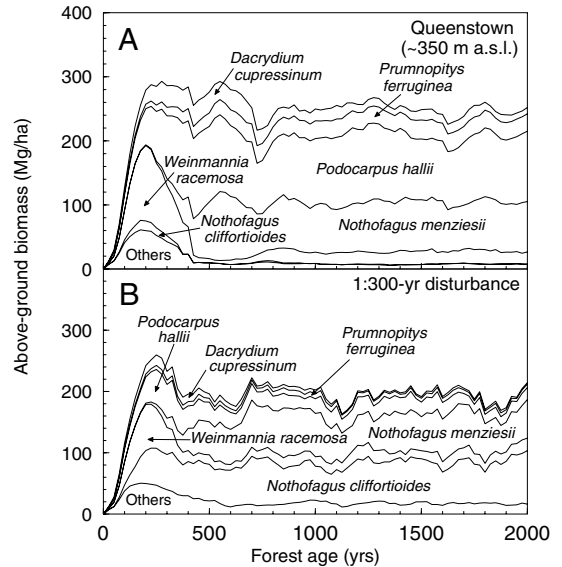


Figure 3. Modelled indigenous forest biomass for a lower elevation site near Queenstown (A). “Others” include *Griselinia littoralis*, *Lepidothamnium intermedium*, *Libocedrus bidwillii*, *Kunzea ericoides*, *Myrsine divaricata*, *Aristotelia serrata* and *Coprosma* species. The effects of a 1:300-year whole-stand disturbance regime on forest biomass are modelled in (B). “Others” include *G. littoralis*, *L. intermedium*, *L. bidwillii*, *Nothofagus fusca*, *K. ericoides*, *Leptospermum scoparium*, *M. divaricata*, and *A. serrata*.

canopy composition varied as the forest matured. At year 100 the broadleaved species *Weinmannia racemosa* and *Griselinia littoralis* contributed >50% of the total forest biomass and the major podocarp species (*Dacrydium cupressinum*, *Prumnopitys ferruginea*, *Podocarpus hallii*) comprised c. 25%. At year 200, the biomass of the beech *Nothofagus menziesii* was negligible and the faster-growing *N. cliffortioides* contributed only c. 5% of the biomass. When a whole-stand disturbance regime was invoked (Fig. 3B) total forest biomass dropped 30% from c. 260 Mg/ha to c. 200 Mg/ha, the biomass of podocarp species reduced markedly to subdominance, whereas the biomass contribution from *N. cliffortioides* rose to a near constant 30% after year 200.

At the higher-elevation site (500 m a.s.l.) the modelled forest, without whole-stand disturbance, exceeded the cool temperature limits of the large podocarp species *Dacrydium cupressinum* and *Prumnopitys ferruginea* but could still be categorised as a mixed beech–podocarp forest (Fig. 4A). The forest differed in composition from that at the lower elevation by an increased occurrence of the smaller cold-tolerant

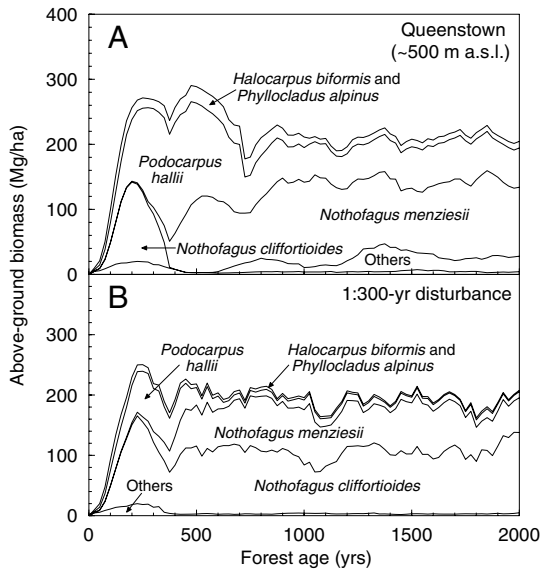


Figure 4. Modelled indigenous forest biomass for a higher-elevation site near Queenstown (A). “Others” include *Lepidothamnium intermedium*, *Griselinia littoralis*, *Myrsine divaricata*, *Dracophyllum traversii*, *Aristotelia serrata*, and *Coprosma* species. The effects of a 1:300-year whole-stand disturbance regime on forest biomass are modelled in (B). “Others” include *G. littoralis*, *L. intermedium*, *D. traversii*, *Hoheria glabrata*, *Kunzea ericoides*, *Leptospermum scoparium*, *M. divaricata*, *A. serrata*, and *Coprosma* species.

podocarp species *Halocarpus biformis* and *Phyllocladus alpinus* and a reduced presence of the broadleaved species *Weinmannia racemosa* and *Griselinia littoralis*. At higher elevation there was a c. 20% long-term, lower forest biomass of c. 210 Mg/ha. When a disturbance regime was invoked (Fig. 4B) the most obvious change to the forest composition was the increased presence of the hardy pioneering beech *Nothofagus cliffortioides* at the expense of the podocarp species. An interesting consequence of applying a whole-stand disturbance regime at the higher-elevation site was the relative robustness of the forest biomass, which declined only 10% to c. 190 Mg/ha. The species composition in these simulations conformed to descriptions of the forests from around Lake Wakatipu by Wardle (1984).

Impacts of exotic species

Christchurch

The model predicted the exotic *Pseudotsuga menziesii*, *Acer pseudoplatanus*, *Pinus radiata*, and *Pinus contorta* could establish in the dry lowland Christchurch

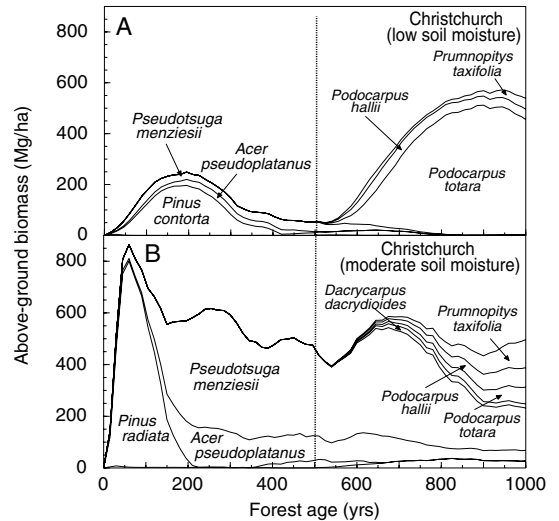


Figure 5. Modelled above-ground biomass at Christchurch under low soil moisture conditions (A), and moderate soil moisture conditions (B), beginning with exotic *Pseudotsuga menziesii*, *Acer pseudoplatanus*, *Pinus radiata*, and *Pinus contorta*. Indigenous species were introduced at year 500.

environment. In lower soil moisture conditions, the most common plantation species in New Zealand, *Pinus radiata*, could not compete against the other exotic species, particularly the hardy *P. contorta* (Fig. 5A). The pattern of succession revealed *P. contorta* would act as a colonising species, attain a biomass of c. 195 Mg/ha by year 200, and then decline until it formed a very small part of the forest. By year 500 the exotic forest could only maintain a very low total biomass of c. 50 Mg/ha due to the dry conditions, which then suited the indigenous species entering the succession, particularly the dominant *Podocarpus totara*.

Conversely, under moderate soil moisture conditions the exotic forest grew to reach a much higher biomass, c. 825 Mg/ha, due to the large fast-growing *Pinus radiata*, which quickly displaced *P. contorta* (Fig. 5B). The exotic forest biomass then steadily declined as *P. radiata* struggled to regenerate beneath the canopy, which by year 500 was dominated by *Pseudotsuga menziesii*. Even when introduced to this fully mature exotic forest the indigenous species were eventually able to establish and grow, and the

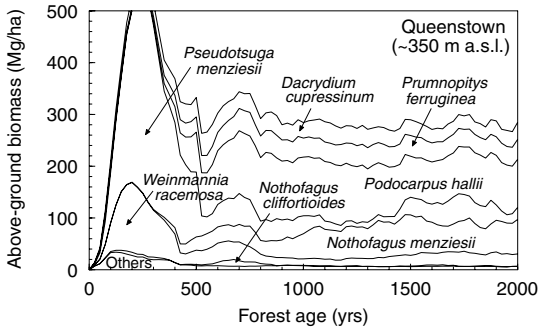


Figure 6. Modelled above-ground forest biomass at the lower-elevation Queenstown site with the exotic species *Pseudotsuga menziesii* included. “Others” include *Lepidothamnus intermedius*, *Griselinia littoralis*, *Libocedrus bidwillii*, *Halocarpus biformis*, *Myrsine divaricata*, *Aristotelia serrata*, and *Coprosma* species.

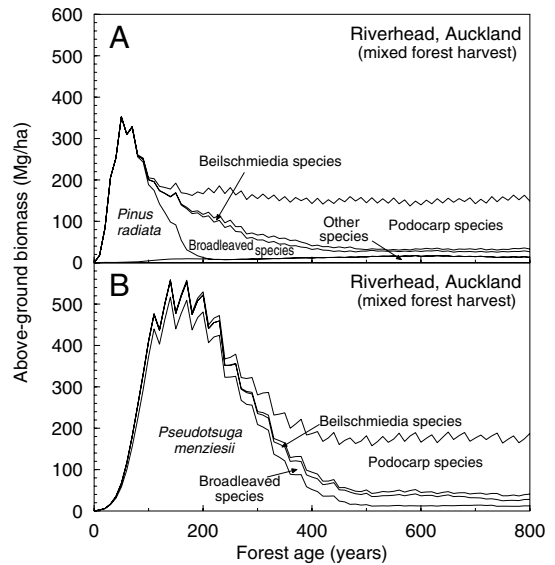


Figure 8. Modelled above-ground biomass at Auckland. (A) Beginning with a *Pinus radiata* plantation followed by a 20% thinning and indigenous species introduced at year 15, harvesting 20% of stems ≥ 30 cm every 20 years, but leaving a minimum of 12 stems/ha. (B) Beginning with a *Pseudotsuga menziesii* plantation followed by a 20% thinning and indigenous species introduced at year 20, harvesting 20% of stems ≥ 30 cm every 30 years, but leaving a minimum of 12 stems/ha.

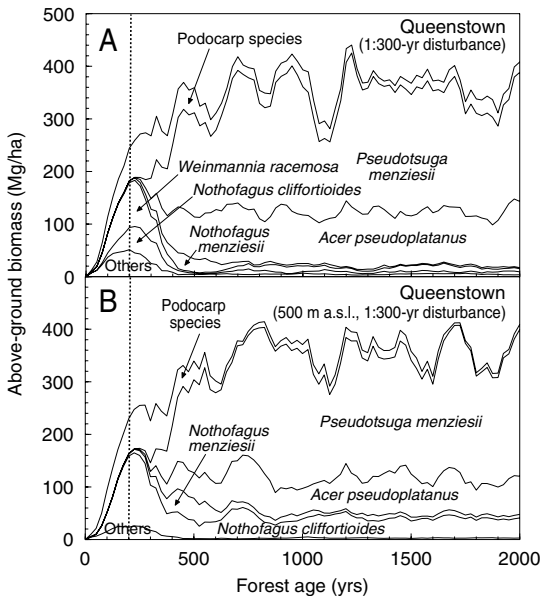


Figure 7. Modelled above-ground biomass at Queenstown with a mean 1:300-year disturbance regime and the introduction of *Pseudotsuga menziesii* and *Acer pseudoplatanus* at year 200. The forest dynamics are modelled for the lower-elevation site (A) and an upper elevation site (B).

model predicted *Podocarpus totara*, *P. hallii*, *Prumnopitys taxifolia*, and *Dacrydium cupressinum* would slowly increase in biomass and tend to displace these exotic species.

Queenstown

When *Pseudotsuga menziesii* was added to the list of species available to the model, the forest simulation for the lower-elevation site at Queenstown predicted it would quickly grow and dominate the forest biomass for >300 years. Without major disturbance, the simulation further showed *P. menziesii* would be gradually displaced by indigenous podocarp and beech species (Fig. 6) but would retain a small presence throughout the rest of the simulated period in contrast to the pure indigenous forest (Fig. 3A).

The introduction of the two exotic species *Pseudotsuga menziesii* and *Acer pseudoplatanus* at year 200 into a simulated forest at Queenstown, subjected to a mean disturbance rate of 1 in 300 years, led to a dramatic reduction in indigenous species biomass (Fig. 7A). In comparison with the equivalent indigenous forest simulation (Fig. 3B), total forest biomass increased by 80% to *c.* 375 Mg/ha. Under this

scenario the exotic species accounted for two-thirds of forest biomass 200 years after being introduced and c. 90% of total forest biomass 300 years later.

At the higher-elevation Queenstown site (Fig. 7B) the shade-tolerant exotic species remained competitively superior to the indigenous species and accounted for two-thirds of forest biomass 200 years after being introduced and c. 80% of total forest biomass 300 years later. Compared with the equivalent indigenous forest simulation (Fig. 4B), total forest biomass was nearly double with a mean of c. 380 Mg/ha. The impact on the native beech species, particularly *Nothofagus menziesii*, was severe.

Production from mixed exotic-indigenous forests

Auckland

Application of the chosen harvesting regime halved the long-term biomass in a *Pinus radiata* initiated forest to c.160 Mg/ha (Fig. 8A) compared to the biomass predicted for the pure indigenous forest (Fig. 1). The exotic pine persisted about the same length of time as the woody colonising species *Kunzea ericoides*

in the pure indigenous forest, being replaced after 200 years, and performed a similar role to *Kunzea* except that the dominant species of the natural forests, *Agathis australis*, was suppressed. Harvesting accelerated the successional sequence so the eventual long-term domination by the shade-tolerant, later-successional podocarp species occurred after 200 years, compared to the 600-year period required in the pure indigenous forest.

In comparison, the longer-lived exotic *Pseudotsuga menziesii* managed to reach c. 500 Mg/ha after 200 years under harvesting (Fig. 8B) and unlike *Pinus radiata* maintained a small presence throughout the simulation period. The long-term biomass was 12% higher at c. 180 Mg/ha in this mixed forest due to the continued presence of *Pseudotsuga menziesii*. Again, *Agathis australis* was unable to establish. This continuous canopy harvesting accelerated the successional sequence so the eventual long-term domination by the late-successional podocarp species occurred after 400 years, compared to the 600-year period in the pure indigenous forest.

Christchurch

Application of the chosen harvesting regime halved the long-term biomass in a *Pinus radiata* initiated forest to c. 180 Mg/ha (Fig. 9A) compared to the mean biomass in the pure indigenous forest (Fig. 2B).

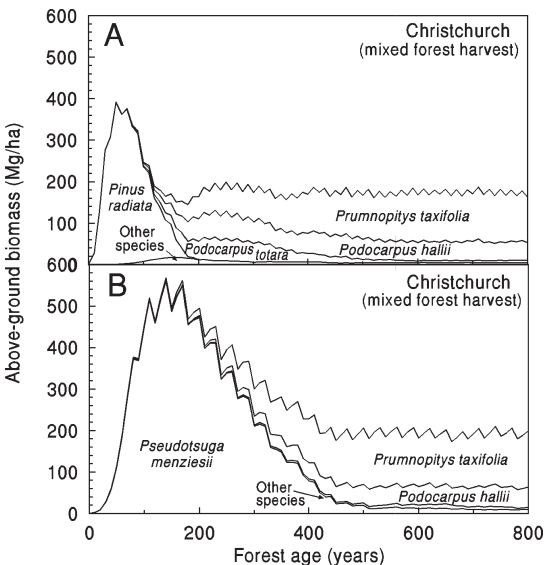


Figure 9. Modelled above-ground biomass at Christchurch under moderate soil moisture conditions. (A) Beginning with a *Pinus radiata* plantation followed by 20% thinning and indigenous species introduced at year 15, harvesting 20% of stems ≥ 30 cm every 20 years, but leaving a minimum of 12 stems/ha. (B) Beginning with a *Pseudotsuga menziesii* plantation followed by 20% thinning and indigenous species introduced at year 20, harvesting 20% of stems ≥ 30 cm every 30 years, but leaving a minimum of 12 stems/ha.

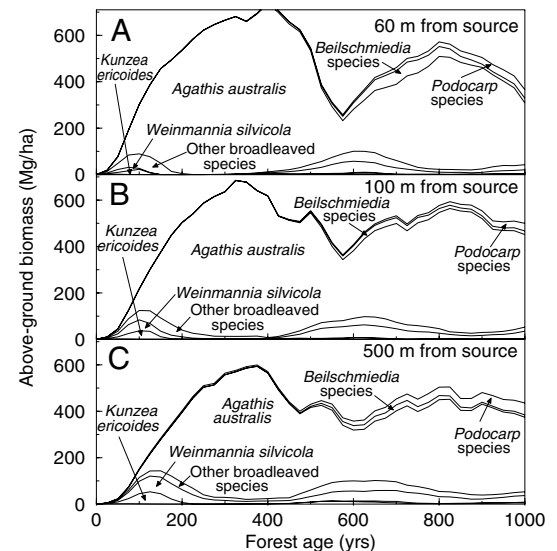


Figure 10. Modelled above-ground biomass at a sequence of receptive sites at Riverhead, Auckland, (A) 60 m, (B) 100 m, and (C) 500 m from the nearest propagule source. The propagule source is assumed to deliver a constant supply of all indigenous species.

The exotic pine was replaced after 200 years, and was present for about the same period as the indigenous colonising species *Kunzea ericoides* and *Leptospermum scoparium* in the pure indigenous forest. Under the continuous-canopy-management regime the eventual long-term domination by the shade-tolerant later-successional podocarp species occurred after 200 years, similar to that of pure indigenous forest.

In comparison, the longer-lived exotic *Pseudotsuga menziesii* managed to reach c. 500 Mg/ha after 200 years under the harvesting regime (Fig. 9B) and maintained a small presence throughout the simulation period. Long-term biomass was 11% higher at c. 180 Mg/ha in this mixed forest due to the continued presence of *P. menziesii*. If anything the successional sequence was delayed in this mixed forest compared to the pure indigenous forest so the eventual long-term domination by the late-successional podocarp species occurred after 400 years, compared to the 150-year period in the pure indigenous forest. In both mixed forest simulations *Dacrycarpus dacrydioides* failed to establish.

Corroboration of the early stages of these successions has been observed in Douglas fir, eucalyptus and other deciduous forests in Canterbury (Norton, 1989; MacMillan, 1973; Pratt, 1999; CDM, pers. obs.). However, most examples are limited by the usual grazing regimes associated with these forests (of both exotic feral and domestic browsing animals), and a general lack of seed sources in close proximity.

Dispersal distance effects

At Auckland the model predicted that separation from the nearest propagule source would influence the pattern of development on receptive sites (Fig. 10A, B, C). The most obvious difference in the forest succession that was related to increased dispersal distance occurred in the growth pattern of the long-lived conifer *Agathis australis*.

Within a forest setting *A. australis* was predicted to establish early, dominate the total biomass for >400 years, and then decline as the more shade-tolerant *Beilschmiedia* and podocarp species (*Dacrydium cupressinum*, *Prumnopitys ferruginea*, *P. taxifolia*) increased in biomass (Fig. 1). This within-forest pattern corresponded to field studies of short-term succession in these forests.

When dispersal of the forest species to a sequence of receptive sites was modelled the initial pattern of succession resembled the within-forest pattern for c. 500 years. However, instead of beginning a slow long-term decline as before, *Agathis australis* was predicted to recover and commence a second growth cycle. The effect was more pronounced at 60–100 m from the propagule source than at 500 m (Fig. 10 A and B, versus C), and beyond 500 m the successional dynamics

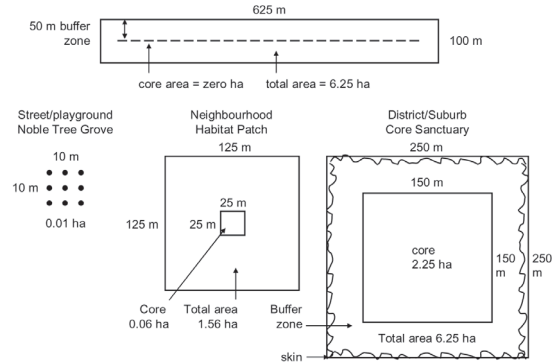


Figure 11. Reserve patch designs, with 50-m buffer zones (see text), in which linear and optimally compact shapes minimise and maximise core biological areas respectively. Linear patches have no core. In a matrix of urban woodland and hedgerows, most of the buffering occurs outside the reserve. Three patch sizes are shown that can accommodate (left to right) increasing populations and sensitivities of plants and wildlife.

showed little change due to the shape of the dispersal tail. This effect suggested that once receptive sites become available, dispersal processes could assist with the long-term maintenance of *Agathis australis* forests in the north of New Zealand.

Greenspace planning

The forest simulation model highlighted some of the challenges facing New Zealand's biodiversity at a landscape scale. To attempt to address these, some results from the exotic species and dispersal process simulations can be linked with greenspace planning, by combining island biogeographic theory (MacArthur and Wilson, 1967) and principles derived from landscape ecology. The major risk, as noted by several studies (e.g. Fahrig, 2003; Goodwin, 2003; Rutledge, 2003), is oversimplification of the relationships between spatial, environmental, life-history and autecological traits. Thus, the overall concept proposed should be treated cautiously, even though Henle *et al.* (2004) have demonstrated broad commonalities in the response of species and populations to fragmentation regardless of whether the organism is plant or animal, and Drinnan (2005) has quantified threshold differences for a range of organisms in Sydney, Australia.

Reserve design theory has indicated that bigger, compact areas are preferable for preserving biodiversity (Fig. 11). In New Zealand this is illustrated by the behaviour of the larger iconic bush birds such as kokako (*Callaeus cinerea*) and kiwi (*Apteryx* spp.), which favour bush remnants in excess of 500 ha and 10 000 ha, respectively, although it is likely that pest-free

status and freedom to travel between habitat patches are more important than a continuous large area *per se* (J. Innes, Landcare Research, Hamilton, *pers. comm.*). In urban and rural environments, reserve area is constrained by land use and commercial factors, requiring utilisation of smaller habitat patches (1–6 ha). This is not necessarily a crucial limitation because most extant New Zealand wildlife (insectivorous birds, lizards, invertebrates) are either small or vagile, and small habitat patches can perform useful ecological functions provided habitat quality (determined mainly by predator control) is not diminished (Henle *et al.*, 2004). For instance, the frugivorous/folivorous wood pigeon (*Hemiphaga novaeseelandiae*) successfully nests in about 30 ha of largely dry-seeded, exotic parkland in the Botanic Gardens, Christchurch, but visits a 5.5-ha indigenous forest patch (< 2 km distant) to feed. Omnivorous bellbirds (*Anthornis melanura*) nest in small outliers close to large remnants, but need very large patches for breeding beyond about 0.25 km from source habitat (H. North, E. Spurr, C. Newell, Landcare Research, Lincoln, *pers. comm.*). In addition, insectivorous fantails (*Rhipidura fuliginosa*) and grey warblers (*Gerygone igata*) are ubiquitous in highly fragmented rural landscapes, and geckoes (*Hoplodactylus*) have survived over several years in a residential rock pile (J. Parkes, Landcare Research, Lincoln, *pers. comm.*).

Young and Mitchell (1994) and Davies-Colley *et al.* (2000) calculated that a climatic edge effect penetrates about 50 m into forest remnants around Auckland. Hence a compact reserve of around 6.25 ha (a 250 x 250 m square) would have a core area > 2 ha

surrounded by a buffer zone of about 4 ha (Fig. 11). Based on the observations above, a 2-ha core area would be close to the minimum necessary to sustain populations of more sensitive plants and animals, assuming the necessary specific species life history and habitat requirements are available. Another key reason for adopting a patch size of around 6 ha in urban or rural settings is due to a local government target of <10% in value or area for reserve contributions. In practice, few multi-hectare sanctuaries have been designated because most reserves are allocated to recreation.

A patch-pattern can therefore be constructed for modified landscapes where available land is limited by including a range of minimum forest patch sizes; *c.* 6.25 ha for core sanctuaries in urban/countryside contexts; *c.* 1.6 ha to provide habitat for most plants, lizards, insectivorous birds and invertebrates and resource-rich 'stepping stones' for larger frugivorous or honey-eating birds; *c.* 0.01 ha to provide groves of New Zealand trees, finer-grained stepping stones, and feeding stations (Fig. 12). These patches would be spaced about 5, 1–2, and 0.2 km apart from similar sized patches, respectively, to achieve spatial connectivity. Such a configuration of forest patches in a landscape (together with riparian and road edge linkages) should allow adequate propagule coverage across the landscape (based on modelled dispersal curves), and assist to support metapopulations of birds and flighted insects, improve the continuity of bird habitat, and the gene flow between plant and animal populations (e.g. Drinnan, 2005; Lindermyer and Luck, 2005; Radford *et al.*, 2005). Other urban or rural habitats (for example the matrix of gardens and borders) would provide additional resources. It is proposed that this kind of patch-corridor-matrix complex would provide the major ecological requirements for most extant biodiversity, and satisfy conditions for social visibility and accessibility (Meurk and Swaffield, 2000; Box and Harrison, 1993; Harrison *et al.*, 1995) reminiscent of the ecological park as pioneered in the densely populated Netherlands.

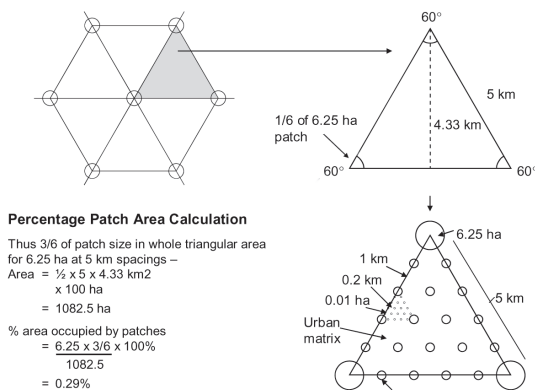


Figure 12. An idealised, nested forest patch configuration of three patch sizes; and method of calculation of percentage area occupied by patches, applied to the largest patch size of 6.25 ha.

Discussion

The forest successions generated for selected sites demonstrated several well-known risks to biodiversity from exotic species in modified landscapes and evaluated options to maintain and enhance the indigenous component. If the profile of indigenous species in the urban/rural landscape could be raised then the range and quantity of food sources for indigenous wildlife would increase and this in turn should improve the rate of dispersal of indigenous tree species across depleted landscapes. Furthermore,

Meurk and Swaffield (2000) have suggested that once the visibility of indigenous species increases this is likely to reinforce their sustainability through social feedback. In addition, the study indicated that there may be feasible options for manipulating forest patches, to manage biosecurity risks, and to integrate production with nature conservation across New Zealand's fragmented cultural landscapes. The practicality of such forecasts has led one territorial authority, the South Island Timaru District Council, to experiment with some of the options presented.

The flexible design of the forest model allowed the effects from geoclimate, soil conditions, species composition, exotic plant impacts, natural disturbance, harvesting, and patch spacing to be simulated. The successional sequences predicted by the model for mixed conifer forest at Auckland, for podocarp forest at Christchurch, and mixed beech–podocarp forest at Queenstown match field observations. The model predicted that persistence and presence of podocarp species in forest around Christchurch was related to available soil moisture. The simulations for sites at Queenstown predicted an upper threshold of tall podocarp species, showed beech would become prominent 150 m above the lake shore, and found that whole-stand disturbance could advantage the early successional native beech *Nothofagus cliffortioides*, the introduced conifer *Pseudotsuga menziesii* and broadleaved *Acer pseudoplatanus*. At the less disturbed, lower-elevation Queenstown site the two exotic species did not achieve the same dominance as the podocarps whereas at the higher-elevation site these species were predicted to displace indigenous tree species irrespective of whole-stand disturbance (Wardle, 1985).

A variety of ecological studies (e.g. Drinnan, 2005; Lindenmeyer and Luck, 2005; Radford *et al.*, 2005) and sociological studies (Harrison *et al.*, 1995) suggest <10% habitat cover in a landscape may trigger a decline in many species and limit human accessibility to nature. Although the estimates in this study support this ecological threshold from a dispersal and reserve design perspective for many indigenous organisms and provide a framework for meeting experiential criteria, there is as yet no consensus on such a threshold. Rutledge (2003) reviewed the landscape ecological literature and found that this threshold may be up to 40% of total land area, depending on the species in question and its life history and habitat requirements. Obviously, larger organisms, naturally rare and specialised species, and those highly sensitive to disturbance tend to have larger habitat requirements. In New Zealand, most large indigenous species are extinct, at least regionally, whereas the remaining indicator birds of bush and wetland (New Zealand's largest terrestrial vertebrates) are increasing in cities in conjunction with maturing urban forest and creation of

new ponds (Crossland, 1997).

Renard and Meurk (2006) applied the greenspace schema described in a planning exercise for the city of Christchurch. The total area required was well within current planning edicts (0.29% for large patches, 1.8% for medium, and 0.29% for groves = 2.38%, Fig. 12), but all of that area would have to be vegetated as forest or woodland groves. To achieve a target of about 10% aerial extent of greenspace indigenous habitat, the c. 2.5% cover contained in the proposed patchwork configuration would need to be complemented by naturalised riparian corridors, larger peripheral reserves, and a slightly increased proportion of native species in the private garden matrix. Since most New Zealand urban gardens already support 15–25% indigenous trees/shrubs (Stewart *et al.*, 2004), and sales of native plants are increasing, such a target seems feasible.

Box and Harrison (1993) and Harrison *et al.* (1995) have proposed standards for nature experience in English cities. Under these standards urban residents should have access to a "natural greenspace" of at least 2 ha within 0.5 km of their home (cf. 1.56 ha within 0.5 km for this study) with much larger areas (20–500 ha) within 2–10 km. In three New Zealand cities these macro-reserve requirement would be met in the border areas of Banks Peninsula for Christchurch, the Waitakere Ranges for Auckland, and the Karori Sanctuary for Wellington. Such large core bush reserves may be needed to maintain viable breeding populations of more sensitive birds that can then feed in the adjacent urban patchwork and matrix. Regardless of whether larger frugivorous bush birds are dependent on large sanctuaries, observations of their distribution within the current greenspace configurations of New Zealand suggest that where there are adequate resource-rich stepping stones or patches, even if only one tree in extent, then wildlife will use them. Ensuring these are spaced uniformly (together with predator control) will likely ensure that the dependent wildlife will also at least forage uniformly across cities and farmland, and ensure human experience of them.

At present c. 8% of New Zealand is covered by plantation forest, virtually all of which is composed of the exotic species *Pinus radiata* and *Pseudotsuga menziesii*. In addition, other pines, such as maritime pine (*Pinus pinaster*), have established wilding populations in the high country. Because exotic trees can grow at higher elevations than indigenous species (Wardle, 1985) and thrive in a range of environments, it is essential to contain wildings (Richardson *et al.*, 1994) and ensure adequate funding of high country weed control. Although further investigation is needed, the simulations of *Pseudotsuga menziesii* at the higher-elevation Queenstown site suggested that it has the potential to establish in parts of the montane beech forest biome (Fig. 7A, B cf. Fig. 4A). Such a spread

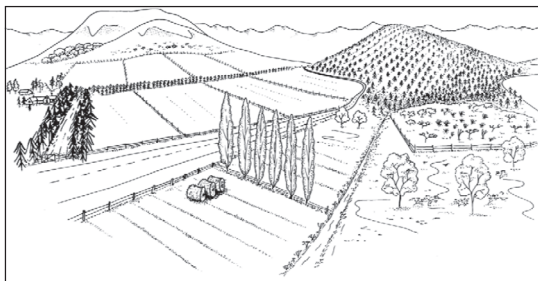


Figure 13. A contemporary utilitarian high-country landscape, based on current trends, with low visibility of indigenous nature to both resident and traveller.

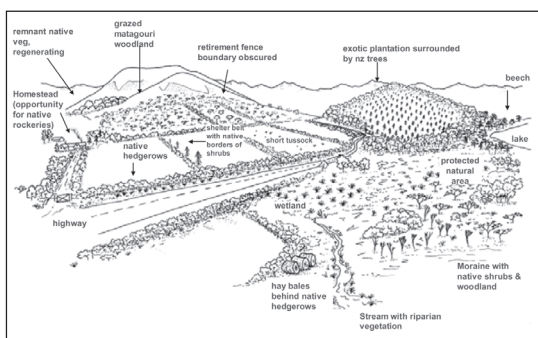


Figure 14. A possible biodiverse high-country landscape with protected primary habitat at biologically communicable spacings linked by a matrix that incorporates indigenous-dominant shelter, field edges, forest buffering and productive systems.

could visibly alter forest composition over substantial areas of the high country and may lead to a reduction in native biodiversity and natural character across these landscapes (Fig. 13). In contrast, the possible alternative of a biodiverse mature cultural high country landscape (Fig. 14) is a goal that may take centuries to accomplish if the evolution of integrated nature and production in the English countryside (Rackham, 1986) is a reasonable model for New Zealand.

This study proposed that production forestry systems be established, based on a mixture of indigenous and exotic species, as a means to increase the visible indigenous component in the rural landscape. Because of risks from wildings, the exotic component of such forests might desirably utilise sterile hybrids [e.g. Leyland cypress, *X Cupressocyparis leylandii* (Floate, 1994)]. In addition, yields of such mixed forests should be estimated so that expected returns can be compared against those from monocultural exotic conifer plantations. Further trialling of manipulated successions and placement of buffer strips

around exotic plantations would help to achieve desired forest composition. Native regeneration could be facilitated in a range of semi-production and border habitats (hedgerows, woodlots, road verges, riparian zones, homestead woods) and by avoiding the propagation of potential weeds in these locations. Because visibility of native species may influence their sustainability (Nassauer 1995; Meurk and Swaffield, 2000), placement should also be addressed.

Conclusions

Enormous changes to the natural environment have taken place in New Zealand in a relatively short time. Residents and visitors are often unaware how vulnerable the distinguishing features of New Zealand could be, at least in the long term, to the impact of introduced exotic species. The lowlands of New Zealand and some other large island nations are now dominated by species from other parts of the world (as are seed banks – Partridge, 1989), a situation that represents a significant reduction in biodiversity, natural character, and ecological integrity. Accordingly there is a conservation imperative to raise the ecological and cultural profile of indigenous vegetation – with consequent benefits for indigenous wildlife.

This study endeavoured to extend understanding beyond site-based ecological restoration developed in New Zealand (Davis and Meurk, 2001) to landscape and planning dimensions. The issues explored and suggestions were derived from historical data, field observations, model predictions, and reserve design theory. The scenarios modelled were concerned with goals involving traditional landscape elements that therefore might be considered familiar and pragmatic (Nassauer, 1995; Swaffield and Hughey, 2001). The long time frames adopted for the simulations and the broad landscape scales considered are important for medium- to large-scale planning and also accommodated potential opportunities within expected mixes of indigenous and exotic elements of the flora.

Based on this and past studies, the forest ecosystem model appeared robust enough to make sensible predictions about the dynamics of native forests and exotic tree species at a range of temporal (decades to centuries) and spatial (local to regional) scales. It reaffirmed that restoration of native forest cover would be unlikely to occur spontaneously in some depleted New Zealand landscapes due to potential biosecurity risks from fast-growing introduced species. The proposed greenspace planning option estimated that habitat requirements to improve biodiversity and visibility in modified landscapes would be relatively modest and not incompatible with land use and economic constraints in urban and rural landscapes.

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