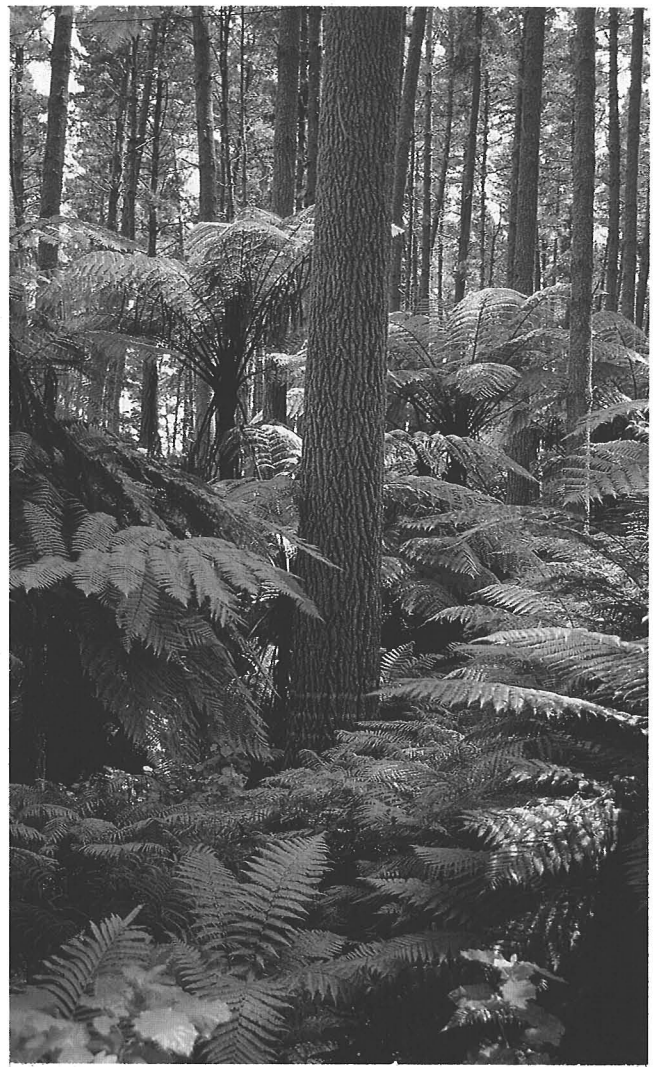


supporting biodiversity in plantation forest management as do other countries such as Britain. There, private landowners have grants available to them that allow up to 20% of their land to be left unplanted and managed as open ground for biodiversity values (Hodge *et al.* unpublished report).

Despite the fact that New Zealand plantation forests are not managed specifically for biodiversity they can support a significant number of species in their understoreys. The importance of this biodiversity to crop production is not clear; however, it likely does contribute to an intangible level of environmental quality not present in densely-stocked plantation forests found in the other countries. Perhaps more importantly as far as the conservation of New Zealand's indigenous biodiversity is concerned, most plantation managers are committed, through the Forest Accord and the Principles, to the conservation of indigenous biodiversity in natural reserve areas and to the conservation of threatened species known to occur in their plantations.

References

- Allen, R.B., K.H. Platt, and R.E.J. Coker. 1995a. Understorey species composition patterns in a *Pinus radiata* D. Don plantation on the central North Island Volcanic Plateau, New Zealand. *New Zealand Journal of Forestry Science* 25:301-17.
- Allen, R., K. Platt, and S. Wiser. 1995b. Biodiversity in New Zealand plantations. *New Zealand Forestry* 39(4):26-29.
- Hodge, S.J., G. Patterson, and R. McIntosh. The approach of the British Forestry Commission to the conservation of forest biodiversity. Unpublished report.
- Maclaren, J.P. 1996. "Environmental Effects of Planted Forests – the implications of continued afforestation of pasture". FRI Bulletin no. 198. New Zealand Forest Research Institute, Rotorua. 180 p.
- NZFOA, 1997. NZ Forestry Facts and Figures 1997. New Zealand Forest Owners' Association Inc., Wellington, New Zealand 22p.
- Ogden, J., J. Braggins, K. Stretton, and S. Anderson. 1997. Plant species richness under *Pinus radiata* stands on the central North Island volcanic plateau, New Zealand. *New Zealand Journal of Ecology* 21(1): 17-29.
- Rowe, D.K. 1996. Interim report on studies related to the effects of land-use changes on native fish. NIWA unpubl. report, 10p.
- UNEP, 1994. Convention on Biological Diversity. UNEP/CBD, Switzerland, November 1994. 34 p.



Understorey biodiversity.

Biogeography and Forest Biodiversity in New Zealand

John Ogden*

Abstract

*The concept of biodiversity is scale dependent. Biogeography is concerned mainly with explaining the larger scale patterns – the origins of the New Zealand flora and the regional patterns of biodiversity within the country (gamma-diversity). Geological and climatic history are important at these scales. Altitudinal gradients illustrate variation at the landscape level (beta-diversity). The conservation of landscape processes is important for maintaining high biodiversity and ecosystem 'services'. Ecologists cannot yet explain differences in diversity at the community scale (alpha-diversity), but arguably the disturbance regime is a key factor. A case study, comparing kauri (*Agathis australis*) and beech (*Nothofagus solandri*) forests, is outlined. If the indigenous conservation strategy, and operational exotic forestry, are to emphasise the sustainability of indigenous biodiversity, then the spatial and temporal scale effects which determine it must be explicitly addressed.*

* Centre for Conservation Biology and School of Environmental and Marine Sciences, University of Auckland.

Introduction

The development of a New Zealand Biodiversity Strategy by the NZIF indicates our concern about the potential loss of some of our indigenous biodiversity, and an acceptance of our international obligations under the 1992 Biodiversity Convention. We should be particularly concerned about the loss of the flora, for its own sake and because plant communities largely constitute the 'habitats' in which other components of biodiversity live. In a very short span of evolutionary time the flora has been subject to enormous changes wrought by forest clearance, increased fire frequency, wetland drainage, urban and rural subdivision, introduced mammals, birds and insects, and an enormous influx of exotic plants. There is no clear end in sight for most of these effects, or for the new class of problems arising from global climate change. The latter is just one of several threats to biodiversity originating outside New Zealand, driven by a global economy on which we seem to have little influence.

Forests, both native and exotic, play a very significant role in maintaining indigenous biodiversity. Lowland forest ecosystems, now much depleted in extent, contain many of our more

unusual plants and animals. Such systems have survived in varying extent and composition throughout the climatic oscillations of the Pleistocene. More recently, forest covered the majority of the landscape. The significance of this is that tree diversity generally reflects total biotic diversity (e.g. Richerson and Lum 1980).

Hal Mooney, Secretary General of the International Council of Scientific Unions (ICSU), has recently emphasised that ecologists do not yet know how many species must be saved to keep an ecosystem functioning – providing the ‘services’ we take for granted. Such services include clean water from mountain catchments, regenerating fisheries and soul-sustaining landscapes (Mooney 1997; quoted by Basu 1997). Large-scale changes in such services can have global effects and unpredictable interactions. We do know that some species are more important than others (‘keystone’ and ‘umbrella’ species) and that different trophic levels are interdependent. Theoretically we can argue that high biodiversity ensures ecosystem stability, but the argument is bedevilled by definitions, semantics and scale effects. The challenge for ecology is to develop a new approach linking biodiversity and ecosystem functioning.

This paper starts by presenting the traditional concepts used in the discussion of plant biodiversity. Traditional views about the origins of our flora are currently being questioned. This debate is important because understanding the origins and wider relations of our plant communities underpins the scientific justification for their conservation. The well-known geographical patterns of biodiversity within New Zealand are outlined, and some comments made on the implications of this for our reserve network. Reserve priorities should be based not simply on species inventories, but on the quantitative understanding of change along major environmental gradients, and an appreciation of the dynamic nature of plant communities as mosaics on the landscape. To preserve biodiversity we must preserve the landscape processes which have selected for or against particular combinations of demographic characteristics in different species, thus determining their ability to grow together in natural communities.

Scales of plant species diversity - a conceptual framework

Scale is central to the perception of diversity. While the general trend of decreasing diversity from the equator to the poles is clear at one scale, at finer scales of resolution more detailed patterns may be superimposed. Whittaker (1972) presented a framework for the discussion of species diversity which, with minor modifications (e.g. Soule 1986), has been widely adopted.

Alpha-diversity relates to the number of species coexisting within a uniform habitat. It is an inventory of the species present *within a community*, often referred to as ‘species richness’. In common with other authors (e.g. Huston 1979; Peet 1974; Wilson and Keddy 1988; Wilson and Sykes 1988), I recognise that equitability (the relative proportions of species) is a component of diversity, but species richness is a simpler statistic. *Beta-diversity* describes the *between community* level of diversity. It provides an index of the diversity across a landscape within one biogeographical region. For example, as the community composition changes along an altitudinal gradient new species are encountered and others drop out, and this species turnover rate is termed beta-diversity. Two stands with the same number of species present (same alpha-diversity) can differ in composition, and thus together they exhibit beta-diversity. Beta-diversity can be measured by a similarity coefficient (e.g. Sorensen’s coefficient) or using ‘between stand distance’ in ordination space (Druitt *et al.* 1990). *Gamma-diversity* can be regarded as the total species inventory for a large geographical region, e.g. regions of New Zealand or the country as a whole. Thus gamma-diversity is the broad-brush approach, dealing with the flora of large areas, and it can be further partitioned into gradients within regions

(beta-diversity) and the composition of communities (alpha-diversity).

The origins of floristic biodiversity in New Zealand

The size of the New Zealand flora (about 2300 vascular plants), percentage of endemism (85%; Wardle 1991), amount of dioecism and the prominence of small inconspicuous flowers (Dawson 1988) all reach intermediate levels between truly isolated oceanic islands (e.g. Hawaii) and much less isolated continental islands (e.g. Britain). The traditional biogeographic explanation for this, and for some striking similarities between the floras of all the southern land-masses, is that the flora comprises an ancient ‘Gondwanan’ element, and more recent elements derived by west-wind drift from Australia (Raven 1973) or by putative ‘island hopping’ from the more tropical islands to the north. This view, expressed first as an explanation for the observed faunal and floristic similarities between South America, Tasmania and New Zealand, appeared to be vindicated when the geological evidence of plate tectonics clearly indicated that these areas were formerly connected.

However, the idea of an ancient Gondwanan flora, rafted with the original continental fragments but remaining largely intact, has recently been questioned. Pole (1994) points out that some supposedly Gondwanan species are also present on true oceanic islands, which were not part of Gondwanaland, and to which the species in question must have migrated over long sea crossings. MacPhail (1997) further points out that, if the earliest fossil records of New Zealand plants are examined, the majority appear to have been present in Australia before they occurred in New Zealand, a feature which would be consistent with long-distance transport across the Tasman Sea. The dispersalist’s argument is that, if some supposedly Gondwanan elements can indeed cross huge oceanic distances, then given sufficient time, maybe all of them could have reached New Zealand by this means! So, once again the origins of the New Zealand flora are under debate. The new techniques of molecular biology may be the means whereby the debate will be settled.

Whatever the origin of our biota, it is clear that there are high levels of endemism at the specific level in most groups, for example, 90 - 100% for Angiosperm trees and Conifers. The supposed Gondwanan element of our flora contains several small genera in primitive families, suggesting that these species are ‘palaeo-endemics’ which have survived the extinction of most other members of the group in remote isolation. In contrast, suites of endemic species in some genera can be explained as ‘neo-endemics’ resulting from speciation in new environments following immigration. Some of the larger genera of alpine plants, e.g. *Celmisia* (59 species), *Ranunculus* (45), and *Epilobium* (57), appear to have reached New Zealand and undergone adaptive radiation in the new mountainous habitats of the Pleistocene (Raven 1973). Such species, genetically close to each other and to related members of the genus elsewhere in the world, are generally thought of as having less ‘value’ than those taxonomically and geographically isolated organisms regarded as palaeo-endemics. Of course, there is always a problem with these arguments, illustrated by the tendency of taxonomists to split large genera into smaller ones. The attitudes of taxonomists (to the grouping of patterns of variation into species or genera) are central to any assessment of biodiversity.

The broad brush – patterns of biodiversity on the New Zealand landscape

Many species have localised distributions within New Zealand and are thus regional endemics. More widespread species often show marked disjunctions in their distributions. Although there is a general tendency for decreasing total diversity with increasing latitude, a much stronger pattern in which areas of high and

low endemism alternate down the country is superimposed (Fig. 1). These patterns have been discussed by Wardle (1963), Burrows (1965), McGlone (1985) and Atkinson (1994), with the two later authors drawing on additional field exploration and (unpublished) taxonomic work by A.P. Druce. Centres of endemism are generally associated with topographically varied but geologically stable landform units (McGlone 1985).

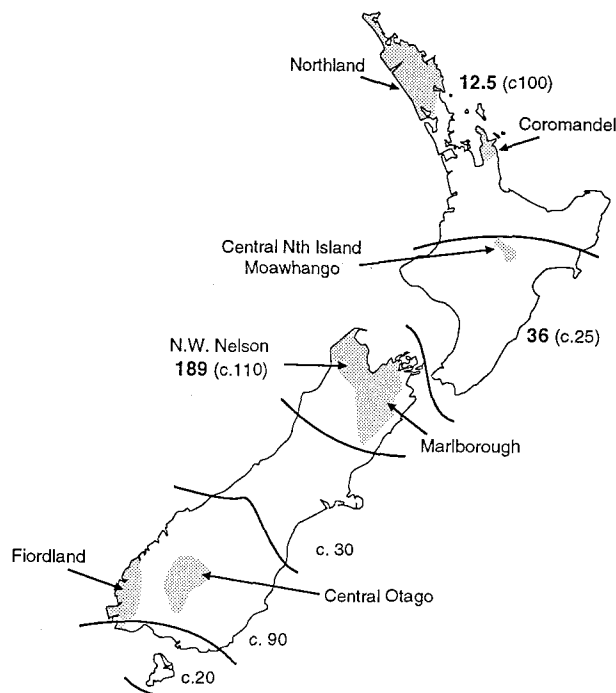


Fig. 1. Numbers of endemic plant species in different parts of New Zealand. Bold numbers from McGlone 1985 (based on Druce pers. comm.), others from Wardle 1963. Centres of highest diversity are shaded.

Regions of high endemism are also regions in which the total floristic list (gamma diversity) is greatest. This is partly due to the inclusion of the endemics, and partly because some more widespread species are not present in the intervening areas of low endemism. The two major disjunctions occur in the southern North Island and the central South Island. For example, nine northern tree species (e.g. *Phyllocladus trichomanoides*; *Libocedrus plumosa*) reappear in north-west Nelson and Marlborough (McGlone 1985), while several alpine species are absent from the waist of the South Island (Burrows 1965). Likewise, the genus *Nothofagus* is disjunct west of the Alps, though the environment there appears suitable and all species are found to both the north and the south. McGlone (1985) draws attention also to a third disjunction, between the high-altitude areas of the central North Island, and the South Island mountains (see also Rogers 1989).

The region of high endemism and diversity north of latitude 38°S coincides approximately with the distribution of kauri (*Agathis australis*) and several tree genera of supposedly tropical affinities (e.g. *Avicennia*, *Ackama*, *Vitex*). According to McGlone (1985) the region contains 125 endemic species, of which 18% are trees and 55% are woody. Together these species comprise nearly 6% of the total native flora of New Zealand. The Northland conservancy has 37 species classed as rare or endangered, compared to an overall average figure of 12 for all conservancies. Although the Nelson-Marlborough region contains even more endemics (189, or about 9% of the flora), they are predominantly herbaceous. This conservancy has 22 rare and endangered species (Molloy and Davies 1992). Both regions are geologically and topographically varied, both escaped inundation

by the marine transgressions of the Pliocene which covered the intervening southern North Island, and both may have served as refugia for the forest flora during the Otira (last) Glacial period. The latter argument cannot be convincingly applied to the centre of high endemism in Fiordland and Otago; the former at least was heavily glaciated. McGlone (1985) points to the geological and historical links between this area and the Nelson-Marlborough region, which have separated by movement along the alpine fault during the Tertiary. Wardle (1963) and Burrows (1965) emphasise high rates of extinction in the intensely glaciated region between them. Both factors may have contributed to the pattern. The apparently low number of endemics on Stewart Island may simply reflect the much smaller area compared to the others under consideration.

The geographical patterns of plant diversity described above are paralleled by distribution patterns in geckos and skinks (Pickard and Towns 1988), large landsnails (Powell 1979, Meads *et al.* 1984), large insects (Meads 1990) and earthworms (Lee 1959). Regions of relative tectonic stability, in some cases periodically isolated as islands or escaping the worst effects of the last glaciation, apparently constitute refuges for palaeo-endemics and local centres of diversity (Ross 1972). Park (1983) drew attention to the urgency for conservation efforts in the Northland and Nelson-Marlborough regions. This known biogeographic pattern, which is an overall feature of the New Zealand biota, should be specifically targeted in New Zealand's biodiversity strategy.

In considering the contrasts between regions of high and low species diversity one can ask whether high diversity is a result of more species per community sample (high alpha-diversity), or a result of a finer mosaic of community types (higher beta-diversity). For example, are species more tightly packed along altitudinal gradients in Nelson than in the Tararua? How do different forest types differ in alpha-diversity? These sorts of questions are conceptually straightforward, but they imply a considerable amount of field effort in geographically separated regions. Relevant data focused on such questions are not yet available, but some instructive comparisons can be made.

The altitudinal gradient of plant species richness

It is well known that the number of woody species generally declines with an increase in altitude (e.g. Whittaker 1967; Beals 1969; Peet 1981) and this has been described in several studies in New Zealand (e.g. Ogden 1971; Clarkson, 1986; Druitt *et al.* 1990). In a quantitative study of species distributions on nine South Island altitudinal sequences, Allen *et al.* (1991) indicated that altitude accounted for $44 \pm 15\%$ of the variation in species composition. Other components of variation included geological substrate and disturbance history. Simple presence-absence data for the woody flora on altitudinal gradients throughout New Zealand are illustrated in Fig. 2. Forest clearance has resulted in few of the North Island sequences extending below 400 m altitude, but some 'spot' data from forests at lower altitudes have been included. The overall impression is of diversity decreasing in a fairly consistent way as altitude increases. The range of possible woody species diversity at any one altitude (i.e. the range of alpha-diversity) is about 35-40 species, truncated to a smaller range in the subalpine zone. Some of the spread in the data can be regarded as sampling error, but it is noteworthy that even geographically close sequences sampled with the same methods show marked differences in alpha-diversity at some altitudes (Ogden 1995).

The least squares linear regression line fitted to these data accounts for 65% of the variance, and indicates an average loss of 3.4 woody plant species for every 100 m of altitude gained. This should be regarded as an expected or null value of the rate of decline in 'species packing' with altitude against which individual sequences can be assessed.

If we take 60 species as the sea-level value, then reduce species number with altitude on the assumption that the number is proportional to the area available on a perfect cone, we get a 'regression' line which is indistinguishable from the least-squares line (lower line on Fig. 2). Of course, the mountains studied are not all conical, but the volcanic Mt Egmont comes close, and shows the closest fit to this line. This analysis, and other evidence (Ogden 1995), implies that the simplest explanation for woody species diversity at any altitude below tree-line is the area of land available at that altitude. This prediction agrees with the generalisations proposed in the general theory of island biogeography of MacArthur and Wilson (1967), and suggests that rare species will be present at rare altitudes (isolated mountain summits) and that maximum diversity will generally be reached in the lowlands. It also predicts that high altitude plateaux will be important centres of diversity.

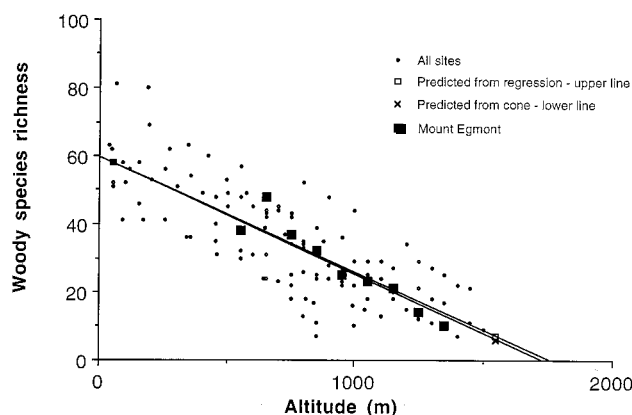


Fig. 2. Total numbers of woody species (trees, shrubs, sub-shrubs and lianes) in samples from different altitudes in New Zealand. The species number at any altitude includes any species recorded at both higher and lower altitudes. It is the number 'potentially present' (Druitt *et al.* 1990) at any altitude rather than the actual number in a sample plot. The upper regression line is defined by: $y = 59.914 - 0.0432x$ ($r^2 = 0.655$). The lower line assumes 60 species at sea-level and a progressive reduction with altitude based on the declining surface area of a cone with its apex at 1500 m (see text). The solid data points are for Mt Egmont (unpublished data, but see Clarkson 1986). See Ogden (1995) for data sources.

Case study: kauri and mountain beech

Kauri forest, characteristic of the high gamma-diversity region of the northern North Island, is generally regarded as the most diverse forest community in New Zealand. Canopy and sub-canopy composition varies across gradients of topography and altitude (Burns and Leathwick 1992). Kauri itself is distributed in patches, often on ridge crests or upper north-facing slopes. These patches have a cohort structure suggesting regeneration following local catastrophic destruction (Ogden *et al.* 1987). In contrast, mountain beech forest is almost a monoculture (low alpha diversity). The species can grow on a wide range of substrates and over a broad altitudinal range, thus 'preventing' the development of high beta-diversities also. In the Craigieburn Range (low gamma-diversity region of the central South Island), this type of forest clothes valleys, slopes and ridges, often with only one or two scattered representatives of other trees and shrubs per hectare. This aggressive occupancy of sites is maintained by a catastrophic or 'dieback' system of regeneration and relatively high juvenile growth rates (Ogden 1988; Ogden *et al.* 1993).

The differences in geographical extent, structure and diversity between kauri and mountain beech forest are outlined in Table 1. The comparison suggests that particular forest types, defined by

particular canopy dominants, have characteristic levels of alpha-diversity. Though kauri forest is much more restricted in latitudinal and altitudinal range, it has about double the tree species diversity of mountain beech forest. Twice as many species in half the altitudinal range implies tighter species packing along that gradient in kauri compared to mountain beech forest. Burns and Leathwick (1992) demonstrated that, at Waipoua forest, the topographic gradient from ridges to gullies (controlling soil moisture and nutrient availability) is more important in determining species composition than is altitude alone. Thus, where more species are present we witness more niche differentiation along a variety of gradients. Communities with high alpha-diversity may be more 'stable' in the sense that their component populations show less fluctuation in abundance, but they are less 'resilient' than simpler systems: mountain beech forest springs back readily following destruction, while kauri forest undergoes a long succession. This suggests that high alpha-diversity can be sustained only in association with high beta-diversity – a landscape mosaic of successional stages.

Biodiversity and plantation forests

Pine plantations, mainly *Pinus radiata*, cover about 5% of the New Zealand landscape (Newsome 1987) – about the same as kauri. Such plantations are not the 'biological deserts' they are sometimes said to be. The exotic monocultural appearance of these forests has obscured the fact that pine plantations in New Zealand sometimes have quite high plant species richness in their understoreys (Ogle 1976, 1989a; Allen *et al.* 1995a; Ogden *et al.* 1997), and have value in maintaining populations of native birds (Gibb 1961; Clout and Gaze 1984; Allen *et al.* 1995b). Plantation forestry involves the development of a crop and an associated assemblage of adventive and native species which increases in indigenous diversity through time. Because this is normally destroyed during harvest and replanting, the level of indigenous plant species richness in planted areas is largely a question of the rotation time and the proportion of the landscape left in indigenous cover (Ogden *et al.* 1997). As in native communities, the build-up of alpha-diversity on any one location is a function of the 'disturbance regime' (felling) in the surrounding landscape and the consequent level of beta-diversity. Plantation forestry can move to sustainable operational practices which retain indigenous biodiversity within the plantation forest matrix if consideration is given to rotation times (disturbance frequency), the proportions of the landscape in different aged pine cohorts (seral stages), and the amount and spatial pattern of areas left in native forest cover (the beta-diversity of the landscape).

Conservation of plant biodiversity

Since human effects are relatively recent, 'natural' and 'semi-natural' landscapes still cover about 50% of New Zealand (Norton 1989a,b), and the country possesses a range of ecosystems from highly-modified to near pristine (Towns and Ballantine 1993). Aspects of vegetation ('habitat') loss and modification by introduced plants and animals are reviewed by Norton (1989b) and Atkinson and Cameron (1993). Loss of indigenous species diversity is widely regarded as the most apparent and serious effect of browsing by mammals.

The introduction of mammalian pests has been halted, but alien plants continue to arrive in New Zealand at the rate of about 11 new species per annum. Huge efforts have been expended since the 1930s to control introduced mammals and techniques are researched and refined each year. Meanwhile, the import of exotic (garden) plants and their subsequent control as noxious weeds is accorded relatively low priority. Weeds are already changing many ecosystems, but continued importation implies an insidious long-term problem in sustaining native plant communities.

The Threatened Species Unit of the Department of Conservation has devised a system of priority ranking using criteria which can, supposedly, allow comparisons across major taxonomic boundaries (Molloy and Davies 1992). This system indicates that vascular plants comprise the largest group of threatened organisms in New Zealand, with 40 plants classed as highly endangered (category A) and a further 44 ranked as requiring some recovery work in the short term. Wilson & Given (1989) claim that ten per cent of New Zealand's flora is under threat of extinction in the wild. In 1991 the threatened plant list numbered 368 species and varieties (about 16% of the vascular flora) (de Lange and Taylor 1991; Wassilieff 1992). Most conservation expenditure, however, is devoted to the protection of the endangered avifauna.

Detailed vegetation data covering all parts of New Zealand (Wardle 1991) emphasise the unrepresentative nature of existing reserves (Mark 1983, 1985). Mountains are high-altitude 'islands' in a 'sea' of lowland. However, this sea of diverse forest in the lowlands is now itself highly fragmented, imposing new problems for the conservation of its biodiversity.

Realisation that lowland forest below 300 m altitude, tussocklands, swamps, estuaries and dune systems were under-represented in reserves gave impetus to the Protected Natural Areas Programme (PNA) initiated in the early 1980s (Mark 1983). Using differences in landform, vegetation, biota and climate, the country was divided into 268 Ecological Districts, and these were

to be surveyed for areas requiring protection (McEwen 1987). The scale of the operation, and the detail of the protocol envisaged, meant that the programme has never received the resources necessary for its full implementation (Ogle 1989b; Dickinson and Mark 1989). Although the programme continues, lowland forests remain under-represented in reserves. Moreover, reserved areas in the lowlands are mostly small fragments, in which modification by browsing mammals and invasion of alien weeds have greatest impacts (Timmings and Williams 1991).

The 'representative' landscape comprises not only a (more or less) static pattern of communities related to altitude, topography and substrate, but also a superimposed set of dynamic patches (successional stages) adding a temporal aspect to local biodiversity. A single generation of the dominant plants lasts for 600 - 1000 years in many cases.

Where the aim is to conserve maximum biodiversity in communities (high alpha-diversity), reserves need to be large enough to include representation by all phases of this dynamic pattern (beta-diversity), and management of the disturbance regime or weed invasion needs to explicitly recognise the time scale over which conservation 'results' are expected. While some small high diversity reserves may not be viable in the long term, with knowledge-based management of larger reserves some weed 'problems' may not be long term either. Almost certainly, where ecologically 'equivalent' alien species have become established we will have to accept some changes as inevitable.

Table 1. Comparison between kauri (*Agathis australis*) and mountain beech (*Nothofagus solandri* var. *cliffortioides*) forests. Data are given as normal ranges.

| | Kauri forest ⁽¹⁾ | Mountain beech forest ⁽²⁾ |
|--|-----------------------------|--------------------------------------|
| Structure | | |
| Basal area m ² ha ⁻¹ | 51 - 117 | 42 - 56 ⁽³⁾ |
| Height m | 30 - 40 | 16 - 19 |
| Density, trees ha ⁻¹ | 337 - 821 | 1409 - 1685 ⁽³⁾ |
| Diversity | | |
| Vascular plant spp. per plot ⁽⁴⁾ | 20 - 44 | 4 - 29 |
| Total vascular plant spp. ⁽⁵⁾ | 231 | 173 |
| Tree species ha ⁻¹ ⁽⁶⁾ | 8 - 27 | 2 - 23 |
| Total tree species ⁽⁷⁾ | 69 | 44 |
| Disturbance | | |
| Frequency at landscape scale | 500 - 1000 years | 50 - 200 years |
| Recovery after windthrow | Succession back to forest | Rapid in-situ regeneration |
| Recovery after fire | Succession back to forest | Often loss of site to grassland |
| Geographical extent | | |
| Latitudinal range | 4° (34 - 38°S) | 10° (36 - 46°S) |
| Altitudinal range | 700m | 1500m |
| Area 10 ⁶ ha ⁽⁸⁾ | 0.2 | 2.5 |

Notes: (1) Data from Ahmed (1984) and Ahmed and Ogden (1991) except where noted otherwise. Based on point-centred-quarter sampling of 25 1 ha stands in mature kauri forest throughout the latitudinal range of the species.

(2) Data from Wardle (1970 part 2), except where noted otherwise. Based on 2400 plot descriptions generally covering about 0.05ha. The data presented relate to the 19 associations with > 50% cover of trees.

(3) From Wardle (1984; Tables 11.3 and 11.4); average of all mountain beech forest types in proportion to the number of plots included.

(4) Based on 20 5m-diameter circular plots in each kauri stand, but plants < 1m tall not recorded, consequently the figures are an underestimate.

(5) From Cockayne (1928); mountain beech data from Cockayne's sub-alpine (beech) forest community, and so the difference between the two communities is again underestimated.

(6) Trees > 10cm diameter (dbh) in the case of kauri, but > 5cm dbh in the case of beech.

(7) All tree species recorded in all plots.

(8) Kauri data from Halkett (1983).

There is a need in New Zealand to integrate the findings of plant ecology and biogeography into the broad conservation strategy. Patterns of plant species distribution and bio-diversity in New Zealand are known, but this information is not clearly reflected in the reserve network. As a generalisation we seek to conserve vegetation types which reflect the pre-European vegetation pattern. In aggregate these reserves will, we hope, preserve the character of the New Zealand landscape and its unique biota. High species diversity is regarded as desirable, and is achieved both by creating reserves which include a variety of different plant communities and by selecting examples of communities which retain high diversity. One approach would be to identify the *largest* remaining lowland forest reserves, and the most intact lowland to montane altitudinal sequences in each biogeographic area of different gamma-diversity in New Zealand, and accord them high priority for the control of introduced mammals and invasive plants.

Acknowledgements

Discussions with Rob Allen, Ian Atkinson, Bruce Burns, Ewen Cameron, Matt McGlone, Susan Timmins and Carol West helped to formulate the ideas on which my original paper (Ogden 1995) on this topic was based. The Robert C. Bruce Trust supported my research on diversity in pine plantations, and Carter Holt Harvey Forests gave permission for the work in Kinleith Forest.

References

- Ahmed, M. 1984. Ecological and dendrochronological studies on *Agathis australis* Salisb., kauri. Unpublished Ph.D. thesis, University of Auckland.
- Ahmed, M. and J. Ogden. 1991. Descriptions of some mature kauri forests of New Zealand. *Tane*, 33: 89-112.
- Allen, R. B., A. Reif, and G. M. J. Hall. 1991. Elevational distribution of conifer-broadleaved hardwood forests on South Island, New Zealand. *Journal of Vegetation Science*, 2: 323-330.
- Allen, R. B., K. H. Platt, and R. E. J. Coker. 1995a. Understorey species composition patterns in a *Pinus radiata* D. Don plantation on the Central North Island Volcanic Plateau, New Zealand. *New Zealand Journal of Forestry Science* 25: 301-17.
- Allen, R., K. Platt, and S. Wiser. 1995b. Biodiversity in New Zealand plantations. *New Zealand Forestry* 39(4): 26-29.
- Atkinson, I. A. E. 1994. Ecological measures for conserving biodiversity: a New Zealand perspective. Systematics Association. Special Volume Series. Oxford University Press (in press).
- Atkinson, I. A. E. and E. K. Cameron. 1993. Human influences on the terrestrial biota and biotic communities of New Zealand. *Trends in Ecology and Evolution*, 8: 447 - 451.
- Basu, J. 1997. Mooney calls on scientists to find out how biodiversity protects ecosystems. *Science International*. No. 64 April 1997. 10-11.
- Beals, E. W. 1969. Vegetation change along altitudinal gradients. *Science*, 165: 981-985.
- Burns, B. R. and J. R. Leathwick. 1992. Vegetation map of Waipoua Sanctuary and environs, Northland, New Zealand. Forest Research Institute Bulletin 143. Ministry of Forestry, New Zealand.
- Burrows, J. C. 1965. Some discontinuous distributions of plants within New Zealand and their ecological significance. II. Disjunctions between Otago-Southland and Nelson-Marlborough and related distribution patterns. *Tuatara*, 13: 9-29.
- Clarkson, B. D. 1986. Vegetation of Egmont National Park, New Zealand. (Illustrated by J. Bruce Irwin). National Parks Scientific Series No. 5. DSIR Science Information Publishing Centre, Wellington, New Zealand.
- Clout, M. N. and P. D. Gaze. 1984. Effects of plantation forestry on birds in New Zealand. *Journal of Applied Ecology* 21: 795-815.
- Cockayne, L. 1928. The Vegetation of New Zealand. 2nd edition. Engelman, Leipzig.
- Dawson, J. W. 1988. Forest Vines to Snow Tussocks. The Story of New Zealand Plants. Pp. 264. Victoria University Press, Wellington, New Zealand.
- de Lange, P. J. and G. Taylor. 1991. Threatened plant symposium. *New Zealand Botanical Society Newsletter*, 25: 17-19.
- Dickinson, K. J. M., and A. F. Mark. 1989. Tussock grassland reserve design: some practical considerations. Pp. 26-30 in *Management of New Zealand's Natural Estate*. ed. by D. A. Norton. New Zealand Ecological Society, Christchurch, New Zealand. Occasional Publication No. 1.
- Druitt, D. G., N. J. Enright, and J. Ogden. 1990. Altitudinal zonation in the mountain forests of Mt Hauhungatahi, North Island, New Zealand. *Journal of Biogeography* 17: 205-220.
- Gibb, J. A. 1961. Ecology of the birds in Kaingaroa Forest. *Proceedings of the New Zealand Ecological Society* 8: 29-38.
- Halkett, J. C. 1983. Kauri forest management review. New Zealand Forest Service. Wellington, New Zealand.
- Huston, M. 1979. A general hypothesis of species diversity. *The American Naturalist*, 113: 81-101.
- Lee, K. E. 1959. The earthworm fauna of New Zealand. New Zealand Department of Scientific and Industrial Research Bulletin 137.
- MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.
- Mark, A. F. 1983. The need to reserve lowland indigenous forests. Pp. 189-205 in *Lowland Forests in New Zealand*, ed. by K. Thompson, A. P. H. Hodder and A. S. Edmonds. University of Waikato, Hamilton, New Zealand.
- Mark, A. F. 1985. The botanical component of conservation in New Zealand. *New Zealand Journal of Botany*, 23: 789-810.
- McEwen, W. M. 1987 (Ed.). Ecological regions and districts of New Zealand. Third revised edition in four 1:500 000 maps. New Zealand Biological Resources Centre Publication No. 5. Department of Conservation, Wellington, New Zealand.
- McGlone, M. S. 1985. Plant biogeography and the late Cenozoic history of New Zealand. *New Zealand Journal of Botany*, 23: 723-749.
- McPhail, M. 1997. Long-distance dispersal. Response to Pole 1974. *Correspondence. Journal of Biogeography* 24: 113-117.
- Meads, M. J. 1990. The Weta Book. A Guide to the Identification of Wetas. Land Resources Division. DSIR. Lower Hutt, New Zealand.
- Meads, M. J., K. J. Walker, and G. P. Elliott. 1984. Status, conservation and management of land snails of the genus *Powelliphanta* (Mollusca: Pulmonata). *New Zealand Journal of Zoology*, 11: 277-306.
- Molloy, J. and A. M. Davis. 1992. Setting priorities for the conservation of New Zealand's threatened plants and animals. Dept. of Conservation, Wellington, New Zealand.
- Newsome, P. F. J. 1987. The Vegetation Cover of New Zealand. National Water and Soil Conservation Authority, PO Box 12041, Wellington, New Zealand. 153 pp.
- Norton, D. A. 1989a. Management of New Zealand's protected natural areas into the 21st century. Pp 3-7 in *Management of New Zealand's Natural Estate*. Edited by D. A. Norton. New Zealand Ecological Society, Christchurch, New Zealand. Occasional Publication No. 1.
- Norton, D. A. 1989b. Scientific basis for the conservation management of New Zealand plant communities. Pp 349 - 381 in *The Scientific Management of Temperate Communities for Conservation*. 31st Symposium of the British Ecological Society, Southampton 1989. Edited by I. F. Spellerberg, F. B. Goldsmith and M. G. Morris. Blackwell Scientific Publications, Oxford.
- Ogden, J. 1971. Studies on the vegetation of Mount Colenso, New Zealand. I. The forest continuum. *Proceedings of the New Zealand Ecological Society*, 18: 58-65.
- Ogden, J. 1988. Forest dynamics and stand-level dieback in New Zealand's Nothofagus forests. *Geojournal*, 17: 225-230.
- Ogden, J., G. M. Wardle and M. Ahmed, M. 1987. Population dynamics of the emergent conifer *Agathis australis* (D. Don) Lindl. (kauri) in New Zealand. 2. Seedling population sizes and gap-phase regeneration. *New Zealand Journal of Botany*, 25: 231-242.
- Ogden, J., C.H. Lusk, and M. G. Steel. 1993. Episodic mortality, forest decline and diversity in a dynamic landscape: Tongariro National Park, New Zealand. Pp. in *Forest Decline in the Atlantic and Pacific Region* ed. by R. Huettl and D. Mueller-Dombois. Springer-Verlag. Berlin Heidelberg.
- Ogden, J. 1995. The long-term conservation of forest diversity in New Zealand. *Pacific Conservation Biology* 2: 77-90.
- Ogden, J., J. Braggins, K. Stretton, and A. Anderson. 1997. Plant species richness under *Pinus radiata* stands on the Central North Island Volcanic Plateau, New Zealand. *New Zealand Journal of Ecology* 21: 17-29.

- Ogle, C. C. 1976. The effect of pines on the diversity of indigenous species. *Bulletin of the Wellington Botanical Society*, 39: 23-29.
- Ogle, C. C. 1989a. Pine forest flora - Opoutere revisited. *New Zealand Botanical Society Newsletter* 17: 12-15.
- Ogle, C. C. 1989b. An overview of reserve design and location in New Zealand. Pp 11-18 in *Management of New Zealand's Natural Estate*. Edited by D. A. Norton. New Zealand Ecological Society, Christchurch, New Zealand. Occasional Publication No. 1.
- Park, G. N. 1983. The Patterns, diversity and conservation status of New Zealand's lowland forests Pp 153-188. In *Lowland Forests in New Zealand*, edited by K. Thompson, A. P. H. Hodder and A. S. Edmonds. University of Waikato, Hamilton, New Zealand.
- Peet, R. K. 1981. Forest vegetation of the Colorado Front Range. *Vegetatio* 45: 3-75.
- Peet, R. K. 1974. The measurement of species diversity. *Annual Review of Ecology and Systematics*, 5: 285-307.
- Pickard, C. R. and D. R. Towns. 1988. *Atlas of the amphibians and reptiles of New Zealand*. Conservation Sciences Publication No. 1. New Zealand Department of Conservation.
- Pole, M. 1994. The New Zealand flora - entirely long-distance dispersal? *Journal of Biogeography* 21: 625-635.
- Powell, A. W. B. 1979. *New Zealand Mollusca*. Collins, Auckland, London.
- Raven, P. H. 1973. Evolution of subalpine and alpine plant groups in New Zealand. *New Zealand Journal of Botany*, 11: 177-200.
- Richerson, P. J. and K. L. Lum. 1980. Patterns of plant species diversity in California: relation to weather and topography. *The American Naturalist*, 116: 504-532.
- Rogers, G. M. 1989. The nature of the lower North Island floristic gap. *New Zealand Journal of Botany*, 27: 221-241.
- Ross, H. H. 1972. The origin of species diversity in ecological communities. *Taxon* 21: 253-259.
- Soule, M. E. 1986. Patterns of diversity and rarity: their implications for conservation. Pp. 117-121 in *Conservation Biology*. The Science of Scarcity and Diversity, ed. by M. E. Soule. Sinauer Associates, Sunderland, Massachusetts.
- Timmings, S. M. and P. A. Williams. 1991. Weed numbers in New Zealand's forest and scrub reserves. *New Zealand Journal of Ecology*, 15: 153-162.
- Towns, D. R. and W. J. Ballantine. 1993. Conservation and restoration of New Zealand island ecosystems. *Trends in Evolution and Ecology*, 8: 452-457.
- Wardle, J. A. 1970. The ecology of *Nothofagus solandri*. 2. The associations. *New Zealand Journal of Botany*, 8: 532-570.
- Wardle, J. A. 1984. *The New Zealand beeches: ecology, utilisation and management*. New Zealand Forest Service, Christchurch, New Zealand.
- Wardle, P. 1963. Evolution and distribution of the New Zealand flora, as affected by Quaternary climates. *New Zealand Journal of Botany*, 1: 3-17.
- Wardle, P. 1991. *Vegetation of New Zealand*. Cambridge University Press, Cambridge.
- Wassilieff, M. 1992. Letters to the Editor. *New Zealand Botanical Society Newsletter*, 28: 19-20.
- Whittaker, R. H. 1967. Gradient analysis of vegetation. *Botanical Reviews*, 42: 207-267.
- Whittaker, R. H. 1972. Evolution and the measurement of species diversity. *Taxon*, 21: 213-251.
- Wilson, C. M. and D. R. Given. 1989. *Threatened Plants of New Zealand*. DSIR Publishing, Wellington, New Zealand.
- Wilson, S. D. and P. A. Keddy. 1988. Species richness, survivorship and biomass accumulation along an environmental gradient. *Oikos*, 53: 375-380.
- Wilson, J. B. and M. T. Sykes. 1988. Some tests for niche limitation by examination of species diversity in the Dunedin area, New Zealand. *New Zealand Journal of Botany*, 26: 237-244.

FRI research on genetic diversity as a component of biodiversity of forests

Michael J. Carson*

Introduction

Forest biological diversity can be considered in terms of ecosystem, species and genomic richness (UNEP). Loss of biodiversity occurs when species disappear from a community, or ecosystem. Historically, species losses have occurred as a natural consequence of evolution, driven by (sometimes catastrophic) environmental change. However, mankind's interest in biodiversity is very largely driven by the recognition that human influences on the environment are producing rapid (in evolutionary terms) and irreversible changes in biodiversity. Implicit in that interest is an assumption that at least some human-directed influences can be managed to either retard or reverse species loss, and maintain biodiversity. The draft NZIF Position Paper recognises the importance of research in protecting New Zealand forest biodiversity (Section 3 i-v), specifically in areas of:

- taxonomic studies ... in natural environments
- interdisciplinary ecosystem studies to understand processes ... and the functional role of biodiversity
- identifying and monitoring indicators of biodiversity
- protecting and maintaining forest genetic resources
- developing management options to maintain and enhance biodiversity.

Species diversity and genetic diversity of forest trees

The FRI has made a major and long-term contribution to an overall research effort addressing various aspects of forest biodiversity, of both indigenous and exotic forests. Much of the research that has assisted our understanding of forest biodiversity preceded, and contributed to, recent public recognition of its importance. For example, a very high proportion of both native and exotic forest plants have been taxonomically classified, as also have around 50% of insect species in

New Zealand. Similarly, FRI researchers are placing a major current emphasis on identifying and monitoring indicators of biodiversity - particularly the use of beetles as an indicator group (Hutcheson, 1994). The rationale for this work is to identify changes in the composition of insect communities that will reflect underlying changes in their habitat. Future research will include studies of indigenous and exotic understorey plant species as indicators of biodiversity.

Just as a large component of biodiversity is concerned with the richness expressed by species variability, so too is genetic diversity within a species of significant importance. The genetic diversity of a production crop needs to be protected, maintained, and if necessary enhanced as part of responsible management of our forest genetic resources.

The genetic resources of New Zealand's major exotic forest tree species have been managed since the 1950s, including low-intensity programmes of species and provenance introduction, test-

* FRI, Rotorua