Vegetation History and Dynamics in New Zealand: Future Scenarios and Improved Trajectories Towards Restoring Natural Patterns

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Abstract New Zealand is a micro-continent that has been more isolated from mainstream (especially Northern Hemisphere) evolution than any other large, ice-free land mass. This has created a land of unusual and often unique ecology, notably lacking land mammals. Native Gondwanan elements, and others considered ancestral to major world lineages, imply some continuity back to Gondwana itself. Together, both old and new arrivals make up a largely endemic biota. These have been decimated both ecologically and socio-culturally (extinction of experience) by large numbers of recent continental imports. We examine opportunities for recovery of some of the lost integrity of natural patterns, at a range of scales, albeit in the absence of an alarmingly high number of extinct and critically endangered, keystone species. Apart from the essential pest-control programmes being carried out assiduously by Government and NGOs, our research has focused on design of landscape factors that can facilitate regeneration, recovery, and connectivity (ecologically and socio-culturally). Earlier landscape-optimising models are being combined with reserve-design theory (island-biogeography concepts) and spatial configurations based on empirical dispersal data, refined by considering the patch condition and proximity requirements of contrasting wildlife guilds. We present some preliminary data. Like the rest of the world, New Zealand is at an ecological crossroads regarding the extent to which it will retain its endemic biota and landscape legibility. We can take action even in the absence of perfect knowledge to apply the most promising strategies and restoration techniques available—or we can wait and watch the decline.

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Introduction

New Zealand is a micro-continent that has been more isolated from mainstream (especially Northern Hemisphere) evolution than any other large, ice-free land mass. Pine, willow, poplar, oak, elm, ash, maple, birch, rosaceous trees, land mammals and most large advanced reptiles are significant South Temperate Zone absentees. Glaciation had a considerable impact on tropical elements—with nowhere to go on an archipelago. This has created a land of unusual and often unique ecology (Sullivan at al. 2010). While many groups have reached New Zealand shores regardless (Goldberg et al. 2008), native Gondwanan elements (leiopelma frogs and tuatara), and others considered ancestral to major lineages (such as the New Zealand wrens, basal to the passerines), imply that there has been some continuity, albeit as archipelagic and temporal stepping stones, through the > 60 million years back to Gondwana itself (Lee et al. 2001; Wilson 2004; Swaffield et al. 2009; Gibbs 2011). These ancient elements have in turn been masked somewhat by many more recent, trans-oceanic arrivals over the past 5–10 million years, which have subsequently radiated in new mountain environments or, in the absence of mammalian predators, evolved some bizarre adaptations and lost redundant functionality, such as bird flight. Together, both old and new arrivals, make up a largely endemic biota (100 % of bats, amphibians and reptiles; 90 % freshwater fish; >80 % vascular plants and invertebrates; and 70 % of land and wetland birds).

One of the most defining influences on the unique biogeography of New Zealand is the lack of land-dwelling mammals except bats (Wilson 2004; Lee et al. 2010). This is the largest ice-free land mass in the world with such a lop-sided fauna. There are bats, sea mammals and evidence of a small marsupial snuffling around in the Tertiary (Worthy et al. 2006). Furthermore, New Zealand was the last major land mass besides Antarctica to be settled by humans, with Polynesians now thought to have arrived around 1280 A.D. (Wilmshurst et al. 2008). These and later peoples brought predatory mammals which have devastated the highly endemic native fauna, totally naïve to this brand of continentally honed predation. And later mammalian herbivores, together with an avalanche of exotic plant species co-adapted to mammal grazing and browsing, and associated with widespread deforestation and land use change, created a pincer movement of defoliation from above and competition from below.

Added to these ecological circumstances is the complex social dynamic. ‘Extinction of experience’ (Miller 2005) has occurred because the human-co-adapted, introduced utility/amenity species, supported by centuries of plant and animal breeding from the immigrant’s homelands, took over the transformed landscapes and created in New Zealand the old familiarity and sense of place that reinforces the dominance of and protectiveness towards exotic (homeland) species in the cultural landscape (Meurk and Swaffield 2000). This has put great strain on the ecological integrity of lowland biota especially. Unfortunately, the transformed landscape is familiar to northern hemisphere tourists, and so it is marketed and further reinforces

New Zealand as an 'unspoilt', clean, green, idyllic and romanticised Northern Hemisphere in miniature.

This short paper summarises key factors of the condition and trend of New Zealand landscapes and ecosystems, as well as opportunities for recovery of some of the lost integrity of natural patterns, albeit in the absence of an alarmingly high level of extinct and critically endangered species—some of which were keystone.

New Zealand Forest and Wetland Vegetation: Excluding Alpine, Seral and Dune Vegetation

Outside of the Southern Alps, and naturally disturbed or excessively wet environments, New Zealand was, and is potentially, forested throughout. The forests and shrublands of New Zealand comprise several broad groupings (Meurk 1995; Wiser et al. 2011; Wiser & De Caceres 2013): rainforest of kauri (*Agathis australis*) in the far north, podocarps throughout, and southern beech (*Nothofagus*) in cool or leached land; floodplain and swamp forest (podocarp-hardwood); dry forest (podocarp and hardwood woodlands); and coastal forest (hardwoods); plus quasi-climax communities of small-leaved divaricating shrubs in very dry or otherwise stressed environments. Wetlands comprise swamps (*Typha*, *Phormium*, sedges, rushes), fens (sedges and restiads), bogs (cushion plants, restiads, *Gleichenia* fern) and salt marshes (mangroves, restiads, rushes, sedges and mat plants) (Johnson & Gerbeaux 2004). These communities expanded following Polynesian fires and have contracted again in the post-European drive to drain and farm their productive soils.

Condition and Trend

Forest canopies have been stable although there is a shifting emphasis to less palatable regeneration and understorey species—due to naturalised deer, pigs, goats and possums (Forsyth et al. 2010; Stewart 2010). Native shrublands and woodlands, apart from unpalatable *kanuka* and daisy shrubs, are often regarded as 'living dead' due to lack of recruitment from palatable seedlings. These landscapes have also been displaced by exotic leguminous or daisy shrubs, hastened by use of herbicides or fire, which in fact favour the quickly regenerating and browse-tolerant exotic woody plants, and cause the gradual shift of dominance away from the native species. Coastal dieback, wetland drainage, and replacement of wet marshes by farmers' ponds (often for attracting and shooting the introduced and prevalent mallard duck) are all contributing to general and widespread attrition of natural vegetation.

Critical aspects of New Zealand's forest biology are that about 75 % of native woody plants bear fleshy fruits and/or nectar (Burrows 1994; Kelly et al. 2010), are largely evergreen, and somewhat shade-tolerant. Many of these species thus depend on birds (or lizards) for dispersal. In contrast, the majority of the dominant exotic trees are dry-fruited or they are warm-temperate to subtropical evergreen broadleaved, shade-tolerant trees that have similar but more aggressive functional characteristics to the native forest species. These also get dispersed by birds and can therefore invade the evergreen indigenous forests.

All this underscores the fact that a primordial bird/lizard-driven ecosystem has been largely replaced by a naturalised mammal-bird-driven system during just 0.001 % of New Zealand's separate history. The prognosis is not good, based on current trends. Various strategies have been debated and tested over the years, though, and new technologies are providing more options, notwithstanding their publicly controversial nature. Killing anything is an ethical/moral dilemma and much conservation in New Zealand, in order to be successful, requires killing plants and animals, or even extermination of whole populations. But what the public (and animal-rights advocates) do not see is the nightly carnage of defenseless unique indigenous species meted out by the exotic carnivores. In light of this, the independent environmental commissioner for New Zealand has been unequivocal about the need for these methods of control (http://www.pce.parliament.nz/publications/all-publications/evaluating-the-use-of-1080-predators-poisons-and-silent-forests).

New Zealand's Department of Conservation and regional councils already target about 500 weedspecies, about 20 % of the naturalised vascular flora, which in total is now larger than the native vascular flora (Sullivan et al. 2004) and continually increasing. As well, there have been several concerning outbreaks of potentially transformative diseases attacking indigenous species such as the phytophthora disease in kauri.

Responses

Apart from the essential New Zealand pest-control programmes and research, we have been focusing on landscape factors that can facilitate regeneration, recovery, and connectivity (not only ecological but also socio-cultural). We are building on preliminary modeling work carried out by Meurk and Hall (2006) that endeavours to design (within practical human constraints and requirements of cultural landscapes) optimum reserve sizes, configurations, linkages, structural integrity (that facilitates regeneration) and composition (continuous fruit and nectar sources for wildlife), while avoiding biosecurity risks. This is essentially defining and implementing a re-born vegetation pattern through space and time for New Zealand's cultural landscape. Much of it is about facilitating natural regeneration (Stewart et al. 2004) along appropriate trajectories, while armies of volunteers are actively planting back the lost forests, wetlands and dune systems (Sullivan

et al. 2009, http://www.dunestrust.org.nz/). In the meantime, those government departments responsible for conservation, biodiversity and biosecurity are developing systems to work smarter with declining budgets by prioritising targets with more quantified indicators.

Our Research Contribution

We have looked to extend the earlier landscape-optimising modeling work through combining reserve-design theory (based on island-biogeography concepts) and spatial configuration based on empirical dispersal data (Meurk and Hall 2006), literature (Walker et al. 2008), personal observation, and refined by considering contrasting guilds of wildlife with different habitats, food requirements, size and likely foraging distances. We already know a substantial amount about receptivity of landscape elements to seedling establishment. Most native forest trees and shrubs in New Zealand are evergreen, bird-dispersed, shade-tolerant and palatable, but are also weak competitors in dense, exotic grass swards (as opposed to the more open bunch-grass natural grasslands). These species generally require a woody canopy that has been through an initial dense phase and suppressed the grass, then matured, opened and let in enough light for woody plant seed to germinate and grow. In New Zealand this "goldilocks zone" can be provided by some early successional species in the families Myrtaceae, Rubiaceae or the genus *Pittosporum*, but also by short-lived, exotic leguminous shrubs, willows, eucalypts and conifers. Thus restoration of habitats and landscapes is now often managed through pre-existing cover, because, as it turns out, removal of this is counter-productive and usually just creates a bigger and endless (new) weed problem. Many naturalised exotics are better and faster at exploiting these disturbances than indigenous species. Indicative guidelines that meet landscape requirements for various indigenous wildlife are shown in Table 1.

To reiterate, predator control is imperative, not just for the ferocious predators like mustelids, rodents, cats and dogs, but the vacuum cleaner-like mice, hedgehogs, possums and pigs—for full ecosystem restoration. Some shade-tolerant exotic trees, shrubs and ferns will need to be managed, and dense herbaceous growth has to be controlled for open ground native species to co-exist (see below). Diseases also threaten at times, as mentioned. While exotic polyphagous pest insects can be an issue for some native plants at some locations; hitherto this has been unusual (Brockerhoff et al. 2010).

The particular innovation that is springing up around the country is the predator-proofed eco-sanctuary (see Fig. 1). This is perhaps the cornerstone of an even more ambitious goal of a pest-free New Zealand (now dubbed the Callaghan concept). Basically, this involves fenced or systematically poisoned sanctuaries in both mainland islands (http://sanctuariesnz.org) (and yes this seems full of paradoxes) and real oceanic islands, where the line is drawn creating a starting point for rolling back the predator wall from pressing against these bulwarks. The widely used

Table 1 Working hypotheses for modeling (ecologically and socially) optimum spatial configuration and other metrics of habitat and patches for a range of different wildlife guilds in New Zealand cultural landscapes (based on sources indicated in text)

Guild	Indicator species	% Habitat cover	Minimum patch or matrix* area (ha)	Maximum interpatch gap (km)
Bush bird—herbivore	NZ Wood pigeon	10–15	5–10	25
Bush bird—omnivore	Bellbird and Tui	10–15	5–10	10
Bush bird—insectivore	Grey Warbler and Fantail	5	0.5–1	1
Wetland bird	Fernbird and Pukeko	5	25–50	50
Forest/scrub lizards and sedentary inverts	Gecko and Leaf Vein Slug	5	5–10	0.005
Open ground lizards and mobile inverts	Skink and Large Moth	5	1	0.05

*Note: the maximum inter-patch gap compatible with effective dispersal of berry fruits is only about 2–3 km from source to receptive sink.

Fig. 1 A uniquely New Zealand 'landscape sculpture' (otherwise known as a scientifically tested, predator-proof fence) is a concept particularly resonant of New Zealand's battle to save its unique wildlife

mammalian pest-targeted pesticide 1080, along with cocktails of other poisons, does mean killing many organisms, and there are some side-effects and by-kill. But, unfortunately, much of New Zealand's native wildlife has near zero-tolerance of exotic mammals and just cannot coexist with them.

One celebrated example is Zealandia (http://www.visitzealandia.com) in Wellington, where local communities operate and various recording systems are being used to monitor the 'halo effect' which is the spread of vulnerable wildlife out from the fenced sanctuary into the surrounding residential and even commercial property (http://naturewatch.org.nz/projects/enhancing-the-halo). It is helped by the fact that Wellington is a hilly, moist place with gully remnants of native bush. The question is whether these birds that explore the great wide world are just easy meat

for cats, rodents and mustelids, or whether we can control the urban domestic and feral animals to effectively establish the halo.

Regardless of how effective removal of invasive and predatory species is, New Zealand will always have more exotic plants, birds, and mammals than indigenous species. Acceptance of this requires a new analysis of the possible vegetation patterns and objectives—what we will end up with are sometimes referred to as 'recombinant' ecosystems (Meurk 2011). A new type of management will also be required to balance the species and ensure survival of all our remaining biota. An approach to this is what we have referred to as 'gradient management' (Meurk et al. 2003).

This is really a scaled-up version of J. P. Grime's stress-disturbance matrix for interpreting and managing herbaceous vegetation especially (Grime 1977; 2002; Meurk 2004). It proposes that different permutations and combinations of plant composition will exist under every conceivable management regime (lying somewhere along the continuum of a stress x disturbance matrix). Some positions on the spectrum will be more or less favourable to indigenous and less so to exotic species. But every species will have a different optimum position, so no single management will suffice to ensure survival of all our biota (particularly that of the lowlands). Generally, indigenous species will do best when conditions are less hospitable, as competition from exotics will be reduced (Moen & Meurk 2001). Accordingly, many levels of stress (e.g. from temperature, drought, fertility) and disturbance (e.g. from natural land and soil disruptions, wind, and grazing) please remove this phrase, I can't seem to - thanks need to be applied in an adaptive management context to generate fully representative spatial and temporal patterns of indigenous species' distributions, environments and successional stages.

The implementation of these concepts to forest, wetland and seral habitats across New Zealand is being achieved in a somewhat *ad hoc* fashion through natural regeneration, numerous planting and pest control guides, and through hundreds of community groups across the country (Sullivan et al. 2009). These groups volunteer their time to restore lost habitats, often in partnership with government departments, businesses and local government. Dozens of native-specialist plant nurseries are also supplying millions of indigenous plants every few years. How well these plants are being selected, propagated, planted and managed, and how well the wildlife is being protected, remains to be seen.

All players are striving to attain a more professional and efficient approach to this urgent task, often in the face of shrinking resources that sometimes seem to be unproductively used for competitive fund raising and administration. They are out there fixing up degraded habitats. They are removing weeds and replanting lost species. Other groups focus on predator trapping and creation of pest-free sanctuaries (Fig. 1). While still others are deliberately planning wider landscape configurations that follow the theoretical pattern devised by Meurk and Hall (2006) that addresses the issues of critical mass of core habitat, minimizing negative edge effects, reserve spacing, and connectivity—both ecological and social (Figs. 2, 3 and 4) (e.g. http://www.kakariki.org.nz/).

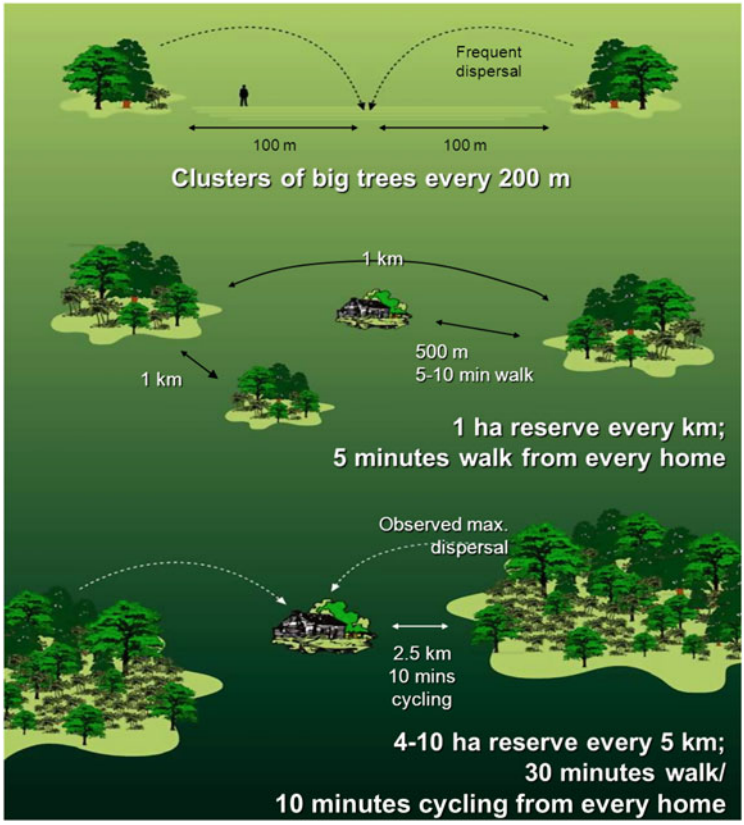

Fig. 2 An optimised configuration of habitat patches, connectivity (within stepping-stone distances)—complemented by continuous habitat corridors, protection for different guilds, and community visibility, identity, and acceptability within the context of cultural landscapes

The intention of all these intiatives is to achieve landscapes with ecological integrity (that function correctly), and natural character with 'the New Zealand look.' This can be described as evergreen broadleaved bushy and emergent trees (early botanists saw an almost tropical appearance), juvenile forms, divaricating shrubs, tussock grasses, and weird wildlife (Gibbs 2011). These landscapes resonate with the 'meaning' of these species to the indigenous people and later immigrants. This is about the landscape concept of 'legibility'—being able to read the stories in the visible patterns of the land that are understandable or interpretable. They may be recombinant systems, but the indigenous component is strong and visible in its own right, not reduced to subordinate 'green fluff'. Only then can we look the world straight in the eye and say we are 100 % pure and clean and green, and legitimately invite tourists here to see an authentic, unique environment. The highway network is the shop window of the country, and this will be a good place to start to repair the

Fig. 3 A real-world example of patch configuration (different-sized forest patches) with varying degrees of separation within a pastoral farmland context. Such a landscape can be said to have natural character (the tree components are predominantly indigenous). The ecological integrity of the patches and corridors are dependent on predator control or extermination

Fig. 4 A landscape topographically similar to the previous (Fig. 3) but biologically depauperate, demonstrating the need and opportunity for restoration of habitats and linkages

damage (Meurk et al. 2012). The recombinant nature of the landscape poses problems for herbaceous systems, but the Gradient management approach (Meurk & Greenep 2003) is one way to overcome this. Still more knowledge and experience are required to understand the best ways to manage these novel combinations.

As part of these recombinant rearrangements (Norton 2009), we also have to consider the staging of manipulation. Are some predators useful as an interim solution, e.g., the meso-predators (cats) that in turn prey on and keep in check the more vicious predators (rodents and mustelids)? And are some exotic nectar-producing plants to be encouraged in the short term, such as Australian Myrtaceae and Proteaceae (which, after all, were here in the Tertiary), providing that they do not themselves become weeds?

The key need is to hold the line on biodiversity, i.e., to retain all remaining species in self-sustaining populations that also contribute to the visual landscape. We can do better with our production forestry (currently dominated by Californian

pines), such as by storing more carbon by increasing the use of slow-growing, heartwood-dense native trees in managed continuous-canopy forestry. This also reduces the need for toxic wood preservatives, necessary for utilizing the fast-growing exotic soft-wood trees in construction timber. Eco-tourism is one of the primary products we have to offer, but we also need to be aware that the cost of international travel is likely to increase in the future. Many trees need to be grown in order to offset the carbon emissions and New Zealand has many areas of young regenerating scrub where this is possible.

There will be major ecological barriers to recovery that still must be overcome, and the fact that New Zealand has insular idiosyncrasies makes this more difficult ecologically. Relative scientific illiteracy and the extinction of experience make this even more challenging. Nevertheless, there is hope for positive change, to some extent by stealth (native plants are a bit like the tortoise in the famous 'tortoise and hare' parable), and through the choices of a younger, and more educated generation of New Zealanders. Our unique New Zealand experiences may yet be brought back from extinction. We can also be smarter and more creative in design, so that we increase the wilderness without raising people's suspicion and fear of losing control over their environment (Nassauer 1995). Just communicating what is possible and establishing demonstrations of the innovative ways for using indigenous species in almost every conceivable urban context, will help (Ignatieva et al. 2008).

Conclusions

Vegetation patterns in New Zealand are complicated by the importation of continental species into an endemic biota that is essentially 'other-worldly' in terms of the global mainstream. This is fundamentally different to typical oceanic islands, which are also vulnerable to invasion but where the biota has a low level of endemism, with completely different drivers. Predator control is the key, but the patterns are dynamic, evolutionary, and can now be directed towards a take-off point for nature to become the principal determinant of those patterns. We can assist by providing the infrastructure of appropriate patch arrangements, and quality of patches to facilitate recovery. Humanity took away the self-determination of nature in New Zealand and now it is in our power to give it back—a little. It is important, not just to the intrinsic value of life, but also for somewhat utilitarian purposes, to our identity as humans, not to mention pure survival. But it takes us past purely material survival to some deeper engagement with the universe and the miracle of existence—however it happened to be. Like the rest of the world, New Zealand is at a crucial crossroad. There are choices we have to make. We can't wait for perfect knowledge, or we will be watching the decline. We must apply the best information we have now to make the best decisions we can. Informed leadership and champions will be needed at all levels to implement a cultural shift.

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