


special issue: 

Feathers to Fur

The ecological transformation of Aotearoa/New Zealand

Life histories, dispersal, invasions, and global change: progress and prospects in New Zealand ecology, 1989–2029

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Abstract: We highlight three areas of significant progress in ecology since 1989 which are particularly relevant to New Zealand, and three major challenges for the next two decades. Progress: (1) The unusual life histories of New Zealand organisms, including extreme longevity and low reproductive rates, are now seen as efficient responses to the low-disturbance environment present before the arrival of large mammals, including humans. (2) Recent data show that long distance dispersal has been far more common than previously supposed, changing our image of New Zealand from a Gondwanan ark to the “flypaper of the Pacific”. (3) Greatly improved techniques for pest control, and innovative species management, have stabilised numbers of many of the most charismatic of New Zealand’s threatened species. Problems: (1) Native species continue to decline, including many previously thought to be stable, and improved phylogenetics and new discoveries have added threatened species. (2) Despite increased emphasis on biosecurity, biological invasions are continuing, driven by increased trade and lags in naturalisation. (3) Conservation efforts risk being overwhelmed by the direct effects of increasing human population, resource use, invasions, and global climate change at a time when human food supplies and economies are coming under increasing pressure from environmental constraints. Conclusions: (1) We need improved ecological understanding and more management tools for invasive and threatened species, especially for species other than birds. (2) In these decades of rapid climate change and habitat conversion, there is an urgent need for more widespread and sustainable integration of native species into New Zealand’s rural and urban lowland landscapes.

Keywords: biogeography; biosecurity; climate change; conservation; disturbance; greenhouse gases; invasive species; island ecology; longevity

Introduction

New Zealand ecology has much to offer the world. It is an example of unusual native ecology, a cautionary tale of human impacts on a naïve biota, and a demonstration of often audacious conservation initiatives to manage threatened species and ecosystems. Jared Diamond (1990a) described New Zealand’s biota as “the most important and interesting biota of any island” (p. 6) and as being “as close as we will get to the opportunity to study life on another planet” (p. 3, a quotation understandably over-used by New Zealander ecologists). Tim Flannery (1994: 55) called it “a completely different experiment in evolution to the rest of the world”, and Gareth Nelson (1975: 494) wrote of New Zealand biogeography, “explain New Zealand and the world falls into place around it”.

New Zealand is such an odd and threatened place that it is regarded as one of the world’s biodiversity hotspots (Myers et al. 2000). Because people arrived in New Zealand only about 1280 AD (Wilmshurst et al. 2008), New Zealand also

regrettably provides one of the best-documented examples of the ecological impacts of the world’s most-invasive species.

Here, to conclude this special issue, we describe three areas of substantive progress in New Zealand ecological research since 1989. The three topics we highlight here are chosen to complement those explored elsewhere in this issue, and inevitably reflect the authors’ idiosyncratic views. The 1989 baseline was the year of publication of “Moas, mammals, and climate in the ecological history of New Zealand”, where the New Zealand Ecological Society reviewed progress on the major ecological problems of the day (see Sullivan et al. 2010, and an overview by Diamond (1990b)). We now know much more about native New Zealand ecology, both before and after human arrival, including how long-distance dispersal and local evolution have worked together to shape this unusual biota. Our pest control and species management programmes have become progressively more ambitious and earned New Zealanders a global reputation as innovative conservationists.

This special issue reviews the current status of New Zealand ecology, updating the 1989 *Moas Mammals and Climate* special issue (NZJ Ecol 12 supplement). Both issues are available at www.newzealandecology.org/nzje/.

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We conclude with an assessment of three important challenges for the next 20 years of ecological research in New Zealand. Native species continue to decline, and invasive species continue to establish and spread, despite current best efforts. Intensifying land use and global climate change will put additional pressure on biodiversity. There is much still to do.

Three areas of progress

New Zealand's unusual life histories: longevity and disturbance

It is widely recognised that many New Zealand bird species are K-selected with long lives and low reproductive rates. It has been less well appreciated until recently how much this also applies to other taxa (but see Tocher 2009), which has several interesting consequences for understanding and managing New Zealand's native biota. Early characterisations of the local biota as competitively inferior (Darwin 1845; review in Healy & Edgar 1980 preface page x) have been replaced (as foreseen by Cockayne 1910) by a growing recognition that the native biota is better adapted to a low-disturbance regime than much of the introduced biota.

Native species can be said to typically maximise future reproduction (Residual Reproductive Value or RRV) rather than current reproduction, as a selective response to high adult survival. Although longevity data in the wild are hard to come by for New Zealand (and elsewhere), there are a number of indicators in birds. Comparing three New Zealand oystercatchers with two overseas species shows the New Zealand species have longer juvenile periods (mean 4.75 years in NZ versus 3.75 years overseas; Dowding & Murphy 2001). Similarly, comparing the endemic takahe (*Porphyrio hochstetteri*) and cosmopolitan pukeko (*P. porphyrio*), takahe live much longer (14–20 vs 3–6 years respectively) and have smaller clutches (1–3 vs 4–6 eggs; Heather & Robertson 1997). That comparison may be affected by the larger body size of takahe (3 kg vs 1 kg), but the same trends are seen in birds of matched size. Brown creepers (*Mohoua novaeseelandiae*, 12 g) are in an endemic genus, and are of similar size to fantails (*Rhipidura fuliginosa*, 8 g) which have presumably not been in New Zealand as long since the species occurs in Australia. Brown creepers have a similar number of eggs per clutch as fantails, but fewer clutches per year (2–3 vs 2–5), a longer juvenile period (1 year vs 2 months) and higher adult survival (80% vs 50% per year) leading to longer-lived adults (mean 5 years vs maximum of 3 years respectively; Heather & Robertson 1997).

Kakapo *Strigops habroptilus* are extremely long-lived, with survival 1985–2007 for adult birds moved to predator-free islands averaging 0.99 per year (Powlesland et al. 2006), implying a median longevity of 70 years. Consistent with this, the last Fiordland bird (“Richard Henry”) could be 100 years old. Although parrots in general are reputedly long-lived, Brouwer et al. (2000) found that life spans rarely exceeded 50 years with a few reliable records of individual birds living up to 70 years, all based on captive birds with abundant food and no predation. In contrast the high kakapo survival rate is for birds in the wild (albeit now intensively managed) and adults were of unknown age when first found. Thus, it seems likely that kakapo are very long lived even for a big parrot (constant 0.99 survival would mean 25% of individuals living >140 years), but more data on survival of known-age kakapo over the coming decades are needed to prove this.

Other animal taxa show similar patterns. Wild common geckos *Hoplodactylus maculatus* on Motunau Island frequently live to >36 years old (Bannock et al. 1999), and one resighted in 2006 was estimated to be 42 years old, the oldest known gecko in the world (<http://extranet.doc.govt.nz/content/frontpage/2005/granny-gecko.htm>). Wild *Hoplodactylus duvaucelii* on North Brother Island also lived to c. 36 years (Thompson et al. 1992). In contrast the oldest known gecko in North America was a captive animal which lived for 21 years (Bannock et al. 1999). Longfinned eels *Anguilla dieffenbachii* at 106 years are the oldest known *Anguilla* worldwide (Jellyman 1995). Native alpine grasshoppers *Brachaspis* spp. in Nelson Lakes National Park live to at least three years old; in contrast alpine grasshoppers overseas typically live only one year (Batcheler 1967). The land snails *Placostylus hongii* and *P. ambagiosus* may live 20 years or more; snails marked as adults in 1979 at Surville Cliffs were found alive in 1991. They have few, relatively large eggs. Less is known about kauri snails (*Paryphanta* spp) but they are also believed to live up to 25 years (Parrish et al. 1995). Perhaps most remarkably, recent work on the land snail *Powelliphanta augustus* suggests the juvenile (pre-reproductive) period lasts more than 14 years (A. James & R. Brown, internal Department of Conservation report, October 2009). Finally, it is worth noting that many of these maximum ages above are from populations currently in the presence of introduced predators, which may therefore be underestimates of longevity in the pre-human situation.

Similarly, the native flora is dominated by long-lived taxa. For a temperate country the flora is unusually dominated by trees, both relatively and absolutely (McGlone et al. 2010). Only about 47% of the native flora is hemicryptophytes and geophytes (mostly herbaceous perennials) compared to a temperate zone mean of 71% in these groups, and only 6% of native species are short-lived plants (annual and biennials) compared to a temperate mean of 17% (Allan 1937; Crawley 1986; Atkinson & Cameron 1993 give a figure of 2% native annuals for the dicot flora). Moreover the climate is clearly suitable for annuals and biennials, since over 30% of the naturalised vascular flora have this life history (Atkinson & Cameron 1993). Even among herbaceous perennials, New Zealand species such as tussock grasses can be extremely long-lived. A demographic study of 81 mapped *Chionochloa pallens* plants recorded no mortality over 1990–2009 (Rees et al. 2002 and D Kelly unpubl. data). Lucy Moore (1955) said native tussocks behaved more like trees, and Mark (1969: 298) concluded that mature snow tussocks (*Chionochloa* spp.) “could be centuries old”. Paired photographs of *Chionochloa* grassland at Porters Pass (Canterbury) taken in c. 1890 and 1978 showed many of the same individual plants still present (Whitehouse 1982).

One possible reason for the unusual longevity of so many New Zealand plants is a relatively low frequency (i.e. long return time) of disturbance due to the absence of both humans and other terrestrial mammals, plus a mild oceanic climate. Most natural disturbance events in New Zealand (vulcanism, earthquake, drought, windthrow, snowbreak, fire) would have had return times on the order of many decades to millennia at any spot, giving ample time for woody plants to dominate. For example, McGlone (2001) estimated the return time for pre-human fire at c. 2000 years. Overseas, the actions of mammals (including ungulates and burrowing rodents) cause disturbance on a return time of months to a few years, creating many gaps for short-lived plants to colonise (e.g. Grubb et al. 1982). The New Zealand mainland previously had many burrowing seabird colonies, but these do not create

good habitat for annual plants. Seabird colonies concentrate such heavy disturbance in a small area around the nests that even annual plants rarely prosper (Bellingham et al. 2010) and these impacts would have been concentrated in a small minority of fixed lowland sites. This contrasts with widespread but lower-intensity mammalian burrowing and trampling in grasslands and savannahs overseas. Forsyth et al. (2010) also emphasise that deer likely represent a much greater trampling disturbance to New Zealand forest understoreys than moa due to double the foot pressure and higher densities.

For animals, disturbance *per se* is less important than adult mortality, so it seems logically inescapable that the absence of the whole guild of nocturnal predatory vertebrates (snakes, whose absence from New Zealand is rarely emphasised, and mammals) must have reduced rates of adult mortality. This reduced mortality could result from both a reduction in the total number of predators per unit area (since snakes are poikilothermic, a greater biomass of them can be supported by a given prey population), and, perhaps, by allowing prey animals to specialise in ways that more effectively reduced vulnerability to the predator guilds that were present. For example, becoming cryptic and nocturnal is an effective strategy against raptors but ineffective against nocturnal mammals (Innes et al. 2010) and snakes. The only nocturnal predators of birds in pre-human New Zealand were two owls (which hunted by sight and sound, not smell and body heat). Nesting adult birds will also be more at risk from nocturnal than diurnal predators, since the adult is permanently on the nest at night. Hence, we suggest that having few predator guilds reduced the mortality rates of adults (either absolutely or relative to juveniles), increasing the relative value of RRV over current reproduction, and favouring longer life and lower reproductive allocation. It is known that native birds currently reach higher densities in mammal-free sanctuaries (Innes et al. 2010), which would increase competition for food and could reduce the relative survival of offspring compared to adults. Greater competition for food also increases selection for fewer, larger offspring, a trend seen in some New Zealand birds which have clutches of few, relatively large eggs (Heather & Robertson 1997), and in snails (see above).

The key consequence of the difference in tolerance of disturbance or predation between the native and exotic biotas is that New Zealand has markedly bimodal communities – a kind of biological apartheid with disturbed rural and urban habitats dominated by naturalised or domesticated plants, birds, fungi and insects, whereas minimally disturbed sites are dominated by native species. The high RRV/high longevity strategy of the New Zealand biota helps explain the relative scarcity of natives in human-modified habitats. An important question is whether low-disturbance native communities are largely safe from invasion, because native species' high-RRV life histories make them superior competitors under low-disturbance conditions (Jesson et al. 2000). Large areas of old-growth native forest are currently widely invaded by few weeds (e.g. *Mycelis muralis*, *Hieracium lepidulum*; Wiser et al. 1998), few exotic fungi (Johnston 2010), and few introduced birds (most notably blackbirds *Turdus merula* and chaffinches *Fringilla coelebs*; Heather & Robertson 1997). There are also few exotic invertebrates common in old-growth forest across groups as diverse as lepidopterans, beetles and earthworms (Brockerhoff et al. 2010). The only exotic animals which currently have thoroughly penetrated native forest are mammals (King 2005) and social hymenopterans (*Vespula* spp. and *Apis mellifera*; Brockerhoff et al. 2010).

It may be premature to conclude that these old-growth

forests will not be invaded eventually by numerous forest-adapted naturalised plants and invertebrates, since the invasion of low-disturbance habitats is inherently slow and most forest-adapted exotic plants and invertebrates have been in the country for less than 150 years (Lee et al. 2006; Brockerhoff et al. 2010). Lee et al. (2010) speculate that the widespread presence of naturalised vertebrates, especially mammals, in these habitats may even facilitate invasion by weeds. Consistent with this, a global meta-analysis by Parker et al. (2006) showed that exotic generalist herbivores had strong negative effects on native plants, reducing competitive barriers to exotic plant invasion.

There are two other interesting consequences. Firstly, the life history emphasis on RRV which depends on high adult survival means that management of threatened species has to allow for the much greater impacts of losing adults than losing reproductive attempts (e.g. Elliott 1996, but c.f. Tocher 2009). Secondly, the great longevity of plants could explain the high incidence of mast seeding in New Zealand (Webb & Kelly 1993), including in herbaceous plants (e.g. *Chionochloa*, *Phormium*, *Aciphylla*), a group which rarely shows masting overseas. Mast seeding is only a viable strategy for species that live many decades to centuries (Kelly & Sork 2002); perhaps New Zealand has more plant species that live long enough for mast seeding to be selectively advantageous. If so, that is another indirect way in which the absence of terrestrial mammals, including humans, has made the New Zealand biota globally unusual.

Goodbye Gondwana: A new appreciation of long distance dispersal

Recent advances in palaeontology and molecular phylogenetics have revealed in unprecedented detail how species have come and gone throughout New Zealand's past. New Zealand has moved from "Moa's ark", a biota dominated by elements of uninterrupted Gondwanan antiquity, to what Matt McGlone (2005) described as "the fly-paper of the Pacific" (see also Trewick et al. 2006; Wallis & Trewick 2009). The greatest challenge to the Gondwanan perspective is the current lack of direct geological evidence for *any* of New Zealand being above water during the peak of the Oligocene marine transgression (Trewick et al. 2006; Landis et al. 2008). However, the persistence of ancient endemic New Zealand lineages of limited dispersal ability, such as moa (Cooper et al. 2001; Haddrath & Baker 2001), along with fossil and molecular evidence, has many biogeographers arguing that land must have been continuously present in Zealandia (Tennyson 2010, McDowall 2010).

Several studies of more recent epochs have highlighted the ephemeral nature of New Zealand ecosystems and the extraordinary dispersal abilities of many taxa on a timescale of hundreds of thousands to millions of years (Pole 1994; McGlone 2006; Trewick et al. 2006). For example, the Chatham Islands, 650 km from the New Zealand mainland, are now thought to have been above the sea for only the past 1–3 million years, and in that time have accumulated a broad diversity of species including freshwater fish, lizards, and flightless insects and including many now endemic species and subspecies (Trewick et al. 2006). The antiquity of the extant New Zealand *Nothofagus* species, once a textbook example of vicariance biogeography and Gondwanan origins, is now in doubt (McGlone et al. 1996; Knapp et al. 2005). New Zealand's two takahe species (*Porphyrio hochstetteri*, *P. mantelli*), both large-bodied and flightless and the latter now extinct, are suggested to have evolved from separate Australian arrivals (Trewick 1996).

The mighty moa-hunting Haast's eagle, *Harpagornis moorei*, the largest eagle in the world until its extinction following Polynesian settlement, was so closely related to Australia's smallest eagle, *Hieraetus*, that they may have diverged less than 2 million years ago (Bunce et al. 2005).

The power of trans-oceanic dispersal, given sufficient time, has been further underscored by the continued natural establishment of Australian species into urban and rural habitats in New Zealand (McGlone 2006, Tennyson 2010) plus ongoing records of stragglers blown across the Tasman. For example, one Australian willie wagtail, *Rhipidura leucophrys*, was recently found on a Chatham Island beach, 3,000 km from home (Gummer 2002). The introduction of foreign bird species into New Zealand has shown that establishment is likely only with a large number of releases and/or released individuals (Forsyth & Duncan 2001), underscoring that transient long-distance dispersal events must greatly outnumber successful long-distance establishment events. Infrequent long-distance dispersal must explain the increasing number of close genetic connections being discovered between many New Zealand species and those of other southern land masses. However, variation in long-distance dispersal seems insufficient alone to explain why some groups (e.g. *Coprosma*) so readily speciate into endemic forms across the Pacific while others (e.g. *Dodonaea viscosa*) remain the same species over similar areas.

It is important to keep this more dynamic view of New Zealand's past in perspective. While species have come and gone more frequently than was believed 20 years ago, the rates of species arrival and turnover are still vastly less than those since people arrived. For example, in over 2 million years prior to human arrival, the Chatham Islands had accumulated 392 plant taxa (de Lange et al. 2008a), 64 breeding bird species (including recent extinctions; Miskelly 2008), and 283 beetle species (Rowan Emberson, pers. comm.). In the 500 years since human settlement, it has accumulated a further 396 wild plants (de Lange et al. 2008a), 16 breeding birds (Miskelly 2008), and 39 beetles (Rowan Emberson, pers. comm.). Since the bulk of the new species arrived subsequent to European settlement 218 years ago, this represents an increase in the successful invasion rate by three to four orders of magnitude.

Improved pest control and species management

The past 20 years have seen a dramatic improvement in technologies to detect, control, and eradicate pests, culminating in the eradication of rats from the 11 216 ha subantarctic Campbell Island (Bellingham et al. 2010). These advances have been due to better poisons, improved baits, GPS-precision bait delivery, and predator-proof fencing. Buoyed by many offshore successes, New Zealand conservationists are thinking big. "Mainland islands", sites on the North and South Islands intensively managed to dramatically reduce pest abundance and diversity, have been appearing across New Zealand, often established by local communities. There is also now a market internationally for New Zealand's mammal-killing expertise, e.g., a Landcare Research team is currently investigating the feasibility of beaver eradication from southern South America.

Alongside successes in mammalian pest control have been successes translocating threatened species back into areas of their past range. North Island kokako (*Callaeas cinereus wilsoni*, previously *C. cinerea wilsoni*), a threatened endemic bird from an endemic family, is a leading example. In 1986, there were about 350 pairs (Innes 2008), the population was

still in decline (Rasch 1992), and the relative contributions of mammalian predation and competition to this decline were still unresolved (Leathwick et al. 1983). Predation has since been shown to be the major factor in kokako decline (Innes et al. 1999), as it has for most native forest birds (Innes et al. 2010). Control of mammalian predators, particularly ship rats and possums, has been implemented in much kokako habitat, using a wide array of poisons and traps (Innes et al. 1999; Sinclair et al. 2006). In the predator control areas, kokako numbers are increasing (about 770 pairs in total in 2008, Innes 2008) and kokako from predator-control areas have been successfully translocated into two existing bottlenecked populations, six islands, and four parts of their former range (L. Molles, pers. comm.). These include the return of kokako to East Cape in 2005 after an absence of 30 years (Molles et al. 2008) and to Secretary Island, Fiordland, in 2008, returning kokako to the South Island (the South Island kokako subspecies is presumed extinct).

There have also been dramatic successes controlling invasive invertebrates and plants. For example, mistflower (*Ageratina riparia*), a dominant and fast-spreading riparian environmental weed in northern New Zealand, was successfully biocontrolled by a specialist rust and gall fly, and subsequent monitoring showed its replacement by native plants (Barton et al. 2007). The New Zealand Biosecurity Act 1993 has seen dramatic advances in the biosecurity capacity of national and regional government agencies. Immediate action by these agencies have successfully eradicated incipient populations of a wide range of pests, including internationally notorious pests such as red imported fire ant (*Solenopsis invicta*), gypsy moth (*Lymantria dispar*; Brockerhoff et al. 2010), mile-a-minute vine (*Polygonum perfoliatum*), and kudzu vine (*Pueraria lobata*, the last tubers of which are currently being targeted; John Mather and Andy McKay, pers. comm.).

While efforts to detect, eradicate, and control pests have advanced considerably, the continuing invasion pressure on New Zealand remains a major challenge for ecologists (see below). Important pests have slipped through the net and established (e.g. Argentine ant, *Linepithema humile*, and varroa mite, *Varroa destructor*) and efforts are ongoing to eradicate others (e.g. the southern saltmarsh mosquito, *Ochlerotatus camptorhynchus*, a vector of the human Ross River virus). Meanwhile, thousands of established invertebrate, plant, and fungi species continue to spread and ecologists struggle to develop effective control measures against the worst of them (Allen & Lee 2006).

Three major challenges

Continuing declines of species

While populations of some critically endangered, charismatic birds like kokako and kakapo are increasing due to intensive management, and a small handful of species thought extinct were rediscovered (including a large flightless weevil thought extinct for 80 years, Young et al. 2008), hundreds of other native species are still in decline. Innes et al. (2010) report that most native forest bird species remain in decline, partly because sanctuaries of various kinds with multi-species pest control (with and without fences) still only occupy 0.24% of New Zealand's mainland area. The situation for vascular plants is also worsening: 6 species are now extinct and, excluding naturally uncommon species, 11.4% of the vascular flora is classed as Threatened or At Risk (de Lange et al. 2008b). New

discoveries and advances in systematics, fuelled by molecular technology, have added species to lists of threatened species (e.g. orange-crowned parakeet, *Cyanoramphus malherbi* (Boon et al. 2000), and the Canterbury Plains small-leaved tree daisy, *Olearia adenocarpa* (Heenan & Molloy 2004)) and extinct species (e.g., the North Island takahe (Trewick 1996), and the Waitaha penguin (Boessenkool et al. 2009)). Species continue to decline despite the many advances in New Zealand ecology and conservation in the past 20 years and the implementation of national and regional governmental biodiversity and biosecurity strategies.

The threat posed by mammalian pests to New Zealand's remaining native bird species in intact wildlands (Innes et al. 2010) should not distract us from the great many threatened or locally extinct species increasingly displaced in lowland agricultural and urban landscapes (de Lange et al. 2008b). Habitat modification is a key driver of species loss (Kingsford et al. 2009) and there is improved awareness of extinction debts for native species in modified landscapes (Tilman et al. 2002). However, in New Zealand's lowland areas with the most extensive habitat loss and the highest densities of threatened species, there is little effective protection under the Resource Management Act for threatened species on private land, and even on Government-owned land, reviews of leasehold areas ("tenure review") continue to prioritise economic uses over environmental protection (Walker et al. 2008). Clearly, more needs to be done. Increasing climate change, agricultural intensification, and invasions (see below), will increase the pressures on wild populations of native species in lowlands already struggling in reduced amounts of habitat. Many native plants will need help to return to landscapes when suitable land-use changes are made, since the ranges of many New Zealand plant species are more limited by dispersal than environment (McGlone et al. 2010) and both pollination and seed dispersal are now less effective due to loss of native birds (Innes et al. 2010; Kelly et al. 2010).

Finding ways to reverse the decline of New Zealand native species will require new pest control technologies, increased public support for intensive targeted pest management in selected wildlands, and, just as importantly, the restoration and reconciliation of urban and rural New Zealand with native species. All are substantial challenges.

Invasions and biosecurity

New Zealand is one of the most invaded places in the world (Allen & Lee 2006), thanks to the unfortunate coincidence of widespread anthropogenic habitat disturbance and extinctions, a biota adapted to low levels of disturbance (see above), a benign temperate climate, a European settler culture dedicated to species introductions, and an economy dependent on global trade. In response to the many pests and weeds amongst these invaders, New Zealand has implemented some of the world's strictest biosecurity legislation and institutional processes (Williams 2000; Allen & Lee 2006). For example, introducing any novel species now requires evaluation and approval by the Environmental Risk Management Agency under the Hazardous Substances and New Organisms Act 1996. As mentioned above, these biosecurity systems have prevented the establishment of some of the world's worst pests. However, new pest incursions are continuing and post-border surveillance and rapid response technologies are being improved to cope.

The continuing incursions are well illustrated by live scorpions found in Auckland International Airport in 2005 (Stokes 2005) and in Queenstown in 2008 (Morris 2008). The

goal is to prevent such isolated incursions leading to established populations. Similarly, live snakes have been intercepted at the border. Snakes need to be excluded indefinitely (see above), and we are confident that there would be rapid reporting and broad public support for a major control operation against any incipient wild snake population. Indefinite exclusion is less certain for the likes of red imported fire ants or Asian tiger mosquitoes (both of which have been detected and controlled around ports) and unlikely for a large number of low-priority species. Delaying the arrival of important pests by decades is likely sufficient economic justification for New Zealand's current investment in biosecurity. However, the distinctiveness of New Zealand's native biota means that there is an ecological imperative to exclude some species indefinitely. Doing this despite New Zealand's economic dependence on global trade will require smarter or more intrusive biosecurity.

Hundreds of species continue to naturalise despite New Zealand's biosecurity systems, fuelled by increasing global trade and New Zealanders' obsession with gardening. More than twice as many shipping containers arrive annually at New Zealand ports now as in 1989 (Williams 2000). Consequently, the naturalised insect fauna continues to grow (Brockerhoff et al. 2010), despite border biosecurity and some effective eradications (e.g. aerial insecticide spraying of urban centres during three lymantriid incursions). For example, New Zealand now has at least 120 aphid species, of which only 13 are native, and while the rate of invasion has dropped markedly since the late 1980s, new aphid species continue to naturalise every few years (Teulon & Stufkens 2002). This included the economically important lettuce aphid (*Nasonovia ribisnigri*) in 2002.

Unlike most new animal pests, almost all new pest plants (weeds) come from cultivated sources in New Zealand. The rate of new plant naturalisations continues to rise (Howell 2008; Gatehouse 2008), with the naturalised vascular flora now at least equalling the native flora nationally and well surpassing it in Auckland City (Esler 2004). In the decade 1990-99, 164 plant species naturalised, 150 of ornamental origin, and including 78 shrub and tree species (twice the long-term average rate of woody naturalisations) (Gatehouse 2008). The future of weeds looks increasingly woody, with unknown implications for New Zealand forests and forest succession.

There has been a gradual transition in biosecurity management from a focus on the most widespread, established pests to the early detection and eradication or containment of incipient pests. However, there are too many naturalised species in their early stages of spread to contain them all, especially plants, insects, and fungi. There is urgent need for better tools for estimating the likely ecological and economic impacts of these species to better set priorities and justify pre-emptive control. There is also urgent need for better technologies to detect and control incipient populations of a wide range of known and potential pests – everything from marine tunicates to freshwater algae to soil fungi.

A cautionary tale here on the difficulty of eradication post-arrival is Dutch Elm Disease, which was discovered in Auckland in 1989 and Napier in 1993. A national eradication programme was initiated that removed the disease from Napier and seemed to be nearing success in Auckland by 1999/00 (Fig. 1), leading Gadgil et al. (2000: 197) to say that Dutch Elm Disease "in New Zealand is under control, and its eradication is a distinct possibility, provided that the current surveillance and tree removal programme is maintained". Unfortunately, pheromone trapping of the beetle vector in Auckland was

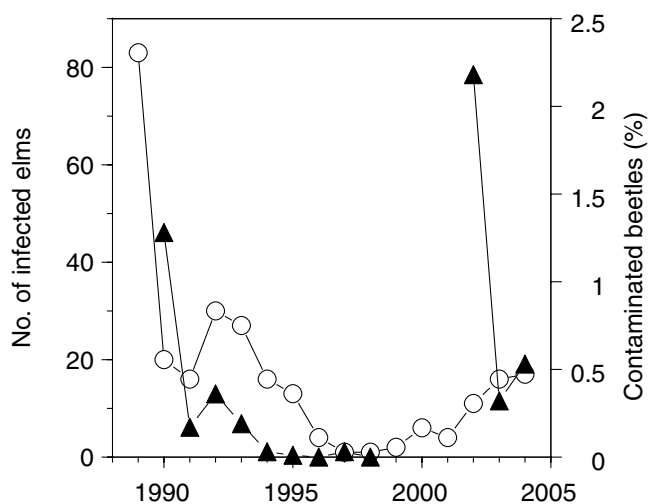


Figure 1. The near-eradication of Dutch Elm Disease from Auckland: infected trees removed (circles) and percent of pheromone-trapped beetles carrying the causal fungus (*Ophiostoma novo-ulmi*) (triangles). Few infective beetles were caught between 1995 and 1998, so pheromone trapping was stopped for three seasons, and during this time the disease rebounded. The national eradication programme was abandoned in 2008 but continues under local government control. “1990” refers to the 1990/91 season. Redrawn from Bulman (2005).

suspended from 1999/00 to 2001/02, during which time the disease rebounded (Fig. 1; see www.nzffa.org.nz archive of reports from Forest Health newsletters, accessed October 2009). The rebound has certainly made eradication more difficult, but it is unclear whether maintaining pheromone trapping 1999–2002 would have helped prevent the rebound. In 2008 Biosecurity New Zealand ceased central Government funding for the eradication campaign, and the programme is continuing with city council funding. Perhaps the key lesson is that funding only 90% of an eradication campaign might waste 100% of the money. The final stages of eradication campaigns can be expensive: for example, when eradicating possums from Kapiti Island, it cost \$50,000 to kill the first 11,500 possums, but \$220,000 to kill the last 80 (Cowan 1992). However, it is very dangerous to scale back funding before eradication is confirmed. As noted above, there is a clear need for better tools for detecting invaders at very low densities (Russell et al. 2008).

While there is a strong ecological and economic imperative to focus on excluding or containing new pests, the ecological impacts of the long list of invaders already here remains poorly understood, and will only become obvious over the next decades and centuries. There is much still to be gained from containing or slowing the spread of established pests, buying time to better understand their impacts and develop better control methods.

Accelerating human impacts and climate change

In this final section we attempt to anticipate the most important threats to biodiversity over the coming 50–100 years. Traditionally there has been a focus in New Zealand on introduced species as threats to biodiversity (see previous section; Allen & Lee 2006; Innes et al. 2010; Forsyth et al. 2010) but a recent review (Kingsford et al. 2009) emphasises that habitat loss and overexploitation remain important locally and globally. Both these drivers seem likely to increase over

the 21st century because of increasing human population and resource use and the consequent need for increased food and fuel production, combined with reduced availability of cheap fossil fuels and disruptions to ecosystems from global change. Conservation programmes have been successful in preventing rare species from tipping over the edge to extinction (Brooke et al. 2008), but few of those species are out of danger, and social disruption due to the above drivers could see extinction rates climb again.

Globally, human population size and the direct impacts of humans are key drivers that perhaps get less scientific attention than they deserve. Human population size has doubled from 3 billion in 1959 to about 6.7 billion in 2009 and is forecast to peak, barring catastrophe (which is not assured), at about 9 billion in mid-century. This implies a need for a substantial increase in food production between 2009 and 2050. That will be difficult given that a number of the world’s crop-growing areas are suffering desertification, salinisation, exhaustion of fossil groundwater, and topsoil loss (Pimentel & Giampietro 1994). Crop yields have increased less rapidly than population since 1990, and are heavily dependent on large inputs of fossil fuels, but “peak oil” is either close or perhaps already here (MacKenzie 2008; Hall & Day 2009). Global fish catches peaked in the late 1980s with a majority of fish stocks now fully or over-exploited; deep-sea fishing is heavily dependent on fossil fuels, and aquaculture has increased but most farmed fish are fed wild-caught fishmeal (Pauly et al. 2002). Of course, such dire predictions have been made before and not yet come to pass, but a recent analysis shows that we are still on the trajectories predicted in the 1971 Club of Rome report, just now very much closer to the crunch points (Hall & Day 2009). The likely consequence of this search for more food, combined with accelerating demand for biofuels, is an increased rate of conversion of marginal land to agriculture and more over-exploitation of animal populations, with consequent impacts on biodiversity.

How these factors might affect New Zealand is uncertain, but we venture some predictions. For food production, New Zealand is relatively well off at present, but has a rapidly growing population for a developed country (up 85% since 1959 and projected to reach 5 million by 2028 according to Statistics New Zealand), and farming is heavily dependent on imports of fossil fuels. If global food scarcity drives up food prices, this is likely to increase conflicts over the environmental impacts of agriculture such as water extraction, stream nutrient loadings, and the clearance of native habitats on private land (as has happened with the recent increase in dairy prices). In addition, if food is globally scarce such conflicts will acquire moral as well as economic dimensions, increasing pressure to favour agriculture over native biodiversity.

An inter-related second major threat is global change from anthropogenic emissions of greenhouse gases. Substantial changes to global climate are almost certain and some are likely to be irreversible for centuries and of large impact, including, notably, an increase in droughts in mid-latitudes which could reduce food supply (Solomon et al. 2009). Preventing climate from entering runaway feedback loops will require large and rapid (within 10–20 years) reductions in greenhouse gas emissions (Monastersky 2009), yet there has been almost no effective political action since the Kyoto Protocol in 1990 (Anonymous 2009). There are three ways in which this could affect biodiversity. Primary impacts are factors like alpine species running out of mountaintop, species restricted to isolated reserves being unable to migrate to match their climate needs, local species being out-competed by

more climatically matched invasive species, and (eventually) “coastal squeeze” where coastal species are caught between coastal development and rising sea levels. Secondary impacts act via human population pressure for more food in the face of droughts. Tertiary impacts are those acting via disruption of social systems that currently fund and support conservation management.

An evaluation of the likely impact of global change on New Zealand biodiversity must begin by recognising that some of the consequences of global change will be unstoppable within decades, yet take centuries to fully develop, due to physical and biological lags. This means that short term impacts (before 2050) are likely to be dominated by secondary effects via human food production described above, while longer-term impacts include more primary effects of elevated temperatures and CO₂, changed rainfall, and higher sea levels. A review for the Department of Conservation of likely impacts (McGlone et al. 2009) showed that temperature has risen little (c. 0.2° C) in New Zealand over the last 40 years, probably because of buffering by the strongly oceanic climate, and in contrast to more rapid warming in the arctic, continental northern hemisphere and Antarctic Peninsula. Because of the slow local rate of warming, and/or inadequate baseline data pre-1950, there are few unequivocal changes known to be already occurring. For example treelines have scarcely risen in New Zealand to date, compared to an expected rise of around 100 m vertically from the 0.9° C warming observed in New Zealand since the year 1900. McGlone et al. identified long-term threats through loss of habitat for alpine species; coastal squeeze with rising sea levels (already up by 0.16 m in the 20th century); and from phenological changes such as alterations in mast seeding cycles changing ecological balances (e.g. McKone et al. 1998; Kelly et al. 2008). However, they concluded that some of the strongest short-term (to 2050) threats come from enhanced impacts of invasive species already in the country, such as wilding pines and mammalian predators (McGlone et al. 2009).

An interesting point of great future importance for tourism and international marketing of New Zealand exports is that our “clean and green” image is untrue for greenhouse gases (GHGs). New Zealand has among the highest annual per capita greenhouse emissions in the world with a 2003 total of 19.3 tonnes of CO₂ equivalent (Atkinson 2007), not far behind the USA and Australia (who in September 2009 were reported as producing 20.6 tonnes to overtake the USA for top spot). The high New Zealand total is partly (c. 48%) due to high emissions of methane and other GHGs from agriculture, but even without those our emissions per capita would still exceed those of Britain (Atkinson 2007). New Zealand has one of the highest rates of car ownership per capita in the world, and since 1990 total vehicle-kilometres travelled increased by 48% from 27 to 40 billion km/year. Over the same period average house size increased 39% (from 140 to 195 m²) so we now have the third-largest houses in the world (again behind the USA and Australia). Thus, New Zealanders have disproportionately large impacts on global climate.

Given New Zealand’s need to protect its international reputation, as well as minimise deleterious changes in climate, we hope it will take rapid action to limit production of GHGs. The technical solutions are already largely obvious and New Zealand has a number of natural advantages (McGlone et al. 1990; Atkinson 2007). In 1990 McGlone et al. (1990: 113) wrote that New Zealand was in a very fortunate position to reduce our climate impact, due to our temperate climate, pasture-based agriculture with nitrogen fixation by clover,

and hydro-dominated electricity system. That remains true, but between 1990 and 2009 the country has moved strongly away from sustainability, as the indicators above attest. The political debate at least until late 2009 has been dominated by delay, extremely modest targets, an aversion to effective economic mechanisms, and in some political circles outright denial of the underlying science.

Changes in New Zealand culture and policies in the next two decades will be more important for conservation than the direct impacts of global warming. Public support for conservation has been strongest when people’s lives have been unaffected. New Zealand’s extensive national park network, mostly on steep, high-rainfall landscapes with few economic uses, contrasts with its meagre dryland and coastal marine reserves. The protection of most native birds contrasts with the legal harvesting of declining grey ducks, *Anas superciliosa superciliosa* (Wright et al. 1995) and there are practically no restrictions on salmonid releases (the Department of Conservation even manages the Tongariro National Trout Centre) despite convincing evidence that they are driving declines in threatened native fish (McIntosh et al. 2010). New Zealand, like most countries, has struggled to conserve native species in economically important rural, urban, and marine habitats, and public support is not assured with growing pressure to further intensify agriculture and fisheries and convert marginal land for new biofuel and carbon crops.

Clearly the next 30 years will be crucial for determining trends in climate, and biodiversity change, for the next several centuries. Ecologists will have major roles to play in much of this, but perhaps necessarily with a much more applied emphasis. Day et al. (2009) argue that we will need more work on how human needs can be met while minimising GHG emissions and damage to biodiversity. We need to forgo the luxury, enjoyed for the last half-century, of pursuing more esoteric and non-applied questions.

Other advances and challenges

The listed areas of progress and challenges could both be greatly extended, and other authors might have focused on other topics. For example, the greater sophistication of computer modelling has allowed some novel insights in subjects as diverse as *Nothofagus* responses to global change (Richardson et al. 2005), environmental controls on scale-insect honeydew production (Dungan et al. 2007), and competition intensity in unmanipulated forests (Coomes & Allen 2007). A second advance is the ability to collate and share large datasets, such as the National Vegetation Survey (NVS) database which has allowed, for example, sophisticated estimates of the effects of climate on forest cover (e.g. Leathwick & Austin 2001). Also, ecology in New Zealand, as elsewhere, has been hugely assisted by rapid progress in statistics and databases. One key advance is the widespread availability of open-source statistical software such as R (R Development Core Team 2009), which implements Generalised Linear Models for appropriate analysis of poisson and binomial data, which are common in ecology.

Similarly, there are important challenges we have not discussed at length. These include the issues of data maintenance, institutional structure, and funding. Long-term studies in New Zealand are not explicitly supported by the current funding system, which emphasises short-term contestable grants. Consequently, some valuable long-term

studies were terminated, such as the then-longest seedfall data set in the world (*Dacrydium cupressinum* on the West Coast: Norton & Kelly 1988), or are under threat of termination, such as monitoring in the Orongorongo Valley near Wellington where much valuable long-term work has been sited (e.g. Cowan et al. 1997; Fitzgerald & Gibb 2001; Efford et al. 2006; Monks & Kelly 2006). We suspect that the fundamental problem is the overall low level of investment in research and development in New Zealand, a point stressed in a series of talks during 2009 by Professor Sir Peter Gluckman, the new scientific advisor to the Prime Minister.

Conclusions

The past 20 years have given us a much clearer view of New Zealand as it was before people arrived and sharpened our understanding of its subsequent transformation. Since 1989, it's been "goodbye Gondwana" and "hello New Zealand". The challenge now is to avoid "goodbye New Zealand" by refining and applying our ecological knowledge to sustain and restore native species in New Zealand's increasingly modified and invaded landscapes. We also must contribute to the global struggle to reconcile a human population increasing in both numbers and affluence with the protection of the other species sharing planet Earth.

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Some exotic weeds of woody habitats (clockwise from top: *Tradescantia fluminensis*, *Vinca major*, *Cytisus scoparius*, *Rubus fruticosus*, *Zantedeschia aethiopica*, *Hedera helix*, and *Ilex aquifolium*), drawn by Liz Grant (<http://www.artbyliz.co.nz/>) for the cover of *New Zealand Journal of Ecology* 15(2) 1991.