special issue:
Feathers to Fur
The ecological transformation of Aotearoa/New Zealand

Feathers to Fur: the status of New Zealand ecological research in 2009

Jon J. Sullivan[1], Dave Kelly[2], Jenny J. Ladley[2]
[1] Bio-Protection Research Centre, PO Box 84, Lincoln University, Lincoln 7647, New Zealand, email: tabebuia@alumni.upenn.edu [2] School of Biological Sciences, University of Canterbury, Christchurch 8140, New Zealand

Published online: 6 October 2009

Abstract: We outline the scope of this special issue of *New Zealand Journal of Ecology*, which reviews progress in New Zealand ecology to 2009, based on a symposium in 2007. Both the issue and symposium update a 1986 conference and 1989 special issue of *NZ J Ecol* called "Moas, Mammals and Climate" which has been influential and widely cited. This issue revisits several themes featured in 1989, including the extent of recent and prehistoric extinctions in the New Zealand fauna; effects of introduced mammalian herbivores replacing now-extinct browsing birds such as moa; the impacts of introduced mammalian predators on native birds (hence the *Feathers to Fur* title); the role of islands as refuges and opportunities for restoration; and the status of bird-plant mutualisms like pollination and fruit dispersal. Several topics not discussed in 1989 are raised, including the unusual size and functional composition of New Zealand's tree flora, and several taxonomic groups (invertebrates, fungi) and habitats (fresh waters) that received little attention in 1989. We summarise four symposium talks which are not included elsewhere in this issue. New Zealand leads the world in ways both unenviable (e.g. levels of impact of introduced species) and enviable (e.g. predator eradication, translocations, rare species management). The recent advances reviewed in this issues have relevance well beyond New Zealand.

Keywords: conservation, disturbance, eradication, extinction, fish, fungi, herbivory, invasions, *Rattus exulans*, trees

Introduction

In the 1980s, progress in ecology in New Zealand was reviewed by a conference symposium (at the 1986 annual conference of the New Zealand Ecological Society) and subsequent special issue of the New Zealand Journal of Ecology (1989, volume 12 supplement), both entitled "Moas, mammals, and climate in the ecological history of New Zealand". These were landmark events, and the 1989 special issue has become the most cited in the history of the journal (see below). A generation later we decided it was time to once again take stock and produce a synthesis of ecological research into important drivers of ecological change, including the implications of this for New Zealand and for global ecology. This special issue and the 2007 conference, again both sharing a single title, "Feathers to fur: the ecological transformation of Aotearoa", reflect on 20 years of progress in New Zealand ecological research. For "Feathers to Fur", we expanded the scope of the 1986 conference to encompass past and present changes to New Zealand's flora, fauna, and fungi in general, and our understanding of the processes driving these changes. While the conference title was suitably alliterative, it was never intended to imply a focus solely on birds and mammals; McIntosh et al. (2010) suggested "mucous to scales" would be a better summary of the fish changes.

More than almost any other land mass, New Zealand's biota has experienced substantial, almost schizophrenic, rates and amounts of ecological change. New Zealand's natural environment has been through the freeze-thaw pendulum swings of the Quaternary glacial-interglacial cycles, mountain building and erosion, frequent massive earthquakes, and some of the largest volcanic eruptions documented. The last 20 years of ecological research have greatly improved our understanding of how these disturbances shaped the New Zealand biota, including surprises such as the extent of maximum marine transgression in the Oligocene when it has been seriously suggested that all of Zealandia might have been underwater (Landis et al. 2008, but c.f. Tennyson 2010, McDowall 2010), accumulating evidence against the ancient Gondwanan ancestry of many New Zealand taxa (McGlone 2005), and the discovery of a fossil mammal from the Miocene (long after New Zealand's separation from Gondwana) (Worthy et al. 2006; Tennyson 2010).

While the New Zealand biota was well used to environmental change, the recent arrival of people with their associated species and fire has caused an unprecedented ecological transformation. Hugh Wilson (2008) likened it to a harpoon hitting a whale. The transition of the vertebrate fauna from feathers to fur, with at least 58 bird extinctions and 31 mammalian introductions since human arrival (Tennyson

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.nz/nzje/.

2010), is just one of the most visible of a great number of interrelated changes. Because people arrived in New Zealand so very recently (c. 1280 AD: Wilmshurst et al. 2008), and because so many novel taxa arrived with them, New Zealand is one of the most detailed examples in the world of the ecological changes caused by humans, both indigenous and European, to naive biotas (e.g., Worthy & Holdaway 2002; Wilson 2004; Allen & Lee 2006). Similar changes probably occurred in all other areas invaded by humans, but the record has either been largely lost through the passage of time, or is only now being uncovered as in the case of bird losses throughout the Pacific (Steadman 1995, 2006).

The "Feathers to Fur" conference and this special issue review how much we've learned about these changes to New Zealand, and look to the many challenges ahead. In this preface to the issue, we briefly summarise the history of these two milestone conferences, and outline additional contributions to the 2007 conference which are not represented as papers in this issue.

A Brief History

The 1986 conference and 1989 journal issue stand as a milestone in New Zealand ecology. The conference, held in Lincoln College (now Lincoln University) on 2–5 September, included a two day symposium and two days of contributed papers. Sixteen of these papers were published in the 1989 special issue of the *New Zealand Journal of Ecology* (issue 12 supplement), which includes four of the journal's ten most cited papers based on ISI Web of Science (McGlone 1989; Holdaway 1989; Clout & Hay 1989; Atkinson & Greenwood 1989). Eight of the issue's 16 papers are among the top 100 most downloaded articles from the journal website since 2003, more than from any other single issue of *New Zealand Journal of Ecology* or its predecessor the *Proceedings of the New Zealand Ecological Society*, and including four of the top ten most downloaded papers (McGlone 1989; Holdaway 1989; Clout & Hay 1989; Anderson 1989). Jared Diamond (1990) wrote an overview of the special issue in *Nature*.

The common themes running through the symposium and special issue were ecological changes brought about by human hunting, burning and grazing, the extinction of moa and other birds, and the invasion of predatory and herbivorous mammals. Among the notable ideas debated were the suggestions that some growth forms disproportionately common in the New Zealand flora, particularly divarication, were adaptations to resist and tolerate moa browsing (Atkinson & Greenwood 1989), that the largest-fruited New Zealand native trees were now virtually reliant on one bird species, the kereru *Hemiphaga novaeseelandiae*, for seed dispersal (Clout & Hay 1989), and that deer might be ecologically partly analogous to moa in their impact on native vegetation (Caughley 1989). These latter two topics featured again in Feathers to Fur (Kelly et al. 2010, and Forsyth et al. 2010, respectively).

The changes in New Zealand ecological research since the 1980s are evident in the common words and phrases used in the full text of all *New Zealand Journal of Ecology* articles from the 1980s and 2000s (Fig. 1). Notable examples of groups of words and phrases that more than doubled in usage between the 1980s and 2000s, as a proportion of all words in that decade, are databases ("database(s)", "data base(s)") (increased 6.5×), fragmentation ("fragmentation", "edge effect(s)", "habitat loss", "habitat modification", "deforestation")

Figure 1: Word maps of the most common words and two-word phrases used in the full text of all articles of *New Zealand Journal of Ecology* from the 1980s and 2000s (excluding common, short English words), generated using www.wordle.net. The size of each word or phrase indicates its relative frequency.

(5.4×), "conservation" (3.6×), statistics ("statistics", "anova", "regression", "glm", "bayesian", "data analysis") (2.6×), mammalian predation ("predator", "predation", "rat(s)", "stoat(s)", "weasel(s)", "ferret(s)", "mustelid(s)") (2.5×), and climate change ("climate change", "global warming", "climate warming", "greenhouse effect") (2.2×). Notable declines are divarication ("divaricate", "divaricating", "divarication") (0.5×) and moa (0.5×). Use of words and phrases associated with browsing, invasion, evolution, and behaviour changed little between the decades. Words and phrases associated with mammalian predation, browsing, and invasion were far more frequent than those associated with fragmentation and habitat loss (1980s: 28–142×, 2000s: 10–23×), and vastly more frequent than those associated with climate change (1980s: 89–444×, 2000s: 78–175×). This reflects New Zealand ecologists' ongoing emphasis on invasions and their impacts (cf Didham et al. 2007).

Feathers To Fur

The "Feathers to Fur" conference reviewed progress since 1986. A one-day symposium of invited speakers was held on 20 November 2007 at the University of Canterbury, followed by two days of contributed papers. In a notable shift from the vertebrate-focused 1986 conference, the first speaker was an insect ecologist, George Gibbs, who assessed whether New Zealand's insect fauna showed unusual features as a result of evolving in the absence of terrestrial mammals (except for New Zealand's once three, now two, bat species)(Gibbs 2010). The conference also broadened taxonomically by the inclusion of ecological changes in New Zealand fungi (Johnston 2010) and freshwater fish (McDowall 2010; McIntosh et al. 2010) and the impacts of invasive invertebrates (Brockerhoff et al. 2010).

Two topics not discussed in the 1989 issue are raised here. Huge advances in the last 20 years in the use of eradication and island refuges for conservation purposes are reviewed by Bellingham et al. (2010), and McGlone et al. (2010) discuss the unusual abundance and odd nature of the New Zealand tree flora.

Four of the "Feathers to Fur" talks are not included in this issue but add important perspectives on New Zealand's ecological transformation. Janet Wilmshurst presented work dating seeds gnawed by kiore (Pacific rats, *Rattus exulans*), which, alongside other evidence, date the first arrival of Polynesians in New Zealand at around 1280 A.D. (Wilmshurst et al. 2008). This work overturns some previous claims of longer Māori occupation of New Zealand, and means that the massive ecological transformation of New Zealand's biota has taken only 730 years. Many of the older trees in New Zealand's forests pre-date human colonisation by centuries (Ogden & Stewart 1995)!

Richard Holdaway reviewed the many advances in our understanding of moa ecology since 1986, and since the last published review (Worthy & Holdaway 2002). New technologies are leading to rapid advances in the knowledge that can be gleaned from the bones of the fallen (e.g., Turvey et al. 2005; Turvey & Holdaway 2005). As Richard put it in his conference paper, ancient DNA has opened up "a brave new ancient world" (see Haile et al. 2007). Radioisotope work is also revealing unprecedented details on what, and where, individual moa were feeding.

Richard Duncan reviewed our recent understanding of how earthquakes have shaped the composition of the forests of the South Island, causing regeneration gaps in forest age-structure that puzzled earlier ecologists (Wells et al. 1999, 2001). Dendrochronology and geological evidence show that the South Island is well overdue for a magnitude 8+ earthquake. As Richard concluded, the trees tell us that we have lived in relatively quiet times.

Leo Condron provided an important soils perspective on understanding forest change, reviewing recent soil chronosequence work on how forest ecosystems progress from nitrogen limitation to phosphorous limitation as soils age (Richardson et al. 2005; Allison et al. 2007; Turner et al. 2007).

Several themes ran through "Feathers to Fur". We now understand in much more detail how exquisitely strange was New Zealand ecology before people (or, at least, how much it was unlike the temperate Northern Hemisphere). We also have a better understanding of how extensive, and rapid, the transformation has been from this unusual outlier of global evolution to the relatively depauperate and invaded New Zealand of today. There is also now an abundance of new evidence, and growing consensus, in the old debates of 1986–1989 about whether deer are ecologically equivalent to moa ("no") and whether moa played a role in the evolution of unusual woody plant growth forms ("yes"; see Forsyth et al. (2010) and Lee et al. (2010)).

Some bibliographic indicators are revealing about trends in science 1989-2010. The papers in this issue have far more authors (3.76 per paper with only 4 of the 13 sole-authored, compared to 1.25 per paper with 12 out of 16 sole-authored in 1989) showing the increasing tendency to work in teams. As a result of the team approach and accumulating information, many of the papers in this issue are substantially longer than the equivalent treatment in 1989. Gender equality shows substantial progress off a low base: none of the 20 authors in 1989 were women, compared to 13 of 49 (27%) in this issue. While all the lead authors in this issue are men, that is only because Janet Wilmshurst's symposium talk was published elsewhere (see above).

Despite the many recent scientific advances detailed in this issue, it is also clear that many extant New Zealand native species and ecosystems remain under threat (Kelly & Sullivan 2010). The transformation of New Zealand continues. For example, most extant native forest bird species are in national decline (Innes et al. 2010), with flow-on effects on weakened pollination mutualisms (Kelly et al. 2010). New Zealanders have yet to face up to the impacts salmonid sports fish are having on native galaxiids (McIntosh et al. 2010) and our knowledge of the impacts of invasive invertebrates, fungi, and plants are still in their infancy (Brockerhoff et al. 2010; Johnston 2010). There are many challenges for New Zealand ecologists for the next 20 years, and there is no time to lose.

Acknowledgements

We thank the principal sponsors of the 2007 "Feathers to Fur" conference: Landcare Research, the Department of Conservation, and Environment Canterbury. We are also grateful to the Department of Conservation and Landcare Research for sponsoring the publication of this special issue. The conference was made possible by support from Biological Sciences at the University of Canterbury and generous inputs from the organising team: Ruth Guthrie, Jason Tylianakis, Philip Grove, Shaun Ogilvie, Lara Nicholson, Matt McGlone, Amy Whitehead, Adrian Paterson (who also suggested the

conference title), Richard Duncan, and Matthew Turnbull. We also record our appreciation to the organisers of the 1986 conference and 1989 "Moas, Mammals and Climate" special issue for their perspicacity.

References

Allen RB, Lee WG 2006. Biological invasions in New Zealand. Ecological Studies Series Volume 186, Springer Verlag, Berlin.

Allison VJ, Condron LM, Peltzer DA, Richardson SJ, Turner BL 2007. Changes in enzyme activities and soil microbial community composition along carbon and nutrient gradients at the Franz Josef chronosequence, New Zealand. Soil Biology and Biochemistry 39: 1770–1781.

Anderson A 1989. On evidence for the survival of moa in European Fiordland. New Zealand Journal of Ecology 12 (supplement): 39–44.

Atkinson IAE, Greenwood RM 1989. Relationships between moas and plants. New Zealand Journal of Ecology 12 (supplement): 67–96.

Bellingham PJ, Towns DR, Cameron EK, Davis JJ, Wardle DA, Wilmshurst JM, Mulder CPH 2010. New Zealand island restoration: seabirds, predators, and the importance of history. New Zealand Journal of Ecology 34: 115–136.

Brockerhoff EG, Barratt BIP, Beggs JR, Fagan LL, Kay MK, Phillips CB, Vink CJ 2010. Impacts of exotic invertebrates on New Zealands indigenous species and ecosystems. New Zealand Journal of Ecology 34: 158–174.

Caughley G 1989. New Zealand plant-herbivore systems – past and present. New Zealand Journal of Ecology 12 (supplement): 3–10.

Clout MN, Hay JR 1989. The importance of birds as browsers, pollinators and seed dispersers in New Zealand forests. New Zealand Journal of Ecology 12 (supplement): 27–33.

Diamond JM 1990. Biological effects of ghosts. Nature 345: 769–770.

Didham RK, Tylianakis JM, Gemmell NJ, Rand TA, Ewers RM 2007. Interactive effects of habitat modification and species invasion on native species decline. Trends in Ecology & Evolution 22: 489–496.

Forsyth DM, Wilmshurst JM, Allen RB, Coomes DA 2010. Impacts of introduced deer and extinct moa on New Zealand ecosystems. New Zealand Journal of Ecology 34: 48–65.

Gibbs G 2010. Do New Zealand invertebrates reflect the dominance of birds in their evolutionary history? New Zealand Journal of Ecology 34: 152–157.

Haile J, Holdaway R, Oliver K, Bunce M, Thomas M, Gilbert P, Nielsen R, Munch K, Ho SYW, Shapiro B, Willerslev E 2007. Ancient DNA chronology within sediment deposits: are paleobiological reconstructions possible and is DNA leaching a factor? Molecular Biology and Evolution 24: 982–989.

Holdaway RN 1989. New Zealand's pre-human avifauna and its vulnerability. New Zealand Journal of Ecology 12 (supplement): 11–25.

Innes J, Kelly D, Overton J, Gillies C 2010. Predation and other factors currently limiting New Zealand forest birds. New Zealand Journal of Ecology 34: 86–114.

Johnston PR 2010. Causes and consequences of changes to New Zealand's fungal biota. New Zealand Journal of Ecology 34: 175–184.

Kelly D, Ladley JJ, Robertson AW, Anderson SH, Wotton DM, Wiser SK 2010. Mutualisms with the wreckage of an avifauna: the status of bird pollination and fruit-dispersal in New Zealand. New Zealand Journal of Ecology 34: 66–185.

Kelly D, Sullivan JJ 2010. Life histories, dispersal, invasions, and global change: progress and prospects in New Zealand ecology, 1989–2029. New Zealand Journal of Ecology 34: 207–217.

Landis CA, Campbell HJ, Begg JG, Mildenhall DC, Paterson AM, Trewick SA 2008. The Waipounamu erosion surface: questioning the antiquity of the New Zealand land surface and terrestrial fauna and flora. Geological Magazine 145:173–197.

Lee WG, Wood JR, Rogers GM 2010. Legacy of avian-dominated plant-herbivore systems in New Zealand. New Zealand Journal of Ecology 34: 28–47.

McDowall RM 2010. Historical and ecological context, pattern and process, in the derivation of New Zealand's freshwater fish fauna. New Zealand Journal of Ecology 34: 185–194.

McGlone MS 1989. The polynesian settlement of New Zealand in relation to environmental and biotic changes. New Zealand Journal of Ecology 12 (supplement): 115–129.

McGlone MS 2005. Goodbye Gondwana. Journal of Biogeography 32: 739–740.

McGlone MS, Richardson SJ, Jordan GJ 2010. Comparative biogeography of New Zealand trees: species richness, height, leaf traits and range sizes New Zealand Journal of Ecology 34: 137–151.

McIntosh AR, Dunn NR, Goodman J, Howard SW, Jellyman PG, O'Brien LK, McHugh PA, Nyström P, Woodford D 2010. Control of interactions between trout and galaxiid fishes in New Zealand. New Zealand Journal of Ecology 34: 195–206.

Ogden J, Stewart GH 1995. Community dynamics of the New Zealand conifers. In: Enright NJ, Hill RS, eds., Ecology of the southern conifers. Melbourne University Press, Melbourne, Australia, pp. 81–119.

Richardson SJ, Peltzer DA, Allen RB, McGlone MS 2005. Resorption proficiency along a chronosequence: responses among communities and within species. Ecology 86: 20–25.

Steadman DW 1995. Prehistoric extinctions of pacific island birds – biodiversity meets zooarchaeology. Science 267: 1123–1131.

Steadman DW 2006. Extinction and biogeography of tropical Pacific birds. University of Chicago Press, Chicago, USA.

Tennyson AJD 2010. The origin and history of New Zealand's terrestrial vertebrates. New Zealand Journal of Ecology 34: 6–27.

Turner BL, Condron LM, Richardson SJ, Peltzer DA, Allison VJ 2007. Soil organic phosphorus transformations during pedogenesis. Ecosystems 10: 1166–1181.

Turvey ST, Green OR, Holdaway RN 2005. Cortical growth marks reveal extended juvenile development in New Zealand moa. Nature 435: 940–943.

Turvey ST, Holdaway RN 2005. Postnatal ontogeny, population structure, and extinction of the giant moa Dinornis. Journal of Morphology 265: 70–86.

Wells A, Duncan RP, Stewart GH 2001. Forest dynamics in Westland, New Zealand: the importance of large, infrequent earthquake-induced distrubance. Journal of Ecology 89: 1006–1018.

Wells A, Yetton MD, Duncan RP, Stewart GH 1999. Prehistoric dates of the most recent Alpine fault earthquakes, New Zealand. Geology 27: 995–998.

Wilmshurst JM, Anderson AJ, Higham TFG, Worthy TH 2008. Dating the late prehistoric dispersal of Polynesians to New Zealand using the commensal Pacific rat. Proceedings of the National Academy of Sciences, USA 105: 7676–7680.

Wilson HD 2008. The changing face of Banks Peninsula. Indigena November: 7–10.

Wilson KJ 2004. Flight of the Huia. Ecology and conservation of New Zealand's frogs, reptiles, birds and mammals. Canterbury University Press, Christchurch, New Zealand.

Worthy TH, Holdaway RN 2002. The lost world of the moa. Canterbury University Press, Christchurch, New Zealand.

Worthy TH, Tennyson AJD, Archer M, Musser AM, Hand SJ, Jones C, Douglas BJ, McNamara JA, Beck RMD 2006. Miocene mammal reveals a Mesozoic ghost lineage on insular New Zealand, southwest Pacific. Proceedings of the National Academy of Sciences, USA 103: 19419–19423.