1 Paradise Lost – the Last Major Colonization

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1.1 Introduction

Non-native or alien species have invaded New Zealand in a manner that is rarely equaled elsewhere in the world. For over a century, and long before biological invasions surfaced on the global research agenda in the late 20th century, alien plants and animals have been the focus of often intense public, legislative, management, and research activity and debate. In the early 20th century, New Zealand provided one of the earliest and most comprehensive national accounts of alien invasions (Thomson 1922), and New Zealand examples of invasion impacts and management commonly feature in the international literature on alien biota. To this day, New Zealand ecologists in general maintain a distinction between native and alien species, which is frequently viewed with bemusement by those from other countries where such categorizations, until relatively recently, have seldom been considered in research (Bannister 1994).

This heightened awareness of alien species reflects both the timing of European settlement, and the stark contrast between the alien and New Zealand resident flora and fauna. When Europeans began to settle in New Zealand in the early 19th century, they found an unfamiliar biota unsuitable as quality pasture for stock, edible fruits, or trees for short-rotation plantation forestry. The aspiration to recreate the resources and recreational opportunities of their largely European homelands saw the introduction of thousands of alien plant and animal species (McDowall 1994). The incidental arrival of plants and animals was also enormous, particularly as the colony looked to provide resources for a growing population and sought to develop primary industries for foreign trade (Guthrie-Smith 1921). In 1870, a few decades after European settlement, the explorer Julius von Haast could claim that he had over 700 non-native plant species to establish (McDowall 1994). A passion for the introduction of alien plants and animals continued until the late-20th century. Introductions were initially from Eurasia and North America. However,

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with increasing trade and transportation links to other countries, the need for commercial crops, pasture and forestry species, and an insatiable desire for novel garden plants, biota were sought from across the globe.

Facilitated by a temperate maritime climate, the lack of significant native herbivores and predators, and expanding areas of human-transformed habitat, an increasing proportion of alien species naturalized. Naturalized alien seed plant species now outnumber natives (Wilton and Breitwiesser 2000), and amongst vertebrates several trophic levels (predators, herbivores) have been dominated by introduced species (King 1990) for nearly two centuries. New Zealand's native biodiversity is renowned for high levels of endemism, ancient lineages, local radiations, and notable taxonomic and functional absences (Diamond 1990). Hence, the alien biota often represents novel functional groups, and species biogeographical and evolutionary histories vastly different from those experienced by the indigenous biota.

Research on alien invasive species in New Zealand was initially driven by concern over economic threats to agro-ecosystems arising from the early spread of pasture weeds. However, the early and rapid decline of many native terrestrial birds created apprehension about the impacts of carnivorous mammals in forest ecosystems (Worthy and Holdaway 2002), and presaged legislation to declare some alien species as noxious pests, to be controlled and eliminated where possible. Although agribusiness and forestry issues continue to drive much of our biosecurity legislation that is focused on the detection and elimination of new and unwanted alien species at the border, environmental issues (particularly the protection of biodiversity) are becoming increasingly important.

In this chapter, we address some of the major themes and debates that have developed through research in New Zealand on alien species, which provide a context for the book. We then introduce the structure and content of the book. The long focus on invasive species in New Zealand provides unique insights that may not be apparent in places that have recently begun to investigate invasions, or where alien species are not long established.

1.2 Themes and Debates on Alien Species

Research on biological invasions in New Zealand has undergone major shifts in approach and emphasis that have been driven by increased ecological understanding, changes in the operational management requirements of agencies controlling alien species, expansion of the diversity of alien organisms being detected, and the need to quantify impacts for risk assessment. Here, we outline some of the major issues, and how they have affected the development of research on biological invasions.

1.2.1 Human Dimension of Alien Invasions

Alien species introductions are obviously dependent on human-assisted transportation to New Zealand, but the important role of humans in the naturalization, establishment and spread of species is only beginning to be understood. Historically in New Zealand, nearly all introduced organisms are selected for surviving outdoors, and generally arrive in sufficient quantity for commercial use. Changing agribusiness requirements and fashions strongly influence alien species introductions (Mack 2001). However, for alien plants, the number of naturalized species is positively related to regional human population densities (Allan 1937). Proximity to human settlement also accounts for the level of alien plant species in native forest fragments (Sullivan et al. 2005), and the pattern and rate of spread of many vertebrate animals are largely a function of the intensity of human activity (Fraser et al. 2000). Habitat modification, coupled with the direct and indirect effects of human disturbance are also important factors maintaining numerical dominance of invasive alien species. What is becoming clear is that the invasion process involves multiple phases (importation, establishment, naturalization, spread, etc.), and that each stage is governed by a different set of key processes. Predicting invasion success requires integration of research on these different phases, and incorporation of a range of key processes.

1.2. Ecological Superiority of Alien Species

Since Darwin's (1845) assertion that the New Zealand vegetation was defenseless against the new and competitively superior alien flora from the Northern Hemisphere, assessment of the susceptibility of the native biota to introduced alien species has been controversial, especially for plants where impacts were less obvious and slower to unfold. Cockayne (1910) and Thomson (1922) challenged the supposed inferiority of the native flora, concluding that alien plant species only prevailed in natural ecosystems where indigenous plant species were weakened by human activity. They considered that local evolutionary processes had produced a native flora strongly adapted to New Zealand conditions and resistant to invasion by Northern Hemisphere plants. However, history and ecological research are showing that a verdict about the outcome of ecological interactions between native and alien plant species is context-dependent, and not necessarily favorable to native species. Although many communities currently comprise mixtures of native and exotic plant species, there is no evidence of stable states, and compositional and structural shifts continue in relation to management and environmental changes (Wilson 1989). For example, in the semi-arid regions of the South Island (which

has one of the longest histories in New Zealand of human disturbance and weed invasion), native and exotic species continue to change within communities, and are poorly correlated with environmental variables (Wilson et al. 1989). Most natural habitats in New Zealand have at least one clear example of a successful invasive alien species, suggesting there are enough safe sites or windows of opportunity, created by natural processes, to allow invasion.

The initial assessment regarding the resistance of New Zealand vegetation and communities to invasion now appears increasingly premature, for three reasons.

- First, early authors greatly underestimated the number, range and intensity of plant introductions, not knowing that in little more than 100 years over 20,000 alien plant species would be imported to New Zealand, and over 2,100 would become naturalized (Wilton and Breitwiesser 2000).
- Second, they failed to consider the invasion process over ecologically realistic time frames. In European landscapes, alien woody species show an average time lag of 147 years between introduction and the initiation of invasion (Kowarik 1995). The onset of alien woody species invasion may well be more rapid in New Zealand than in Europe, due to the absence of original predators, less intensive forms of land use, and milder climatic conditions. However, natural spread for long-lived, slow-growing, woody species is usually incremental, and is further impeded by the availability of safe sites or regeneration opportunities. In forests, for example, entry points for introduced plant species are usually gaps created by disturbance or tree senescence that occur at century-level frequencies (Stewart et al. 1991). Hence, the invasion potential of most species will not be recognized for many decades, and a residence time of at least a century will be required to adequately assess the ability of an alien woody species to spread into natural communities.
- Third, assumptions about the relative resistance of native vegetation focused on widespread forest communities, which frequently have an inherent resistance due to low irradiance levels and slow canopy turnover times. Such a prognosis is less convincing when we consider non-forested terrestrial habitats and aquatic systems that clearly demonstrate the potential for alien plants to invade and modify ecosystems, often displacing indigenous plant species (Scott et al. 2001; Closs et al. 2004).

The obvious impact of alien animal species is in sharp contrast to that observed for plants. While plant introductions (in terms of number of species) have been far more numerous, animal introductions have more frequently represented new functional groups, notably for introduced mammals (King 1990). The opportunities available to introduced mammals, particularly through predation of native fauna with few co-evolved defenses, have allowed a large and rapid impact by the comparatively few species introduced. In general, the large effect of alien animals on native New Zealand plants and ani-

mals is not in question. Rather, the key debates involving alien animal species have centered on whether they are the only cause of native species decline (and the relative culpability of different alien species), or whether other factors (e.g., habitat loss, climate change) are also involved (Worthy and Holdaway 2002; McDowall 2003). Ecological systems are frequently complex, and causal factors driving historical versus recent trends may be different. Thus, there are numerous factors potentially involved in native species' decline, providing some justification for diverse perspectives on which particular alien animal, if any, should be targeted for control.

1.2.3 Invasion Impacts Are Complex

The impact measurement for invasive weeds or herbivorous mammals in agricultural systems is relatively simple: loss of pasture production. Both the impact criteria and the consequences of alien species activity are often not clear in natural systems dominated by native species. Here, research has struggled because both the goals and the interactions are more complex.

Some alien species in New Zealand have clearly extended their niche breadth compared with that in their native range, and we have been slow to detect this expansion. For example, the perspective of the Australian brushtail possum (*Trichsurus vulpecula*) as primarily herbivorous in New Zealand forests was challenged by video footage of the species eating native bird eggs and pre-fledged young. For several decades, possum research focused on vegetation impacts associated with canopy dieback, ignorant of the more immediate threat on native birds (Brown et al. 1996).

The application of ecosystem-level studies has further expanded our perspective on invasive species impacts in New Zealand. For example, traditionally, mammalian herbivore effects were assessed primarily in relation to vegetation composition and regeneration. However, in the last decade, research on multiple-trophic-level interactions and above- and below-ground processes has extended our understanding and demonstrated significant, if somewhat idiosyncratic, influences of deer herbivory on the composition and diversity of soil organisms through the nonrandom selection of vascular plant traits, which in turn influences decomposer processes (Wardle et al. 2001). The long-term significance of deer herbivory on these ecosystem features has yet to be determined, but this is a compelling indication of how alien species may have subtle impacts far beyond those generally measured. Similar multi-trophic and ecosystem-level impacts of alien plant species are also emerging (Standish et al. 2001, 2004; Standish 2004). Deliberate or accidental introductions of cryptic alien organisms causing diseases are also being implicated in multiple trophic changes (Beggs 2001; Norbury et al. 2002), although for some groups such as introduced plant viruses the consequences of transfer to native species are largely unknown (Davis and Guy 2001).

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