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PERSPECTIVE

Species Invasions and the Limits to Restoration: Learning from the New Zealand Experience

David A. Norton

Species invasions impose key biotic thresholds limiting the success of ecological restoration projects. These thresholds may be difficult to reverse and will have long-term consequences for restoration because of invasion legacies such as extinctions; because most invasive species cannot be eliminated given current technology and resources; and because even when controlled to low levels, invasive species continue to exert substantial pressure on native biodiversity. Restoration outcomes in the face of biological invasions are likely to be novel and will require long-term resource commitment, as any letup in invasive species management will result in the loss of the conservation gains achieved.

Recent theoretical advances have emphasized thresholds and alternative stable states as key drivers influencing the outcomes of ecological restoration (*1*). One consequence of these emerging perspectives is the recognition that restoration must address not only the degrading factors but also the altered feedbacks that lead to self-perpetuating novel ecosystems—ecosystems that are different from those that would have existed before human impacts, especially as the impacts of climate change increasingly alter biotic interactions (*2*). The importance of addressing abiotic thresholds in restoration, such as those associated with changes in soil or water conditions, is widely recognized (*1*). Although some biotic thresholds can be easier to address than abiotic thresholds (*3*), biotic thresholds resulting from species invasions are likely to be difficult to reverse and have long-term consequences for restoration projects. Biological invasions can be both the cause of degradation (for example, through predation on native species) and the driver of ecosystem change during restoration (through altering the abundance of resident species or through the establishment of new species), and can result in irreversible changes in ecosystem composition and structure. As a result, the control of invasive species is a key focus of many ecological restoration projects (*4*).

Here I explore how species invasions can impose biotic thresholds limiting the success of ecological restoration projects. I use New Zealand as a case study because the impacts of biological invasions are particularly pronounced as a result of the archipelago's isolation, high endemism, and recent human settlement (within the past 700 to 800 years). New Zealand highlights the many challenges that biological invasions present both to other islands and increasingly to continental areas. At least 30 mammals, 34 birds, 2000 invertebrates, and 2200 plants are fully naturalized in New Zealand (*5*). Although control of these species is the major focus of ecological restoration, eradication is usually not possible except on some offshore islands or within fenced enclosures, and invasive species management therefore needs to be ongoing (*4*). Furthermore, control or eradication is usually able to target only a subset of invasive species (primarily mammalian predators and some plants), while others are left largely unmanaged (such as invasive birds or invertebrates).

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Fig. 1. Forest canopy trees such as *Beilschmiedia tawa* are dependent on kereru (*H. novaeseelandiae*) for dispersal of their large (>1.4 cm in diameter) fruits, because other potential dispersers are extinct or very rare. [Photos: D. Norton and A. McIntosh]

A key consequence of biological invasions, especially on islands, has been the reduction in the abundance of, and in some cases the extinction of, resident biota (*6*). The long-term implications of this are poorly understood but are likely to be important for a range of ecological processes, including reproductive mutualisms (*7*). For example, large-fruited plants (>1 cm in diameter) in New Zealand, including some dominant forest canopy trees (Fig. 1), are now reliant on one avian disperser, the kereru (*Hemiphaga novaeseelandiae*). Other potential dispersers are either very rare or extinct [including the moa (Dinornithidae)] because of predation by invasive mammalian carnivores (*8*), and no invasive birds are capable of dispersing the fruit of these trees. Kereru themselves are far less abundant today than they were historically. Reduced dispersal is likely to result in long-term shifts in forest canopy composition. From a restoration perspective, it is clear that even with control of mammalian predators, the future composition of New Zealand forests will be different from that before invasion.

The need for intensive mammalian pest control in New Zealand is well supported by numerous examples contrasting the survival of indigenous biota in areas with and without such control (*5*). However, the impacts of animal pests may not be reversible, even when they are controlled to very low densities. For example, red deer (*Cervus elaphus scoticus*) are widely dispersed through native forests and have a strong negative influence on populations of understory plants. Seedling growth is often very slow, and even at low densities, deer prevent regeneration because they consume almost all seedlings of preferred species that are present within the browse layer (*9*). As a result, reducing deer numbers, even to low levels, will not necessarily result in the restoration of pre-disturbance conditions. Changes in the abundance of seed dispersers will also limit restoration success in these forests, even if the elimination of deer were possible, because severely depleted plant species may not be able to reestablish themselves.

Invasive plants are very prevalent in New Zealand ecosystems. Although many naturalized plants appear to be having little obvious impact on native biodiversity, some present substantial challenges for restoration and limit the ability of restoration projects to achieve desired outcomes. Of particular concern are a suite of invasive grasses (such as *Dactylis glomerata*, *Bromus* spp., *Festuca rubra*, and *Holcus lanatus*) and forbs (such as *Echium vulgare*, *Hieracium* spp., and *Trifolium* spp.) that are now widespread through open communities (such as herbfield, grassland, and shrubland). An absence of natural enemies and adaptation to anthropogenic disturbances, including grazing, have favored these species. The long-term survival of native species such as the endangered limestone wheatgrass (*Australopyrum calcis*), which grows in naturally open sites associated with limestone outcrops, is seriously compromised by competition with these invasive plants (*10*). The restoration of open communities is very difficult without ongoing human intervention to control invasive plants and/or to establish seedlings of native plants. Even when native species have been established, further intervention will be required to ensure ongoing recruitment.

Fig. 2. Seedling of the native forest tree *Pittosporum eugenioides* regenerating under a canopy of the invasive woody weed gorse (*U. europaeus*) that has become established on abandoned farmland. As the gorse senesces, native forest species will replace it, although the subsequent forest composition may be different from that which develops through a succession dominated by native successional species. [Photo: D. Norton]

Some invasive species can play positive roles in restoration, although they may lead to unexpected outcomes. For example, the European legume gorse (*Ulex europaeus*) acts as a nurse plant for native forest regeneration in many areas of New Zealand, because it readily invades old fields once livestock grazing has been removed. Gorse shades out the invasive grass sward, creating suitable microsites for the regeneration of native woody species (Fig. 2). However, plant succession under gorse follows a different trajectory from that occurring under the native seral species kanuka (*Kunzea ericoides*), at least during the early stages of forest development, with a lower species richness of native forest species and an absence of some native species that are present in comparable kanuka successions (*11*). Furthermore, gorse-dominated successions are more invaded by bird-dispersed exotic woody plants than are kanuka-dominated successions.

Management responses to deal with the threats posed by invasive species present a number of challenges that need to be addressed if restoration is to be successful. Livestock exclusion is actively undertaken as part of restoration projects. However, livestock removal can have undesired outcomes; simply removing browsing animals may not solve the problem. For example, livestock exclusion was implemented to restore habitat for the threatened Whitaker's skink (*Cyclodina whitakeri*) at its last mainland site. However, monitoring over the following 22 years showed that this skink declined from 0.01 skinks per trap night (1984–1989) to 0.0005 skinks per trap night (2000–2006). Removing grazing animals did not restore skink abundance as intended; instead, reduced grazing allowed introduced pasture grasses to proliferate, resulting in periodic rodent irruptions supporting a guild of other introduced mammalian predators, which in turn depleted the Whitaker's skink population (*12*). The removal of livestock grazing can also have unintended consequences for native plants. For example, although restoration of the critically threatened shrub *Olearia adenocarpa* and its habitat requires the removal of grazing by domestic and invasive mammals to enable remaining mature plants to survive, the removal of grazing pressure also results in invasive grasses and herbs preventing the establishment of new plants (*13*).

Ecological restoration is a critical tool for mitigating native biodiversity loss in the face of anthropogenic impacts. Although it might be possible to reverse many abiotic thresholds (for example, through reinstating a disrupted disturbance or hydrological regime), reversing biotic thresholds that have been crossed as a result of the impacts of invasive species is very difficult. This occurs because of legacies resulting from invasions (such as species extinctions); because even when controlled to low levels, invasive species still exert substantial pressure on native biodiversity; and because most invasive species cannot be eliminated with current technology and resources. In these situations, the future ecosystem condition even with restorative management will be different from that which would have occurred at the site had biological invasions not occurred. The New Zealand examples highlight the magnitude of the challenges that face ecological restoration anywhere in the face of biological invasions, challenges that are likely to be even greater when biological invasions are coupled with other drivers of ecosystem change (*14*, *15*).

Three general predictions can be made about the outcomes of restoration in ecosystems that have undergone substantial biotic change as a result of species invasion.

1) Outcomes will be novel in that the ecosystems resulting from restoration will contain species assemblages and interactions that are new for the site and will include exotic species.

2) With multiple species invasions, control or eradication of one or some species will not necessarily result in desired outcomes because of changes in interactions among other species.

3) Where eradication is not possible, restoration will require ongoing management of invasive species if specific outcome conditions are desired.

To be successful with ecological restoration, we must recognize the severe limitations that species invasions impose on achieving traditional restoration outcomes. Ecological restoration in the face of biological invasion needs to be adaptable in the manner in which it sets outcome targets. These might range from establishing areas where restoration involves intensive and ongoing pest management, including the use of predator-proof fencing, to accepting the idea that native species can be sustained within novel ecosystems that include a range of exotic species. However, underscoring all restoration work involving invasive species is the need to ensure that resources are available to enable the ongoing sustainability of the project. Ecological restoration in systems with invasive species involves long-term resource commitment. Any letup in invasive species control, especially of mammalian predators, will result in the restored ecosystem quickly reverting to a highly degraded state as exotic species increase in abundance and/or reinvade, with the conservation gains achieved quickly lost.

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PERSPECTIVE

Pollination and Restoration

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Pollination services underpin sustainability of restored ecosystems. Yet, outside of agri-environments, effective restoration of pollinator services in ecological restoration has received little attention. This deficiency in the knowledge needed to restore pollinator capability represents a major liability in restoration programs, particularly in regions where specialist invertebrate and vertebrate pollinators exist, such as global biodiversity hotspots. When compounded with the likely negative impacts of climate change on pollination services, the need to understand and manage pollinator services in restoration becomes paramount.

Robust pollination services underpin the plant reproductive continuity of a restored ecosystem and rely on an understanding of how to support pollination processes and vectors after restoration activities. In agriculture and horticulture, the economic value of pollination is well recognized, with 75% of crop species and 35% of crop value dependent on pollination by animals (*1*, *2*). The importance of pollinators in agricultural production has been highlighted by the emergence of colony collapse disorder and varroa mite infestation in honeybee hives (*3*). This has led to remediation measures that include importation of hives from countries free of these disorders to use of electric vibrators to replicate buzz pollination in tomato crops.

Conversely, reestablishment of pollination services in restored native ecosystems is not well understood, yet biotically driven pollination services, particularly animal-based pollination services, sustain reproductive potential and genetic resilience in many ecosystems. To date, little has been done in the restitution of pollinator services in ecological restoration projects (*4*, *5*). This is despite a plea 10 years ago for fauna-mediated pollination services to be "…[reintroduced] as part of critical habitat management and restoration plans" (*6*). For example, due to a lack of pollination knowledge, one of Australia's largest urban woodland restoration programs at Kings Park and Bold Park in Perth, involving $5 million and reestablishment of 1 million plants, could not consider pollinator enhancement as part of the programs.

Specialist pollinators are often the first casualties when ecosystems degrade. However, the most pervasive ecosystem impact will arise from the loss of generalist pollinators (*7*–*9*), as witnessed with colony collapse disorder and honeybees. Similar pollination consequences will occur in natural and restored natural ecosystems if generalist pollination services are disrupted.

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For the global biodiversity hotspots that represent 44% of the world's vascular plant species and contain most of the specialized plant-pollinator mutualisms and interactions (*10*, *11*), restoring pollination services may be critical for ensuring restoration success. However, with 60% of global landscapes disturbed by humans and at least 70% of the land area in the 25 biodiversity hotspots cleared, future restoration capability will depend on the ability of pollinators to migrate and establish across often highly fragmented habitat matrices. In such fragmented landscapes, nonflying or restricted-range pollinators, such as terrestrial mammals, lizards, and many invertebrates, are doomed as pollinators particularly when the alienated matrix is ecologically hostile. In these cases, highly specific and obligate pollination interactions are most at risk and likely to pose the greatest challenge to conservation biologists and restoration ecologists.

Only a handful of research papers specifically investigate pollination networks and persistence in the face of climate change (*7*, *8*), yet climate change represents a major threat to pollination services. Climate-change trends predict alteration in timing of greening, flowering and senescence, and overall shortening of the growing season (*12*), factors with direct impact on pollination mutualisms. However, climate change will also lead to a decrease in precipitation and a shift in seasonality of rainfall, particularly in mediterranean regions, resulting in reduced plant vigor, delayed plant maturation, and a decline in nectar production capacity, with potentially devastating effects on nectar-dependent mutualists.

In addition, global warming may lead to partial or total asynchrony between pollinator life cycles and flowering phenologies. In the case of obligate pollination systems, this may lead to a breakdown of pollination mutualisms (*13*, *14*). Both have important implications for restoration, where species mixes may need to source nonlocal native plant species from a climate zone that matches the predicted new climate regime at the target restoration site. Such actions would necessitate the careful consideration of the invasive potential of introducing such plant species.

Ecosystems with high levels of specialized plant-pollinator interactions present substantial risks in achieving restoration success. These are heightened when the associations involve mutual dependencies between pollinator and plant leading to coextinction (*15*)—the "buy one, get one free" phenomenon. In turn, decay or shifts in pollinator assemblages servicing a plant species can lead to undesirable consequences such as lowered seed set or increased inbreeding, as seen in some plant species (*16*, *17*). In cases of one-on-one commensal relationships, as found in orchids, extinction risks for the plant partner can be substantial. This is exemplified in sexually deceptive orchid-wasp relationships in the southwest Australian biodiversity hotspot where the first recorded orchid extinction for the region may be a direct result of habitat loss, altered fire regimes (e.g., prescribed spring burning), and/or pollinator loss (*18*). Conservation and restoration of these highly specialized pollinator associations will require detailed knowledge of the ecological requirements for both plants and their pollinators.

Though many factors will influence the capacity of pollinator guilds to become established in restored landscapes, there are continental-scale trends that provide some guidance for restoration practitioners. For example, plants in biodiversity hotspots are more likely to exhibit higher levels of pollinator specialization due to increased competition for pollinator services in species-rich plant communities (*19*), resulting in ecological restoration that may involve specialized, obligate, and potentially unrecoverable pollinator associations. In the case of Southern Hemisphere continents, nonspecialist-to-specialist vertebrate pollination occurs along a continental gradient from east to west (*20*). Thus, in southwest Australia, which has the highest recorded incidence of bird pollination, 15% of plant species are pollinated by birds that exhibit generalist foraging strategies (*21*). In contrast, some tropical South American hummingbirds exhibit a high level of coadapted dependency on particular plant species (*20*), placing these relationships at greater risk. Thus, undertaking restoration in a South American context is likely to involve more plant species where specialized vertebrate pollinator commensalisms and mutualisms need to be considered and factored in than for southern Australian ecosystem restoration.

A key component in facilitation of pollinator activity in restoration is proximity to natural landscapes that support pollinator communities (*22*).

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