Ecological Restoration in the Light of Ecological History

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Ecological history plays many roles in ecological restoration, most notably as a tool to identify and characterize appropriate targets for restoration efforts. However, ecological history also reveals deep human imprints on many ecological systems and indicates that secular climate change has kept many targets moving at centennial to millennial time scales. Past and ongoing environmental changes ensure that many historical restoration targets will be unsustainable in the coming decades. Ecological restoration efforts should aim to conserve and restore historical ecosystems where viable, while simultaneously preparing to design or steer emerging novel ecosystems to ensure maintenance of ecological goods and services.

“[Nature] is ever shaping new forms: what is, has never yet been; what has been, comes not again.”—Johann Wolfgang von Goethe, 1783, On Nature (1)

Ecological restoration is rooted in ecological history. To facilitate the recovery of degraded or damaged ecosystems, knowledge of the state of the original ecosystem and what happened to it is invaluable. However, systematic monitoring of ecosystems, whether deeply degraded or nearly pristine, rarely spans more than the past few decades. Restoration ecologists are forced to assess ecological history by indirect means, ranging from documentary sources (e.g., written descriptions, historical photographs, maps, and paintings) to paleoecological records from natural archives (e.g., tree-rings, rodent middens, and sediments of lakes, peatlands, oceans, and estuaries). Fortunately, both documentary and natural archives can provide records of environmental variables and ecosystem properties in many parts of the world.

Restoration ecology looks to ecological history as a means of identifying appropriate restoration targets—the state of the ecosystem before disruption—and assessing sources of damage (e.g., fire suppression, acid rain, and cultural eutrophication). Restoration targets in the “New Worlds” of the Americas, Australia, and Oceania are identified as the “natural” states existing at the time of European discovery and conquest, that is, just before disruptions associated with land clearance, agriculture, grazing, and wildfire control. Ecological history plays a straightforward role in these applications in identifying the natural state of the landscape and constituent ecosystems (2–4), including the range of variability in disturbance and other properties (5–7).

Deeper consideration of ecological history is leading to revision of this approach. First, the notion of “natural” is being redefined based on increasing awareness that pre-European native cultures often exerted substantial influence on ecosystems, from simple hunting/harvesting to fire management and direct vegetation alteration (8–11). The nature, duration, and intensity of these impacts varied widely in space and time (10, 12), but few terrestrial or estuarine ecosystems escaped some effects of human activity. Second, climate has changed in the past 500 years, owing to natural causes and more recently to human activities (13). For many ecosystems, restoration to a historic standard is anachronistic. The environment has drifted, and so too have the targets. Ecosystems of even the recent past may be unsustainable under an early 21st-century climate. Finally, human activities leave ecological legacies that may be difficult or impossible to override in restoration. These legacies include extinctions (moos, mastodons) and industrial activities (brownfields, mine lands). Moreover, more subtle human imprints are being revealed, including the terra preta soils of the pre-Columbian Amazon (12) and soil-nutrient mosaics dating to 17th- to 19th-century English settlers in Massachusetts and 2nd- to 3rd-century Roman settlers in France (14, 15). For many parts of Europe, Asia, and Africa, undisturbed landscapes are too remote in time to provide restoration targets, which may instead comprise cultural landscapes (16, 17).

Despite these complications, predisturbance restoration targets remain worthy goals in many contexts. A key task for the future will be to determine where this remains viable and, conversely, where alternative targets must be considered. Historical studies will remain valuable in determining ecosystem structure and function before disruption (2–5) and in assessing the nature and timing of ecosystem responses to disruptions (4–9, 18–20). Paleoecology, together with observational, experimental, and modeling studies, can identify factors that prevent spontaneous or assisted ecosystem recovery once the obvious factors have been eliminated or mitigated.

Paleoecological and paleoenvironmental records spanning the last 10,000 to 20,000 years are now available for much of the globe, most densely in glaciated terrain but also in many other regions (21, 22). These records provide important perspectives for restoration, not all of them comforting. First, environmental and ecological changes are normal; perhaps the most natural feature of the world in which we find ourselves is its continual flux. The past 20,000 years witnessed a transition from a glacial to an interglacial world, with numerous climatic excursions throughout. Few major terrestrial ecosystems have existed in situ for more than the past 12,000 years (23, 24), and most are considerably younger, some arising only within the past few centuries (24). Every terrestrial locale has been occupied by a series of ecosystems—often contrasting in structure and function—since the

Fig. 1. The Big Woods (Minnesota) landscape, dominated by mesic forest, was savanna and prairie until about 1300 C.E., when droughts and consequent fine-fuel reduction led to reduction of surface fires, allowing tree invasion and expansion (27). [Photo: S. T. Jackson]
last glacial period. In the long run, no inherent natural ecosystem or landscape configuration exists for any region. Second, a multitude of ecological realizations arise and dissolve as the environment changes. Different species assemblages develop, leading to ecosystems with differing structure and function. The late-glacial “no-analog” communities—assemblages of plants, vertebrates, and insects with no modern counterpart—are the most dramatic example, but community assembly and disassembly are characteristic of the entire Quaternary (25). Third, the paleoecological record provides numerous case studies of multiple, alternative “natural” states, owing to historical contingencies affecting species migration, site colonization, and extinction (26). These cases are not always subtle, involving contrasting ecosystems (forests, grasslands, woodlands, and steppe) (Fig. 1) (26, 27).

These observations have the potential for setting restoration ecology adrift from its moorings in notions of objectively identifiable natural states of ecosystems. If natural states are elusive, if the environment is always changing and ecosystems are always coming and going, and if multiple realizations are normal, then the premises underlying ecological restoration to a historic standard come under question. Does ecological history render ecological restoration “quaint”?

Ecological restoration finds new moorings in emphasizing restoration of ecosystem function, goods, and services. Restoration ecologists increasingly recognize the ongoing and often inevitable development of novel ecosystems, resulting from species invasions, climate change, land-use legacies, and altered biogeochemical cycles (28, 29). Restoration efforts emphasize managing for change, which is accepted as inevitable, and interventions are directed toward ensuring that desirable ecological goods and services, including aesthetic values, are maintained (7, 30).

The paleoecological record gives restoration ecologists permission to accept environmental and ecological change and to intervene in ways that will foster biodiversity and vital ecosystem functions. In many cases, this will lead to ecosystems unlike those of the past (7, 25, 28). Restored ecosystems may have combinations of species that have never co-occurred. Many such ecosystems will be contingent not only on scientific and societal judgments but also on particular combinations of climate events, disturbances, extinctions, and migrations (26). As artificial or capricious as these ecosystems may seem, they must be embraced as such if environmental change is inevitable, multiple ecological realizations are natural, and contingencies and legacies are embedded in virtually all natural ecosystems.

Even in the face of inevitable environmental change and ecological novelty, efforts to conserve and restore historical ecosystems should be con-

Fig. 2. Contrasting ecosystem trajectories from historic through present to future configurations, indicating degree of change from the historic ecosystem (e.g., physical environment and species pool). Trajectories 1 to 3 indicate systems in three different states today: relatively unchanged (1), moderately altered (2), and severely altered (3). Colored bands indicate costs of restoration to the approximate historic state. Dotted lines represent realistic interventions for each trajectory; pursuit of A is more difficult and expensive than B. For trajectory 3, the only viable option is to slow the rate of change and direct the system to maintain or improve its value in terms of ecosystem services (C). Paleocoeology can help assess viability of different levels of intervention by identifying historical states and their range of variability, determining how far existing systems have drifted from these historic states, assessing the thresholds between required levels of intervention, and guiding design of novel and sustainable ecosystems capable of providing ecological goods and services.

Paleoecology will play important roles in all of these efforts. Paleoecological and paleoenvironmental studies inform our understanding of existing and historical ecosystems, determining the circumstances under which they arose, gauging the range of environmental variability they have experienced, and identifying environmental thresholds at which they will require different levels of intervention. By integrating the “reverse monitoring” of paleoecology with conventional “forward monitoring” and targeted experiments, we can diagnose the point(s) at which existing ecosystems will be unsustainable. At the same time, paleoecological studies will continue to reveal past ecosystem realizations and their properties at local, regional, and global scales. Paleoecological insights, together with modeling, experimentation, and observation, will advance our capacity to engineer ecosystems successfully. Obviously, the more time we purchase by slowing the rates of global change in all its dimensions, the more we increase our capacity for successful adaptation. We face serious risk that global change will outpace our scientific capacity to prescribe adaptive strategies, let alone implement them.

References and Notes
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 (3). 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 (6). 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).

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 novae-zealandiae). 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

Fig. 1. Forest canopy trees such as Beilschmiedia tawa are dependent on kereru (H. novae-zealandiae) 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]