Paleoecology reveals lost ecological connections and strengthens ecosystem restoration

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Biodiversity loss is one of the major challenges facing our planet, with extinction rates currently up to 100 times the background (1). Changes in the distribution and abundance of species can disrupt vital ecological processes and interactions (2). Restoring these connections has emerged as an essential component of biodiversity conservation, providing potential for renovating ecosystem services and enhancing the capacity to adapt to future change (3, 4). In PNAS, Bush et al. demonstrate how paleoecological, historical, and ecological evidence can be used to uncover lost connections between fauna and flora in the Galápagos Islands, providing a basis for restoration of these iconic landscapes (5).

Restoring ecosystems through species reintroductions and replacement requires a deep consideration of how long-term changes in species distribution and abundance have affected ecological processes (6, 7). This is particularly true in island ecosystems, which have endured rampant extinctions during the past few hundred years (8). The absence of predators on many islands made naive island fauna particularly vulnerable to overexploitation, and the introduction of nonnative animals and plants caused further devastation. In addition, island ecosystems often lack the complexity and functional redundancy that contribute to resilience on the mainland, and loss of keystone species can have cascading effects (9).

The ecological implications of extirpation on islands are often not well understood and islands are therefore a particular focus and challenge for restoration efforts. Bush et al.’s study (5) utilizes fossil pollen and coprolithic fungal spores from sediments from a highland lake on San Cristóbal in the Galápagos Islands to track the effects of extirpation of tortoises and their subsequent replacement by domestic stock. Intriguingly, the authors go beyond reconstruction of the vegetation surrounding the El Junco Crater Lake and deduce changes in tortoise behavior that had profound effects for ecological function and plant community composition. Tortoises (Chelonoidis) were overharvested by whalers along the coast of San Cristóbal in the 1790s. The authors suggest that the resulting loss of competitive pressure in the lowlands alleviated the need for seasonal migration of dome-shelled tortoises to upland areas. As a result, diverse shrublands in the highlands surrounding El Junco Crater Lake were replaced by a novel Miconia-dominated vegetation, which persisted even when domestic stock replaced tortoises as the dominant herbivore guild from the 1920s. Though early restoration attempts involved planting Miconia, Bush et al. advocate for removal of domestic stock and restoration of preimpact shrub species such as Alternanthera and Acalypha, alongside reintroduction of tortoises. Their plans would not only promote habitat restoration but would also bolster the socioeconomic value of these highland ecosystems through enhanced tourist experiences (5).

Fine-resolution studies covering recent centuries, such as those by Bush et al. (5), are especially valuable in understanding the ecological connections that underpin successful restoration. Another intriguing example, by Wilmshurst and coworkers in New Zealand, concerns the pollination of an endangered plant (10, 11). Dactylanthus taylori (Pua o te Reinga/wood rose) is an endemic cryptic root parasite of hardwood trees and shrubs. It was once widespread on the north island but its range is now severely restricted due to overharvesting and destruction by introduced possums (Trichosurus vulpecula) and rats (Rattus rattus). Furthermore, its only current pollinator is the lesser short-tailed bat (Mystacina tuberculata), and this close mutualism has restricted potential sites for reintroduction. However, analysis of pollen and ancient DNA in coprolites identified the to kākāpō (Strigops habroptila) as another pollinator of D. taylori. This nocturnal, flightless parrot is also critically endangered and survives only on small islands that are free of rats. These islands potentially provide further reintroduction sites for D. taylori (10, 11).

Reintroducing to a former range, termed inter situ conservation, is being successfully applied in Hawaii (12). On the island of Kauai, Zanthoxylum and Kokia are rare trees that are currently found only in high-elevation sites, a range restriction formerly attributed to a need for wetter conditions. However, paleoecological evidence has shown that these species were formerly widespread in the lowlands but retreated to their current inaccessible locations as indigenous forest was converted to agriculture near the coast (12). Inter situ conservation restores formerly contiguous populations, thereby restoring genetic connectivity.

The studies above concern reintroduction of locally extirpated species, but can paleoecological data help restoration even when a species is extinct? In Dart River Valley, New Zealand introduced deer have replaced extinct moa populations as the dominant herbivore in southern beech (Nothofagus) forests (13). Comparison of fossil pollen in moa coprolites showed a much greater diversity of pollen than...
that found in present-day deer pellets, suggesting that grazing pressure is now higher than in the past (13–15). A further indication of overgrazing is that more palatable species are currently restricted to rocky areas that are inaccessible to deer. The authors argue that deer numbers need to be controlled if former plant diversity is to be restored (13, 15).

Another important component of ecosystem restoration is the removal of nonnative species. However, the indigenous status of species is not always clear. In the Galápagos Islands, fossil pollen data showed that *Hibiscus diversifolius*, once thought to be invasive and subject to eradication efforts, was in fact returning to areas of former habitat (16). Similarly, on the Azores and Tenerife, paleoecological studies have established the native status of species once thought to be invasive (17, 18).

Returning habitats to “pristine” conditions is often unrealistic or undesirable. In some cases, cultural landscapes may have biodiversity and social significance that informs restoration efforts by reintegrating customary management practices (19, 20). Knowledge coproduction and collaboration with local communities can aid in exploring future desired states that remain resilient and adaptable to future environmental and social change (19, 21). In highly transformed ecosystems where a return to former conditions is impossible, a pragmatic approach with emphasis on restoring process and ecosystem services of nonanalog communities will be needed (3, 22, 23).

**Toward a Synergy of Restoration Ecology and Paleoecology**

Islands are particularly vulnerable to human disturbance and overexploitation, which can cause loss of unique biodiversity with cascading effects in ecosystems. However, the potential contribution of paleoecology and related disciplines goes beyond island restoration and Bush et al.’s paper (5) is significant in exemplifying a huge and largely untapped synergy between paleoecology and restoration ecology. In addition to fossil pollen, spores, and ancient DNA, used in the studies above, paleoecologists can use charcoal, stable isotopes, and geochemistry to reconstruct changes in fire, climate, hydrology, and erosion, for example. Aligning multiple paleoecological proxies can assist in distinguishing climatically driven from anthropogenically driven changes and provide the basis for exploring ecosystem resilience and defining restoration targets based on historical ranges of variability (24). Combined with present ecological and local knowledge, these long-term data can be applied to, for example, restoration of historic fire regimes, defining the ecological character of wetlands, restoring past variability, and informing vegetation and reforestation plans that are historically and ecologically justified (6, 25). Even when a return to past conditions is impossible or undesirable, the process-based understanding that is gleaned from paleoecological studies can be linked to changes in ecosystem services and can underpin modeling and scenario planning in uncertain future conditions (22, 26). Thus, a range of restoration approaches can be explored that consider landscape history alongside ecological and customary knowledge in order to explore future scenarios ranging from near-natural to novel ecosystems (see Fig. 1).

![Fig. 1. Process of exploring future scenarios for restoration based on a transdisciplinary understanding of landscape history.](https://doi.org/10.1073/pnas.2206436119)
perspectives into restoration plans codeveloped with communities, policy makers, and managers will require paleoecological data to be presented in forms that are accessible, relevant, and useful to stakeholder communities. Calibration of paleo-proxies against modern data and modeling of the interactions between multiple drivers will increase the relevance of long-term data in exploring future scenarios. The United Nations decade of restoration ecology provides a focus for creative collaboration between paleoecologists and the restoration ecology community to help imagine and rebuild sustainable landscapes and ecosystems (19, 21, 27).

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