In 2021 giant tortoises were seen hunting birds, which may be the return of a 'lost' interaction. What implications could such restored interactions have for rewilding projects and conservation efforts for other species?

The first documented case of giant tortoises hunting tern chicks, described in Zora and Gerlach (2021), is potentially a 'lost' interaction restored following rewilding efforts on Frégate island. Lost interactions are defined as those that historically existed between species in an ecosystem but have disappeared due to ecosystem degradation (Jordano, 2016). Human rewilding and conservation projects increase the likelihood of restoring such 'lost' interactions. Given the growing popularity of such projects, examining the implications of these restored interactions is critical. These implications can be considered at the individual species level, the ecosystem level, and, more broadly, the biosphere and human society levels. As the examination of actual and proposed conservation efforts indicates, ability to restore functional interactions can determine the ultimate success or failure of rewilding projects and, as such, warrants careful consideration and planning.

'Lost' interactions can return following rewilding efforts

Pair-wise species interaction is defined as the effect that two organisms living together in a community have on each other (Agrawal, 2022). Such interactions can disappear or be reduced to an extent where their functional ecological role is lost, thus becoming 'lost' interactions (Jordano, 2016).

In June 2020, a 'novel' aggressive hunting behaviour was reported in the giant tortoise, *Aldabrachelys gigantea* (Zora and Gerlach, 2021). A female tortoise was filmed reaching out for a tern chick with its jaws wide open and the tongue retracted, killing the chick and eating it. The retracted tongue is characteristic of aggressive tortoise behaviour, while normal feeding behaviour features a protracted tongue (Natchev *et al.*, 2015). Zora and Gerlach (2021, p. R990) concluded the tortoise's behavior was deliberate and was "not infrequent for this individual". Prior to this, other tortoises on Frégate had been seen eating birds or pursuing tern chicks, but the hunting and consumption had never been observed together, so can be seen as a seemingly novel interaction or a restored lost interaction.

This interaction became possible because of rewilding: human conservation efforts made the Frégate island ecosystem "exceptional" due to the unusual combination of large populations of tree-nesting terns and giant tortoises living together (Zora and Gerlach, p. R990). Noddy terns had recolonized the island after successful mixed woodland habitat restoration, with a colony of 265,000 living in a 1.9-hectare area, while tortoise numbers had reached 3,000 as a result of bringing tortoises from Aldabra atoll in the 1950s, releasing captive ones from other islands and wild breeding on Frégate. Seychelles giant tortoises – a keystone species and ecosystem engineers on this island – were able to take advantage of the fact that noddy tern chicks fallen out of tree nests are not typically defended by parents and prefer to stay on logs where even a slow-moving tortoise can capture them (Zora and Gerlach, 2021).

In this case, the restored interaction may not matter, as predation by tortoises would not exert selective pressure on terns (Zora and Gerlach, 2021). However, in other cases restored interactions may determine the very success or failure of conservation projects.

Restored pair-wise species interactions can determine success of rewilding projects

Rewilding generally attempts to rebuild ecosystems that have previously been disturbed by human activity, by reintroducing plants and animals that would have been present had the ecosystem not been disrupted (IUCN, 2021). Forup *et al.* (2007) argue that, while most efforts to restore damaged ecosystems focus on structural aspects of biodiversity, such as species richness and abundance, an alternative approach would be to consider the functional aspects, such as interaction patterns between species.

The importance of species interactions for ecosystem functioning was recognised as far back as Charles Darwin (1860), who wrote about plants and animals, which are physically far apart, but bound together by a complex web of interactions.

Pair-wise interactions between species (listed in Figure 1) can be restored through rewilding and exert evolutionary pressures on other species in the ecosystem. The traditional approach of focusing on restoring direct interactions between individuals can be a starting point in conservation efforts (Pianka, 2011, p. 228).

Figure 1

Type of Interaction	Species A	Species B	Nature of Interaction
Competition	–	–	Each population inhibits the other
Predation, parasitism, and Batesian mimicry	+	–	Population A, the predator, parasite, or mimic, kills or exploits members of population B, the prey, host, or model
Mutualism, Müllerian mimicry	+	+	Interaction is favorable to both (can be obligatory or facultative)
Commensalism	+	0	Population A, the commensal, benefits whereas B, the host, is not affected
Amensalism	–	0	Population A is inhibited, but B is unaffected
Neutralism	0	0	Neither party affects the other

Source: Pianka, 2011, p. 228.

For example, reintroducing beavers in Scotland restored the ecological relationship between beavers and fish. Beavers, which are ecosystem engineers, create deeper pools by building dams in shallow streams. Deeper pools mean increased availability of food for fish and protection from predators. Comparison of a stream modified by beaver activity and an unmodified one indicated brown trout (*Salmo trutta*), particularly larger individuals, became more abundant (Needham *et al.*, 2021).

While the Scottish beaver reintroduction appears successful, human ecosystem engineering efforts which have focused on a narrow species-on-species interaction approach can be disastrous. The introduction of cane toads in Australia in 1935 to control cane beetles led to the proliferation of a more problematic pest and the decline of many Australian reptiles and carnivorous mammals (Beckmann and Shine, 2009). While, in contrast, rewilding projects do not introduce a foreign species and, instead, attempt to restore lost interactions that have existed in the past, the cane toad example is important for conservation planners as it shows they need to be mindful that the effects of the restored pairwise interaction may affect multiple other species and the broader ecosystem.

Reintroducing apex predators can shape ecosystems by restoring interactions crucial for trophic cascades

Rewilding projects restore interactions that affect both the biotic and abiotic components of ecosystems. Each ecosystem features abiotic components, such as soil, water, atmosphere, and biotic organisms like animals, plants, bacteria (MSU, no date). Biotic and abiotic components are linked through a complex web of interactions – direct and indirect – and restoring a particular lost interaction could have unintended consequences.

Successful conservation projects, like the reintroduction of wolves (*Canis lupus*) in Yellowstone National Park in 1995-1996, illustrate the complexity and the broad range of species interactions that can be restored when a keystone species – one that holds the ecosystem together – is reintroduced. During the 70 years wolves were absent from Yellowstone, native ungulates, in particular elk, proliferated, leading to a decrease in abundance and growth levels for young deciduous woody plants (Beschta and Ripple, 2016). In the two decades since wolf reintroduction, elk numbers have declined, with positive effects on vegetation growth and a reduction in soil erosion. Of the 24 studies assessing the state of deciduous plants in riparian areas, examined by Beschta and Ripple (2016, p. 93), all but two found "increases in plant height, stem diameter, stem establishment, canopy cover, or recruitment", with the vegetation changes indicative of the re-establishment of a tri-trophic cascade which includes "an intact large predator guild, elk, and woody plant species". While vegetation recovery in these areas is at an early stage, it demonstrates that restoring a lost interaction can play a positive impact for conservation efforts. The wolf reintroduction led to increasing diversity in the composition, structure, and function of native plant communities, which in turn supports the food web and habitat structure of various animal species and is of fundamental importance for making these ecosystems resilient (Beschta and Ripple, 2016).

Restored interactions have wider implications on biosphere and societal support for conservation efforts

Another important consideration when planning rewilding initiatives is that there are multiple stakeholders as the effects of the conservation project are much broader than the target ecosystem itself. Successful rewilding, which results in greater plant variety and resilience, will impact other ecosystems and the biosphere if it helps to slow down climate change through improved carbon capture.

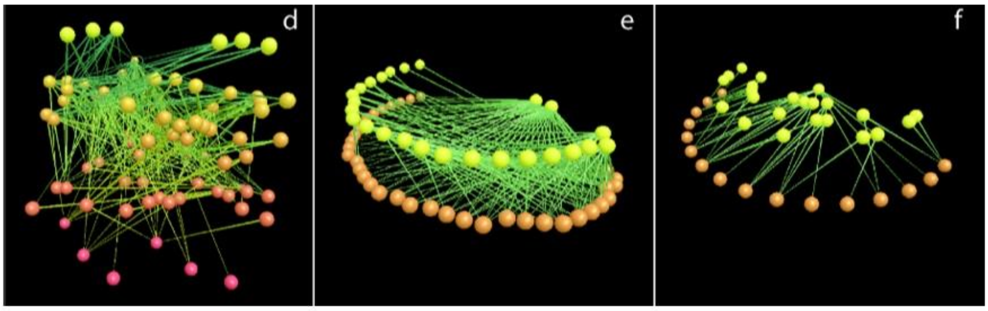
The UKWCT (no date), in its response to questions about the proposed reintroduction of the wolf to Scotland, identifies other factors which can determine the success of rewilding. The intended objectives may be to restore the wolf-deer lost interaction and, through that, control deer numbers in Scotland, but the UKWCT recognizes there could be effects on human safety and on agriculture through wolf hunting of livestock. Given the high level of uncertainty about impacts and the fact public opinion is divided, modeling is used to predict the impact of wolf reintroduction on deer numbers. Modeling results suggest wolf numbers will stabilise to 25 wolves per 1,000 km^2 and it will take 60 years for deer numbers to fall to seven per km^2. Cost-benefit modeling predicts a deer estate could make £800 per year per 10 km^2 with wolves and no need for culling deer, compared £550 without wolves. Another benefit would be the reduction in Lyme disease, which is spread by deer ticks, while grouse moors will also benefit as the presence of wolves leads to a reduction in the number of foxes. On the cost side, analysis suggests that taxpayers may face costs for compensating farmers for sheep killed by wolves and also for changing the current financial incentives to farmers for free range grazing. Certain impacts are harder to model as they could be positive or negative depending on the context: for example, ecotourism in Yellowstone benefited from wolf reintroduction, but in Scotland, where the territory is smaller and wolves are likely to range farther from the designated areas, the impact may differ (UKWCT, no date).

In this broader context, public and policy-maker support for the restoration of lost interactions may determine whether certain rewilding projects are allowed to proceed and given time and funding to ensure their success.

Rewilding should focus on networks of 'restored interactions' and modeling those can inform conservation effort planning

It is clear that conservation planners should consider all levels of potential impact of restoring lost interactions – the pair-wise, the ecosystem and the biosphere and societal-level ones – when planning rewilding projects. Jordano (2016, p. 2/4) warns, people do not currently understand the "minimum set of functional links that are needed to support and restore damaged ecosystems". He illustrates the complexity of interactions in Figure 2, with Panel d showing a typical food web capturing all interactions in an ecosystem with multiple trophic levels; Panel e displaying the pairwise pattern of mutual interdependencies among two distinct sets of animals (orange nodes) and plants (yellow nodes); and Panel f depicting interactions among species whose closer relationships are shown through multiple distinct groups of associations.

Figure 2



Source: Jordano, 2016, p. 3/4.

As conservation efforts to restore ecosystems damaged by human activity are urgent, Jordano (2016) states that it is essential to identify – through experimentation and modeling – the minimum amount of complexity of interactions that needs to be restored in order for ecosystems subject to conservation or rewilding to survive and thrive. The experimentation approach is also recommended by Forup *et al.* (2007), who suggest that for plant-pollinator interactions, a comparison of the pollination webs between restored and reference sites can provide a useful indicator of whether ecological restoration efforts have succeeded. However, Moreno-Mateos *et al.* (2020) suggest a longer, centuries or millennia, timeframe is needed to restore complex interaction networks in degraded ecosystems, and recommend using whole-genome sequencing to study eco-evolutionary feedbacks.

In planning which interactions to restore it is important to consider the conclusions of Borst *et al.* (2018, p. 1/15), who found, based on analyses of 58 food webs from terrestrial, freshwater, and coastal systems, that "carnivores are more strongly facilitated in foundation species' food webs than predicted based on random facilitation, resulting in a higher mean trophic level and a longer average chain length". What the findings from both Beschta and Ripple (2016) and Borst *et al.* (2018) indicate is that when deciding which lost interactions to restore through rewilding projects, priority should be given to those involving carnivores and keystone species.

The findings have important implications for conservation because, as Jordano (2016) pointed out, current knowledge on interactions is limited and, so urgent conservation efforts may have to focus on restoring the minimum number of interactions needed to make ecosystem improvements sustainable.

Concluding remarks

Restoring lost interactions is a crucial objective of rewilding efforts. The complex interactions between species and the implications at the individual species, ecosystem, and broader biosphere and societal levels need to be well understood and modelled before conservation efforts are carried out. Such an approach will enable conservationists to prioritise which interactions to restore in order to ensure that the repaired ecosystem becomes resilient and that public and financial support for rewilding initiatives is secured and maintained.

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