In July 2020, on the partially rewilded island of Frégate, a Seychelles giant tortoise (*Aldabrachelys gigantea hololissa)* was recorded hunting and eventually devouring a tern (family *Laridae*) chick, even though these tortoises were previously thought to be herbivorous, occasionally eating carrion[31]. The directness of the tortoise's attack, the retraction of its tongue in contrast to protraction while eating plants, and anecdotes of similar events all suggest this incident was not isolated, but the return of an interaction that was lost until tortoises were reintroduced and seabirds recolonised Frégate[31]. While the rarity of tortoises hunting and the already poor survival rate of fallen chicks mean that this occurrence is unlikely to affect the 265,000-strong noddy tern (*Anous tenuirostris)* colony on Frégate, restored interactions in other species are a cornerstone of conservation. An ecosystem, by definition, consists of interactions between organisms and their surroundings, and the absence of certain interactions suddenly removes or presents selection pressures, often leading to decreasing biodiversity. Abiotic conditions, such as water availability, may also be affected[13]. Consequently, the prevention of ecological extinction, where a population is too small to meaningfully affect a community, is ideal. When this opportunity has been missed, however, species reintroduction is used to prevent ecosystem collapse or allow rewilding. The Seychelles giant tortoise is a good example[9], spreading seeds and eroding stones underfoot, thus facilitating the restoration of Frégate's woodland. Although restored interactions can have enormous positive implications for conservation, they also mandate caution, for two opposing reasons. Firstly, due to the potential for trophic cascades, a reintroduced species can rapidly restructure a community and make other conservation efforts, like culling, counterproductive. On the other hand, a restored interaction may simply be negative to an ecosystem's condition, especially when humans are involved.

A flagship success story of returning lost interactions to an ecosystem is the reintroduction of grey wolves (*Canis lupus)* to Yellowstone National Park[7]. Once, wolves were seen as pests, due to the threat they posed to nearby livestock, so farmers and even the park administration hunted them to extirpation around 1926[8]. Within a few years, local conditions were described as "deplorable" by visiting biologists. This was mostly due to elk (*Cervus canadensis)* and coyote (C*anis latrans)* overpopulation without wolves as a selection pressure[7,14]. By 1995 the controversial decision was made to reintroduce 21 wolves, with immense positive results[7]. Their population increased to 123 by 2020, and the number of packs tripled, with the result that grey wolves are no longer endangered in the region[17]. Their greatest impacts, however, have been on other species, through a top-down trophic cascade[2]. One element of this is the carcasses they now leave behind throughout the year, in contrast to 1926-1995 when most elk deaths were concentrated in the winter. Scavenging wolf kills is an essential source of nutrition for bears (family *Ursidae*), as well as many smaller animals like ravens (*Corvus corax)* and red foxes (*Vulpes vulpes*)[5]. Another way wolves benefit small animals is by outcompeting coyotes, which thrived in wolves' absence but saw a 50% decrease upon their return[14]. This has led to healthier populations of rodents, upon which coyotes prey. Most notably, however, wolves reduced Yellowstone's elk population from 17,000 to below 6,000 between 1995 and 2019[18], partially since they each kill 16-22 annually[12], but also because elk were forced to move often and avoid open areas, reducing their nutrition[18]. The restoration of this behaviour in turn led to the recovery of riparian habitats, as riverside quaking aspen (*Populus tremuloides*) and grey willow (*Salix glauca*) trees experienced less browsing[7]. Mild browsing can encourage growth, but between 1926 and 1995 it was so severe that few new aspens survived, and most existing aspens by 1995 were over 70 years old[30]. This changed after average browsing intensity by elk halved between 1995 and 2003[21], with aspen recovering and grey willows' average stem height increasing from 25-74cm to 149-268cm[1]. Un-browsed willows also recover biomass 14x faster than browsed willows after being cut, which provides beavers with enough material to build dams[7]. This has been demonstrated by the ninefold increase in North American beaver (*Castor canadensis*) colonies in Yellowstone since 1995[7].

While the reintroduction of a keystone species like the grey wolf has the potential to vastly change an ecosystem through a trophic cascade, beavers, which happened to be at the end of this cascade, affect their surroundings through ecosystem engineering[29]. This is the process by which a species creates or substantially alters a habitat, and in the case of the beaver this involves building a dam. The North American beaver was extensively hunted for its fur in the 19th century, almost to extinction, which greatly reduced the amount of wetland on the North American continent. Since the start of the 20th century, however, the beaver population has recovered to more than 10 million, and the restoration of their interactions in riparian ecosystems has been essential to environmental conservation in North America[29]. By slowing the flow of water, beaver dams both allow the sedimentation of minerals like nitrates[24], and raise the water table[13]. These processes improve plant productivity, and the latter is particularly important in semi-arid areas, where beavers' ecosystem engineering has been shown to substantially increase the area of vegetation around a body of water. This vegetation may also display higher biodiversity than if the dam was absent; in one study the difference was found to be over 33%[29]. In the future, the resurgence of the beaver is likely to make many areas more resistant to the effects of climate change. In western Canada, for example, ecosystems with a beaver dam retain 160% more open water when facing a drought[10], which prevents the spread of forest fires. Furthermore, this water retention helps to preserve peatland, a type of ecosystem that exhibits significant carbon sequestration, but which decomposes to release CO_2 when drained, constituting almost 5% of man-made CO_2 emissions[11].

Another form of interaction with the ecosystem that is of importance to conservation is the disturbance of soil by large terrestrial herbivores[23]. American bison (*Bison bison*) provide an excellent example through the practice of wallowing, which consists of rolling around in a depression in the ground, called a wallow[19]. Wallowing is a social practice that promotes cohesion within a group of bison, as well as relieving itchiness caused by moulting and insects[19]. Repeated use of a wallow enlarges it, compacts the soil beneath it, and leaves behind dead skin and body oils, all of which increase its water retention[19]. An active wallow is normally quite difficult to inhabit, but once they are abandoned wallows regularly play host to many organisms which are not common in the rest of the ecosystem[19]. These include amphibians, which can use wallows to breed due to their ability to hold water, but even the vegetation in a wallow is different, with 16% plant of species found in wallows not being found in the surrounding grassland[16]. The moisture, detritus, and distinct flora of wallows also result in a greater abundance and diversity of arthropod life, which in turn benefits insectivorous birds, like the grasshopper sparrow, which has been documented to fare better when living near bison[19]. Over the 19th century, American bison were nearly hunted to extinction, and the enclosure of prairie land for agriculture further threatened the species, as well as many others that depended on bison. As a result, the prairie has lost a significant amount of biodiversity. Recently, however, there have been many efforts to reintroduce bison to grassland ecosystems across the United States[26], as it is better understood how their interactions with the landscape[23] create trophic cascades and increase biodiversity.

Not all restored interactions are beneficial, and some pose an obstacle to conservation. When wolves were reintroduced to Yellowstone, the behaviours this elicited from elk increased species evenness[7], but the wolves were almost too successful, as the elk population dropped to 3,915 in 2013, the lowest it has been without culling[18]. If hunters had not previously lobbied for an end to the cull, elk would have become at risk of extirpation. Another issue of "lost" behaviours returning and undermining conservation is in the form of domesticated cats (*Felis catus*)[28]. Unlike their ancestors, they do not need to obtain their own food while in captivity. If they become feral, however, they once again begin to hunt, and the return of this behaviour can be extremely problematic. Cats have been involved in 26% of recent extinctions of reptiles, mammals and birds[28], and their ongoing presence makes reintroductions and rewilding difficult. In South Australia, for example, an attempt in 2001 to reintroduce brush-tailed bettongs (*Bettongia penicillate*) in Yathong Nature Reserve saw every tracked bettong die within 13 months, and the failure of the program was attributed to feral cats, which constituted 74% of predation[22].

Equally challenging are restored interactions between animals and humans. A prominent case of this involves the reintroduction of grizzly bears (*Ursus arctos horribilis*) to the Pyrenées. While this project has technically been very successful, raising the population to a 100-year high in 2021, it has hidden expenses[3]. Due to the bears killing 200-300 sheep a year, the French government has been forced to provide hundreds of thousands of euros in compensation[3]. Perhaps more costly is the damage done to public opinion of conservation, particularly in the local area, a phenomenon well-documented in many other campaigns. In Scotland, the return of the Eurasian beaver (*Castor fiber*) has been met with opposition, on account of "incompatible goals" among stakeholders[6]. This is primarily a result of concerns that beaver dams will negatively impact agriculture and fishing. These fears are not, however, simply founded in self-interest, and actually bear ecological importance; dams hinder the movement of inland salmon (*Salmo salar*) and trout (*Salmo trutta*) through streams[6], which was not a major problem when beavers were extirpated 400 years ago, but which today could compound the already worrying decline in these species' populations[6]. A similar attitude, of a Scotland "not fit" for reintroductions, surrounds the prospective release of the Eurasian lynx (*Lynx lynx*)[15]. While national populations normally support such schemes[20], the opposite is true of the rural communities most affected, and without their cooperation it is difficult to succeed. Today, for example, there are calls to reintroduce the hunting of wolves around Yellowstone, in response to attacks on livestock. This type of regression in policy can reverse essential progress in conservation.

Ecosystems are defined by their interactions. Removing these interactions is a destabilising force, repeatedly linked to decreased species richness and evenness, as well topographical changes. When behaviours that were suppressed by depopulation return, via reintroductions or population recovery, they restore valuable influences on the community and the habitat. Often, these effects are disproportionate to the biomass of the population bringing them about. In Yellowstone National Park, the return of an apex predator created a series of substantial shifts, revitalising the ecosystem in only a few years[5,7,8,30]. In other areas, the more gradual recovery of ecosystem engineers has been accompanied by recovering biodiversity as well[19,29]. Furthermore, the restoration of interactions in other species provides opportunities for further conservation, such as in the case of short-haired bumblebees, whose pollination could address declining biodiversity in English meadows if their population returns from the brink of ecological extinction[4]. When manipulating keystone species' prevalence as an ecological tool, it is still important to avoid certain major pitfalls. In many situations, meticulous publicity is necessary to demonstrate how inconvenient restored interactions are a necessary sacrifice. At the same time, one must respect objections to reintroductions and rewilding and consider whether the ecosystem's condition permits the interaction's reinstatement without adverse consequences. Nevertheless, returning "lost" interactions to an ecosystem is a staple of conservation and rewilding, as it is becoming ever more apparent that an organism's niche is essential not just to its own survival, but to the prosperity of the whole ecosystem.

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