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Comment: What if Wolves don't change rivers, or the Lynx lacks bite? Rethinking a rewilding orthodoxy

Hugh Webster

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Could the reintroduction of apex predators such as Lynx be the catalyst for ecosystem recovery?
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Rewilding seeks to establish resilient, self-sustaining ecosystems by restoring natural processes and complete (or near-complete) food-webs encompassing all trophic levels (IUCN 2021). However, rebuilding food webs in nature-depleted landscapes will often require reintroductions, which can be controversial – especially when the species involved are apex predators, returning to landscapes and communities from which they have long been absent (e.g. Hetherington 2018).

Some see reintroductions as subtly diminishing the perceived 'wildness' of the animals concerned, especially where they may have recovered naturally if given sufficient time and opportunity (see for example *BW* 32: 43–48). For many species, however, human intervention represents the only route available for recolonising lost parts of their range. Numerous species have already been reintroduced to the UK, but when it comes to the reintroduction of large carnivores, a daunting range of obstacles remains (Stier *et al*. 2016).

Living alongside apex predators is challenging, and in Britain, where the last of our free-living, native large carnivores was exterminated hundreds of years ago, we have lost many of the traditions and cultural coping mechanisms that facilitate some level of coexistence elsewhere in the world (Van Eeden *et al*. 2018). As a result, proposals to reintroduce Eurasian Lynx *Lynx lynx* (referred to hereafter simply as Lynx), and especially Wolves *Canis lupus*, generate controversy whenever they are raised (e.g. Defra 2018).

Against this backdrop, it is especially important that rewilding advocates can rationalise *why* they might want to reintroduce large predators, and demonstrate an understanding of what we might reasonably expect from reintroductions versus what remains harder to predict. This will help to determine the goals, overall purpose, and technical and biological limitations of any future reintroductions (Seddon *et al*. 2007).

Balance versus chaos

Ecologists now agree that nature exists in a dynamic, often chaotic, state in which different species may rise to prominence at different times (Simberloff 2014). Despite this, the idea of a natural balance – with a preordained endpoint – is still popular, not least among environmentalists who realise that there is, undoubtedly, an optimum set of environmental conditions for the survival of our own species.

One problem with this concept is that it can encourage a belief that ecosystems may be restored to a historical 'balanced' state by simply leaving nature alone, or by replacing some key missing ingredient. In support of this view, there is evidence that reintroductions can precipitate dramatic changes within living communities – what are known as trophic cascades – that may eventually restore ecosystems to something resembling an earlier version of themselves (e.g. Painter *et al.* 2015). This narrative of nature-driven recovery captures the imagination, particularly when the vital missing ingredient happens to be a charismatic large predator.

Contrasted with conservation's traditional focus on trying to save what we have left and the sometimes heavy-handed management used to preserve imperilled wildlife, the possibility of revitalising degraded ecosystems via the re-introduction of lost native species offers a more optimistic vision. And yet, while we know that trophic cascades can occur, we should ask whether the reintroduction of apex predators will deliver the kind of restorative effects that are widely claimed of them – especially when the impacts of human land-use are now so pervasive that they are likely to influence almost any ecological interaction (see Alston *et al.* 2019).

Consider one apex predator, the Eurasian Lynx, a medium-sized cat being considered for reintroduction to Britain (see Hetherington 2008). The 'need' for this reintroduction is often advanced on ecological grounds, including restoring the Lynx to its role as a top-down regulator of smaller mesopredators, such as the Red Fox *Vulpes vulpes*, which has become super-abundant in parts of Britain, creating a problem for ground-nesting birds and other species. But how likely is it that reintroduced Lynx could suppress our abundant and adaptable Foxes, or bring about any of the other ecological changes promised of them?

The Lynx effect

Studies from Norway (Sunde *et al.* 1999) and Sweden (Helldin *et al.* 2006) suggest that preda-

In Switzerland, the return of Lynx has not prevented the Fox population from increasing. Nature Picture Library/ Alamy Stock Photo

tion of Foxes by Lynx can be significant. This, in turn, can benefit Capercaillie *Tetrao urogallus*, Black Grouse *Lyrurus tetrix* and Mountain Hares *Lepus timidus* (Elmhagen *et al*. 2010), which offers hope that the reintroduction of Lynx to Britain could catalyse a similarly beneficial set of changes.

In more productive agricultural landscapes, however, Foxes may simply be too numerous for Lynx to control. A Swiss study by Molinari-Jobin *et al*. (2000), in a landscape more similar to most of the British countryside, recorded that although Foxes were the third most common prey item (average 4.8 Foxes per Lynx per year), this had no obvious impact on the Fox population; indeed, Foxes actually *increased* over the period that followed Switzerland's Lynx reintroduction.

Studies on the response of Roe Deer populations to the presence of Lynx have shown varied results. Don Hooper/Alamy Stock Photo

It has also been suggested that Lynx might help to reduce numbers of deer in Britain, the current abundance of which is thought to be inhibiting woodland regeneration (Hobbs 2009). Specifically, it is claimed that the return of Lynx could create a 'landscape of fear' (Laundré *et al*. 2010), changing the behaviour of deer, and discouraging excessive herbivory of trees, simply through the threat of predation (akin to the trophic cascade suggested to have been precipitated by reintroducing Wolves to Yellowstone: see below). Notably, Lynx may have a stronger influence on deer behaviour than human hunters do (Bonnot *et al*. 2020) since they observe no closed season, hunt in even the thickest vegetation and exhibit no bias towards 'trophy' males.

Yet studies show that the effects of Lynx predation vary. In Switzerland, where returning Lynx encountered naïve populations (without previous experience of large carnivores) of Roe Deer *Capreolus capreolus* and Chamois *Rupicapra rupicapra* clustered in hunting sanctuaries that provide supplementary food over winter (similar to the winter feeding of Red Deer *Cervus elaphus* on some Scottish sporting estates), Lynx predation drove both a drop in prey numbers and a change in prey behaviour (Haller 1992). In contrast, in Sweden and Norway, Lynx recolonisation alongside similarly naïve Roe Deer populations had no detectable effect on habitat selection by the latter (Ratikainen *et al*. 2007; Samelius *et al*. 2013), all of which suggests that the landscape-of-fear phenomenon does not apply equally to all landscapes nor to all predator–prey relationships.

Lynx predation may have the greatest impact where deer densities are already limited by environmental factors, such as forb abundance, rainfall, snow depth and temperature (Linnell *et al*. 1996), or when combined with pressure from other large predators such as Wolves (Jedrzejewska & Jedrzejewski 1998), or humans for that matter. Indeed, in areas of intense hunting by humans, or during extreme events such as harsh winters, Lynx predation can reduce even high-density deer populations (Hetherington 2018).

To illustrate further the ecological limits of what reintroduced Lynx might achieve, it is worth remembering that in Yellowstone National Park,

Wolves in Bavaria, Germany. This species is currently recovering its range in Mainland Europe after centuries of persecution. Arterra Picture Library/Alamy Stock Photo

before Wolves were reintroduced in the mid-1990s, there existed a diverse predator guild that included Grizzly Bears *Ursus arctos* and Black Bears *U. americanus*, Cougars *Puma concolor* (which, although eradicated alongside Wolves in the 1930s, had recolonised Yellowstone naturally by the 1980s), Coyotes *Canis latrans* and two species of lynx, namely Canada *L. canadensis* and Bobcat *L. rufus*. Yet, despite this impressive suite of predators, Elk *Cervus canadensis* were still present at levels that were damaging the ecosystem. So, expecting the Lynx alone to solve Britain's deer problem may be optimistic.

We might still expect reintroduced Lynx to reduce British deer numbers (mainly Roe Deer) in some scenarios, especially in tandem with sustained human hunting effort or where deer numbers are already low. But the level of impact is likely to be highly situation-dependent: as Hetherington (2018) states, 'we don't yet completely understand all the intricacies of how lynx and other species interact with one another'.

Equally, it may be that Lynx can reduce Fox numbers in some landscapes, especially in Highland Scotland where Fox densities are lowest. Newsome *et al.* (2017) note, however, that in general 'suppression of mesopredators will be strongest where top predators occur at high densities over large areas'. Whether that is a realistic prospect in Britain remains unclear but, given the uncertainty described above, rewilding advocates may be wise to temper, rather than raise, expectations when discussing the likely ecological effects of Lynx reintroduction.

Furthermore, any impact that Lynx *might* have will of course be limited to the area(s) that can support resident populations, leaving the need for human hunters to continue controlling deer and Foxes over the substantial part of our landscape that is more heavily developed – i.e. densely populated and criss-crossed with road and rail infrastructure – and therefore likely to be inhospitable to Lynx (Basille *et al.* 2009).

What about Wolves?

Despite the Wolf's remarkable recolonisation of mainland Europe over recent decades (Chapron *et al.* 2014), clear evidence of subsequent ecosystem changes or of trophic cascades mediated by its return remains elusive. Effects, where they have been documented, appear to be highly context-dependent and have occasionally been the *opposite* of what might have been predicted. For example, in Sweden, the presence of Wolves is associated with higher abundance of and greater browsing damage by Moose *Alces alces*. Here, Ausilio *et al.* (2021) emphasise that 'the return of large predators to landscapes with strong anthropogenic influence may result in alternative effects than those described in studies on trophic cascades located in protected areas.'

One study in France did suggest that the recovery of a Roe Deer population after a severe winter might be slower in the core of a Wolf pack's territory compared with the fringes (Randon *et al.* 2020), and another study, from Białowieża National Park, in Poland, found that browsing intensity on saplings was lower where Wolf presence was greater, particularly where woody debris created an 'escape impediment' for prey species (Kuijper *et al.* 2013). In general, though, the return of Wolves across Europe has yet to have much influence on ungulate populations, high densities of which encouraged the Wolf's spread in the first place.

The evidence globally for trophic cascades set in motion by Wolves is certainly greater than that for stalking predators, such as Lynx (Samelius *et al.* 2013), with the most famous and oft-cited example coming from Yellowstone National Park, in the USA. There, hunting by Wolves is suggested to have reduced numbers of Elk and also, perhaps more significantly, affected their behaviour (Creel *et al.* 2005; Painter *et al.* 2015). Specifically, fear of entrapment by hunting Wolves is suggested to have driven shifts in Elk habitat selection, thereby releasing riparian Quaking Aspen *Populus tremuloides* from excessive browsing and catalysing a cascade of effects across the ecosystem, even including changes in hydrology. In support of this fear of entrapment hypothesis, it is worth noting that between 1930 and 1968 hunting by humans kept the Yellowstone Elk herd significantly smaller than it is today and yet there was no recovery in aspen, which could suggest that the effects observed since the reintroduction of wolves were behaviourally mediated rather than consequences of population regulation.

While this story has helped to shape the modern rewilding zeitgeist, the true impact of Wolves in Yellowstone is the source of significant debate (Hayward *et al.* 2019). Painter *et al.* (2015) acknowledge that Yellowstone's Elk, throughout the key period, were additionally subject to 'other influences including increased predation by bears, competition with an expanding bison population, and shifting patterns of human land use and hunting outside the park'. In fact, the decline of

Quaking Aspen stands have expanded in Yellowstone, but the reason for this is still debated. K. D. Leperi/ Alamy Stock Photo

the northern Yellowstone Elk herd pre-dates the return of Wolves. Others have questioned whether the recovery of riparian Quaking Aspen was due to a reduction in herbivory (Kauffman *et al.* 2010) or to some other, climatic factor – such as increasing summer precipitation – which varied contemporaneously.

A further challenge in establishing the importance of Wolves in driving the dynamics of the northern Yellowstone Elk herd and subsequent ecosystem changes comes from the fact that the wolves' reintroduction was a one-off, with neither controls nor replicates (MacNulty *et al.* 2016). The Wolf biologist David Mech considers the whole Yellowstone story 'controversial' and warns that 'in any case, any such cascading effects of wolves found in National Parks would have little relevance to most of the wolf range because of overriding anthropogenic influences' (Mech 2012).

This controversy has not discouraged some ecologists from suggesting that the reintroduction of Wolves might regulate Scotland's Red Deer population, thereby improving conditions for forest regeneration (Nilsen *et al.* 2007; Manning *et al.* 2009). A more recent study (Bull *et al.* 2018) warned, however, that any such control (via so-called top-down forcing) of deer populations would probably require a very high density of Wolves (possibly contained within a fenced reserve). Importantly, these authors also note that the mere fact that a Wolf population is large enough to be self-sustaining does not necessarily mean that it will be able to limit or reduce the numbers of deer.

Meanwhile, even Wolves have not regulated Yellowstone's Bison *Bison bison*, the numbers of which have increased over recent decades (Beschta *et al.* 2020) to the point that they are now regularly culled or translocated by the park authorities to avoid problems with overgrazing, mass starvation or disease (Geremia *et al.* 2021). Even the vast Greater Yellowstone ecosystem is not so large or so wild that some human intervention is not still occasionally necessary.

A different perspective

If all this sounds negative, it is only to highlight the risk of building the case for reintroductions on the promise of ecological nirvana, or of sanctifying charismatic species (Mech 2012). None of this is to say that the reintroducing of predators cannot yield ecological benefits – clearly it can. But we need to realise, and publicly acknowledge, that no single outcome is guaranteed. Radically altered ecosystems, like disassembled engines, will not necessarily be restarted simply by replacing one component, however integral that component once was.

Nature is unpredictable. That is, after all, part of the joy of rewilding. So, perhaps, rather than claiming that predator reintroductions offer a simple fix for complex ecological problems, it may be wiser to champion their capacity to thrill and surprise us. Reintroductions also provide unique opportunities to advance our scientific understanding of the varied and seemingly context-dependent effects of predation (Ausilio *et al.* 2021).

Finally, just as we should be wary of overselling the potential ecological or financial benefits of reintroductions, we also need to be open about the potential costs (see Martin *et al.* 2020). One can easily imagine the ramifications if a reintroduced Lynx was to begin killing sheep after farmers had been assured that this could never happen.

The hazards of an overly utilitarian approach

Similarly, when we seek to justify predator reintroductions exclusively on the basis of functional benefits, we risk jeopardising that justification if these effects are not seen to materialise. Consider recent research claiming that the presence of Wolves reduces deer–vehicle collisions (Raynor *et al.* 2021), seeking specifically to provide hard data on the economic spin-offs associated with the presence of predators. But what will be the reaction if a future study reports an increase in diurnal activity among Roe Deer precipitated by nocturnal Lynx predation (see Bonnot *et al.* 2020), which is then responsible for an increase in deer–vehicle collisions?

Perhaps the best justification for predator reintroductions is one that focuses on their potential to enrich the human experience: if you know that Lynx are back in a forest, it instantly feels wilder. Predators thrill and excite us all. Those suffering from 'ecological boredom' or 'nature deficit disorder' may be shaken from their torpor. Our managed landscapes could recover some element of their intrigue and mystery. You cannot put a value on wonder; we can be sure only that without wild things and wild places we would all be immeasurably poorer. That is one thing we can guarantee.

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Hugh Webster (@DrHWeb) is a writer and conservationist specialising in the behavioural ecology of large carnivores. He has worked with SCOTLAND: The Big Picture on identifying psychological barriers to rewilding, and is a scientific consultant for the African environmental education charity Coaching Conservation. In his spare time, he writes the Natural Storytelling blog and seeks out quiet spaces.