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Essays and Perspectives

Rewilding ecological communities and rewiring ecological networks

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ABSTRACT

Rewilding encompasses management actions such as reintroductions and translocations with the purpose of restoring ecological processes and ecosystem functions that were lost when species were locally extirpated. The success of a species introduction is conditioned by multiple factors, in particular, ecological interactions. To predict the fate of the introduced population and the community-level outcomes of the introduction, species interaction patterns need to be considered. Here I propose that ecological network models can help in rewilding projects in at least three ways. First, combining ecological information and probabilistic models it is possible to infer the most likely ways whereby the introduced species will integrate the community and which will be its role in the topology of the food web. Second, by determining the species more likely to interact directly or indirectly with the introduced species, it is possible to identify those species that may affect the success of the introduction and those that are more likely to be affected. Third, by constructing potential interaction networks representing the rewilding scenario, one can infer the possible ways by which the overall structure of the network will change and thus devise more efficient plans to monitor the community. Network models can be an important asset in rewilding, helping in feasibility and risk assessment as well as in monitoring the consequences after species release.

Introduction

Over the past decades, conservation biology underwent a shift from a field whose main mission was to evaluate extinction risk and halt diversity loss, with particular focus on threatened species (Meine, 2010), to a more process-centered view, whose focus is the conservation of functional ecosystems (Tylianakis et al., 2010). The functioning of ecological systems depends on the integrity of the ecological networks formed by the multiple interactions that species establish with each other (McCann, 2007; Molnar et al., 2004). The main strategy for the conservation of ecosystems is arguably the establishment and management of large interconnected reserves (Lovejoy, 2006). Larger areas can harbor a greater diversity of habitats, organisms and thus of ecological processes (Peres, 2005). However, maintaining large areas does not guarantee ecological processes will be preserved. In fact, most regions of the planet are already largely defaunated (Dirzo et al., 2014), and without large stocks of organisms in neighboring areas, reserves may be nothing more than large patches of empty forests (Redford, 1992) amidst the urban and agricultural landscape matrix.

The extirpation of large vertebrates began when humans expanded their distribution in the Pleistocene and continued in historical times, having profound consequences for ecological systems (Malhi et al., 2016). Large bodied vertebrates are often key players in ecosystems, participating in several processes such as nutrient cycling (Doughty et al., 2013), long-distance seed dispersal (Pires et al., 2017) and exerting top-down control on species on lower trophic levels (Ripple et al., 2015; Terborgh, 2001). Moreover even smaller-sized vertebrates, which might be able to compensate to some extent the absence of large-bodied species, are now declining in most areas (Donatti et al., 2009). This scenario calls for more active restoration approaches in order to reestablish animal populations in the wild (rewilding) and their ecological interactions (rewiring), thus reinstating ecological processes and ecosystem functions (Seddon et al., 2014).

Soulé and Noss (1998) proposed the use of the Pleistocene as a baseline for ecosystem restoration in North America and introduced the rewilding concept. Rewilding was originally defined as "the restoration and protection of big wilderness and wide-ranging large animals – particularly carnivores" (Soulé and Noss, 1998). The use of the Pleistocene fauna as a baseline implies in the introduction of taxon substitutes, such as large felids, feral horses, cattle and elephants, that would be able perform the

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roles that vacated since the native megafauna, like saber-toothed cats, lions, camels, sloths and mastodons died out (Donlan, 2005; Galetti, 2004). More recently the definition has been loosened and rewilding now encompasses both the reintroduction of locally extinct species (Galetti et al., 2017; Svenning et al., 2016) and conservation translocations using surrogate species whose ecological roles would be equivalent to the species that have been lost (Seddon et al., 2014). Different from traditional reintroduction, which focuses on recovering declining populations, the ultimate aim of rewilding is to restore ecosystem processes that were lost due to local extirpation, generating a self-regulated community, without the need of continued management (Sandom et al., 2013; Svenning et al., 2016).

To reestablish ecological processes, a rewilding project envisages rewiring an emptied food web with the desired links. Rewiring is the reconfiguration of the interaction patterns of network elements (Watts and Strogatz, 1998). I refer to network rewiring as the establishment of novel ecological interactions, which will generally involve the introduced species, but also reconfigurations of the interaction network that occur as an indirect effect of a species introduction.

If the goal in rewilding is to restore certain ecological processes, the viability of the introduced population over time has to be secured. However, a number of examples from accidental introductions and biological invasions show that the introduction of a species into a local food web may trigger cascading effects via direct and indirect pathways that can result in diversity decline and changes in ecosystem properties (Lodge, 1993). Thus, a rewilding program should also be able to ensure that the negative impact on other populations will be minimal. Considering the amount of resources a rewilding initiative demands and the potential mishaps, it is compulsory to use techniques that allow foreseeing the suite of possible outcomes after an introduction.

The "Guidelines for Reintroductions and Other Ecological Translocations" (IUCN/SSC, 2013) from the IUCN Reintroduction Specialist Group (RSG) highlight the need of assessing the match between the abiotic and biotic needs of the candidate species and features of the target area. Basic information about the abiotic conditions determining species occurrence are available for many species, especially the ones that are often considered as potential rewilding candidates. Distribution modeling techniques allow predicting, sometimes with a very high level of confidence, where are the suitable regions for a species (Elith and Leathwick, 2009). Yet, without careful consideration of how biotic interactions affect the dynamics of the managed population and how the introduced species will affect other organisms, a reintroduction program is sentenced to failure. In short, the main challenge of any reintroduction is how to guarantee that the introduced species will subsist in a biotic context where it is able to sustain its population and will not harm the others.

Here I first review a set of cases where success and failure of species introduction was related to the effects of biotic interactions. Next, I argue that approaches derived from network science can be an asset for planning, assessing the viability, and for monitoring the success of rewilding.

Biotic interactions and rewilding success

As soon as individuals of the candidate species are released they will create novel interactions with several other species, which will influence the likelihood that the population establishes and will have consequences to the local community. Looking at the outcomes of past reintroductions and translocations is the key to understand how biotic interactions affected their success or failure. Most of the early attempts of reintroduction were ill-planned, with no post-introduction monitoring (Seddon et al., 2007). Available data regarding introductions in the 70s and the 80s show many programs were unsuccessful in reestablishing populations, although the causes of failure were mostly unaddressed (Griffith et al., 1989; Seddon et al., 2007). Examining more than 500 cases of reintroduction to understand what aspects were being reported, Seddon et al. (2007), found that only 7% of the studies addressed the ecological effects of the introduction, i.e., the interactions of the released species with the environment and other organisms.

The RSG (Reintroduction Specialist Group) reports include detailed analyses on the consequences of introductions, but tend to report mainly the successful attempts. Actually, this is a trend in the restoration literature (Fischer and Lindenmayer, 2000; Moehrenschlager et al., 2013), which may be harmful to our understanding on the reasons underlying failure or negative impacts of introductions and translocations. Yet, most of the reports on introductions and translocations covered by the RSG list interactions with predators, pathogens, competitors and resource availability (prey or plants) as potential causes determining the success of introduction attempts.

Predation, either by native or invasive predators, is often identified as a major determinant of post-release mortality, limiting the success of released individuals to form a viable population (Innes et al., 1999; Moseby et al., 2011; Seddon et al., 2007). High mortality due to predation after release has been associated mainly with the naivety of captive-bred individuals (Aaltonen et al., 2009; Biggins et al., 2011). Exposure to predators during captivity has been shown to reduce predation-related mortality for different species (e.g., Heezik et al., 1999). A careful assessment of the predator–prey interactions the rewilding candidate establishes in its location of origin may allow determining the potential predators in the target area and how the introduced species will integrate the local interaction network. Such knowledge may help devising strategies that minimize loss due to predation, including rearing schemes that foster anti-predator behavior.

Large-bodied rewilding candidates are presumably less likely to be victims of predation, especially in already defaunated areas. Still, other natural enemies such as pathogens may induce high mortality in released individuals. The stress produced during capture and transportation may affect the immune system of introduced individuals making them more susceptible to pathogen infection, a phenomenon described for different species such as beavers (*Castor fiber*; Nolet et al., 1997) and the Eurasian lynx (*Lynx lynx*; Schmidt-Posthaus et al., 2002). Knowledge of the pathogens carried by resident organisms and their potential to infect the introduced species is essential to the development of countermeasures that reduce mortality risk.

Another important source of mortality related to the biotic component is starvation. Examples include introductions of the river otter (*Lontra canadensis*; Day et al., 2013), the Arabian oryx (*Oryx leucoryx*; Mésochina et al., 2003), and the Canadian lynx (*Lynx canadensis*; Devineau et al., 2010). Failure of several reintroduction attempts of African predators has also been associated with reduced prey availability in the target area or inefficient hunting skills of captive-bred individuals (Hayward et al., 2007). In a compilation of carnivore introduction success, Jule et al. (2008) found that starvation was the second cause of mortality after human related causes such as shooting and vehicle collision. Competition with resident species for resources may also hinder the establishment of the introduced population (Hayward et al., 2007; Jule et al., 2008).

Starvation may only become a prevalent mortality cause when populations grow unchecked due to low top-down control. In the Oostvaardersplassen, a fenced nature reserve in the Netherlands where cattle, red deer and horses were introduced, populations undergo die-offs as the availability and quality of the forage drops during the winter (Vera, 2009). In the absence of predators,

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