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COMMENTARY

Reversing defaunation by trophic rewilding in empty forests

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ABSTRACT

Defaunation has a major driver of biodiversity loss in tropical forests. Here we discuss how to reverse defaunation by re-introducing key species in defaunated or restored forests.

Key words: Atlantic forest; climate change; defaunation; howler monkeys; reintroduction; tortoise.

Defaunation, the global, local or functional extinction of animal populations or species, has become one of the ubiquitous drivers of biodiversity loss in the Anthropocene (Dirzo *et al.* 2014). Tropical ecosystems are increasingly affected by defaunation, particularly of large vertebrates (Peres & Palacios 2007, Corlett 2013) leading to severe ecological disruptions and to the loss of important ecosystem processes and services (Effiom *et al.* 2013, Kurten 2013, Bello *et al.* 2015). While the proportion of 'empty forests' continues to increase in the tropics, 'rewilding' projects, including the reintroduction of formerly extinct species, continue to attract much debate and attention (Seddon *et al.* 2014, Svenning *et al.* 2016).

The idea of rewilding has faced much controversy primarily because of early focus on the goal of recovering Pleistocene ecosystems. Pleistocene rewilding as first proposed by Galetti (2004) for tropical savannas in South America and Zimov (2005) for steppe ecosystems were thought as experimental fenced parks (the so-called 'Pleistocene parks') to test the role of megafauna in key ecological processes such as herbivory and seed dispersal. In fact, both authors never mentioned the term 'rewilding' that was first proposed by Soulé and Noss (1998) for restoring only top predators in North American landscape. The term 'rewilding' did not get much attention until Donlan *et al.* (2005) popularized the controversial idea of introducing ecological/phylogenetic analogues of extinct Pleistocene megafauna to North American ecosystems. Thus, the idea of rewilding was first met by strong rejection by the scientific community because it was linked to the idea of introducing exotic species such as lions, cheetahs, elephants, and camels to replace the function of extinct Pleistocene megafauna in natural ecosystems (Rubenstein *et al.* 2006, Caro 2007, Oliveira-Santos & Fernandez 2010, Rubenstein & Rubenstein 2016). Although no introduction of elephants or lions was actually attempted in the Americas, every now and then there are still papers heating this debate (Nogués-Bravo *et al.* 2016).

While there is a general consensus that restoring the ecological functions lost from natural ecosystems is vital for maintaining self-regulated ecosystems (Seddon *et al.* 2014), there is no consensus if the ecological function of extinct Pleistocene species should or even can be replaced by living species under our current climate scenario (Richmond *et al.* 2010).

A less radical type of rewilding is the reintroduction of living species that have been recently lost from their habitat. This strategy can be particularly important in forests undergoing restoration. For example, as tree plantations in former agricultural lands embedded in highly modified landscapes that hamper natural faunal recolonization (Rodrigues *et al.* 2011). In the lack of active reintroductions of some groups of native animals, plant species may not be able to persist due to limitations in key ecological interactions (Hobbs & Cramer 2008).

Here, we discuss 'trophic rewilding' (*sensu* Svenning *et al.* 2016) via species reintroductions as a strategy for restoring ecological processes in defaunated or planted forest patches. Trophic rewilding has the goal of restoring trophic interactions to achieve self-regulating ecosystems (Svenning *et al.* 2016). Focusing on the reintroduction of locally extinct species is less radical and may prove less ecologically and socially contentious than Pleistocene rewilding.

A defaunated rain forest with great potential and benefit from this approach of trophic rewilding is the Atlantic forest of

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South America, a biodiversity hotspot (Myers *et al.* 2000) where ~12 percent of the original forest is left, mostly in small (<50 ha) forest patches (Ribeiro *et al.* 2009). Fragmentation has been a major driver of defaunation in the Atlantic Forest, as an abrupt decline of vertebrate community integrity has been observed in landscapes with less than 30 percent habitat cover remaining (Banks-Leite *et al.* 2014), and six of the seven biogeographical regions of the biome have less than half of this threshold (Ribeiro *et al.* 2009). In addition to heavy fragmentation, hunting has decimated most of the mammalian fauna even in large forest remnants (Galetti *et al.* 2009, Jorge *et al.* 2013).

Forest restoration is then necessary to further mitigate species extinction in this biome, while providing new habitat for reintroducing those species locally extinct by both fragmentation or hunting (*e.g.*, Bernardo 2012). Ambitious forest restoration programs have thus been established. For instance, The Atlantic Forest Restoration Pact, a coalition of more than 250 institutions including governments, NGOs, private companies and academia, launched the goal to restore 15 million ha by 2050 (Melo *et al.* 2013). Following this call, and the legal requirements to restore over 20 million ha of native ecosystems in private farms to comply with the Forest Code (Soares-Filho *et al.* 2014), many large-scale forest restoration projects have been implemented across the Atlantic Forest and mobilized an unprecedented amount of resources to reestablish highly diverse tropical forests in agricultural landscapes (Rodrigues *et al.* 2011, Latawiec *et al.* 2015).

Most restoration projects consider that once a forest type is established, preferably with a large array of native species, the area will gradually be colonized by new species, including fauna. This hypothesis has been called as the 'field of dreams' myth: 'build it and they will come' (Hilderbrand *et al.* 2005). However, it is not the case for the Atlantic Forest, where key large-bodied species are no longer found in forest remnants (Jorge *et al.* 2013), so they would not be able to colonize adjacent restoration sites, which further compromises the self-sustainability of the restored community. While small to medium-sized birds have been found in restoration sites, large-bodied birds are absent (Silva *et al.* 2015). Thus, there remains an urgent need to reverse defaunation in order to re-establish important ecological (Brodie & Aslan 2012, Seddon *et al.* 2014) and evolutionary processes (Galetti *et al.* 2013).

The best candidate species for trophic rewilding projects would have to fulfill the following criteria: (1) species that have suitable captive stocks, either in zoos, wild animals screening centers or private captive breeding; (2) species that are habitat generalists but provide an unique ecological service that is absent in most restored or remnant defaunated forests; (3) species which do not represent a high health and economic risk to humans (*e.g.*, top predators, disease vectors, agricultural pests); (4) species that can be easily managed if they reach high abundances; and (5) species with small home ranges. The ideal sites for refaunation include: (1) areas where the impact of hunting and domestic dogs or other invasive species is minor; (2) landscapes with habitat large enough to maintain a minimum sustainable population size; (3) forest patches with sufficient resources to support the populations of reintroduced species.

TABLE 1. *Potential candidates for refaunation projects in Neotropical defaunated forests.*

Group	Refaunation candidates	Common name	Home range (ha)	Ecological/ economical risks	Ecological benefits	Failure causes	Reintroduction sequence
Mammal	*Agouti paca*	Paca	1.5–3.5	Overbrowsing, seed predation	Seed predation	Hunting, predation by domestic dogs	1
Mammal	*Alouatta* spp.	Howler monkey	0.4–1.1	None	Seed dispersal, nutrient cycling	Loss of group cohesion, dog predation	1
Mammal	*Bradypus* spp.	Sloth	2.8–5.9	None	Nutrient cycling	Pet trade	1
Reptile	*Chelonoidis carbonarius*	Tortoise	0.6–600	None	Seed dispersal of large seeded plants	Pet trade	1
Bird	*Crax/Penelope/Pipile*	Cracids	150–200	None	Seed dispersal	Hunting, predation by domestic dogs	1
Mammal	*Dasyprocta* spp.	Agouti	3.0–8.5	Overbrowsing, seed predation	Seed dispersal of large seeded plants	Hunting, predation by domestic dogs	1
Mammal	*Tapirus terrestris*	Tapir	190–302	Crop raiding	Seed dispersal of large seeded plants	Hunting, predation by domestic dogs	1
Bird	*Tinamus solitarius*	Tinamou	Unavailable	None	Seed predation	Hunting, predation by domestic dogs	1
Mammal	*Pecari tajacu*	Collared peccary	123–305	Crop raiding	Seed predation, soil engineering	Hunting, predation by domestic dogs	2
Bird	*Ramphastos/ Selenidera/Pteroglosus*	Toucan, toucanets	86-191	Increase in nest predation	Seed dispersal of large seeded plants	Pet trade, Hunting	2
Mammal	*Leopardus* spp.	Ocelot, margay	319–3710	Poultry predation	Top predator	Hunting, predation by domestic dogs	3

FIGURE 1. Potential candidates for trophic rewilding programs for defaunated Neotropical forests. (A) Guans (*Penelope spp.*) (Photo M. Galetti), (B) Toucanets (*Selenidera spp.*) (Photo Edson Endrigo), (C) Tortoises (Chelonoidis spp.)(Photo M. Galetti), (D) Agoutis (*Dasyprocta spp.*)(Photo M. Terranova), (E) Tapirs (*Tapirus terrestris*)(Photo M. Galetti), (F) Collared peccaries (*Tayassu tajacu*)(Photo M. Galetti)

The sets of species fulfilling these criteria vary among regions, and must be sorted out regionally. Here, we suggest a list of potential candidates for trophic rewilding for Atlantic Forest (Table 1; Fig. 1), but other authors have been discussing for other ecosystems (Louys *et al.* 2014, Sandom *et al.* 2013, Corlett 2016). For each species, the expected ecological benefits must be weighed locally against the ecological and economic risks and the chances of failure, but continuous monitoring is necessary. In addition, just as in restoring plant communities, there should be suitable sequences for inserting species. For example, generalists of the lower trophic levels should be reintroduced first, followed by more specialist species, which would benefit from a richer trophic web. Finally, apex predators should be inserted only after their prey populations have been safely established (Table 1).

Trophic rewilding programs are already taking place in a few defaunated rainforests. For instance, in Tijuca National Park in Rio has already reintroduced agoutis (*Dasyprocta leoporina*) and howler monkeys (*Alouatta clamitans*) (Cid *et al.* 2014). In this forest patch of about 4000 ha, 23 large seeded tree species rely on scatter hoarding rodents and the introduction of agoutis has resurrected this extinct plant-animal interaction (Zucaratto & Pires 2015). In restored forests we still lack examples of trophic rewilding but this is an open opportunity for collaboration between wildlife managers and forestry ecologists. If well managed, small forest fragments and restored forest can became important for maintaining important ecosystem services.

Trophic rewilding programs have usually attracted high interest, support and enthusiasm from the local people and will be an essential management tool for the success of forest restoration projects and they are certainly more feasible, controlled and accepted than Pleistocene rewilding projects. Although more empirical data is necessary to fully understand how to reestablish extinct ecological interactions, it will be an important alternative to reverse defaunation in tropical ecosystems and its consequences for vital ecosystem services.

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