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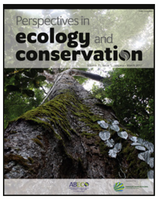

Research Letters

Rewilding defaunated Atlantic Forests with tortoises to restore lost seed dispersal functions

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ABSTRACT

The extinction of frugivores has been considered one of the main drivers of the disruption of important ecological processes, such as seed dispersal. Many defaunated forests are too small to restore function by reintroducing large frugivores, such as tapirs or Ateline monkeys, and the long-term fate of large-seeded plants in these areas is uncertain. However, such small fragments still host many species and play relevant ecosystem services. Here, we explore the use of two tortoise species, the red-footed tortoise (*Chelonoidis carbonarius*) and the yellow-footed tortoise (*Chelonoidis denticulatus*), as ecological substitutes for locally extinct large seed dispersers in small forest patches in the Brazilian Atlantic Forest. We employed prior knowledge on the known occurrences of *Chelonoidis* species and used ecological niche modeling (ENM) to identify forest patches for tortoise rewilding. Based on habitat suitability, food availability and conservation co-benefits, we further refined our analysis and identified that the more suitable areas for tortoise reintroduction are forest patches of northern Atlantic Forest, areas with high defaunation intensity. Giant tortoises have been used to restore lost ecological services in island ecosystems. We argue that reintroducing relatively smaller tortoises is an easy-to-use/control conservation measure that could be employed to partially substitute the seed dispersal services of extinct large disperser species, mitigating the negative cascading effects of defaunation on reducing plant diversity.

Introduction

Tropical ecosystems are facing fast deforestation and defaunation rates (Dirzo et al., 2014). For instance, large tracts of forests and savannas in Brazil are being converted into agricultural and pasture lands, thereby threatening many wild populations and endemic species (Laurance et al., 2014). Fragmentation leaves behind an archipelago of small patches that can hardly sustain viable populations of large-bodied forest-dwelling species (Turner, 1996). The extinction of large vertebrates can trigger cascading effects of important ecosystem services such as carbon storage (Bello et al., 2015). Because many forest patches are deemed too small to maintain relatively high levels of biodiversity in the long term, the value of these areas for conservation has mostly been neglected (Laurance et al., 1997). However, even though such forest patches cannot harbor large vertebrates, they contain important components of biodiversity, particularly tree species (Tabarelli et al., 2005; Gardner et al., 2007; Farah et al., 2017). Consequently, the long-term fate of the populations of plants that rely on large seed dispersers is uncertain (Cordeiro and Howe, 2003; Galetti et al., 2013).

Rewilding—introducing ecologically similar species to perform ecosystem functions analogous to those of extinct species—is being increasingly used in both temperate and tropical ecosystems as a strategy to restore functionality in heavily degraded ecosystems (Svenning et al., 2016). A notable example of a highly fragmented environment that could benefit from rewilding programs is the Brazilian Atlantic Forest, which although figuring as a biodiversity hotspot, has been under great overexploitation and intense urbanization since Brazil's colonization (Ribeiro et al., 2009). Given that a significant part of Atlantic Forest remnants does not support

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large-sized species (Morcatty et al., 2013), small/medium-sized species, once efficient dispersers, present the best alternative to restore and maintain the biome's ecological functions.

Tortoises (Family Testudinidae) have been used to restore seed dispersal and herbivory functions in island ecosystems due to their generalist diet and fruit-based preferences and their capacity of ingesting large quantities of relatively large fruits and seeds (Hansen et al., 2010, 2008; Griffiths et al., 2011). Moreover, there is mounting evidence that tortoises are important seed dispersers and can disperse large-seeded plants in their natural ecosystems (Strong and Fragoso, 2006; Jerozolimski et al., 2009). The current absence of tortoise in several Atlantic Forest remnants is probably consequence of the historical hunting combined to fast landscape conversion (Wang et al., 2011). Tortoises are still highly appreciated as food and for pet purposes in the Amazon (Morcatty and Valsecchi, 2015a,b), but there are no recent records of intense hunting of tortoises in Atlantic Forest remnants.

Here, we explore the use of two tortoise species, the red-footed tortoise (*Chelonoidis carbonarius*), and the yellow-footed tortoise (*Chelonoidis denticulatus*), as ecological analogs for large seed dispersers in small remnants of Brazilian Atlantic Forests that cannot support large frugivores. We employed prior knowledge on the known occurrences, and habitat preferences of both *Chelonoidis* species, forest food availability and ecological niche modeling to calculate a feasibility index and propose sites for tortoise rewilding.

Methods and study site

The Atlantic Forest (AF) of South America was once one of the largest tropical and subtropical forests in the world, originally covering around 150 million hectares along the Brazilian coast and part of Paraguay and Argentina (Ribeiro et al., 2009). Currently, 100 million people live in the AF domain and the anthropogenic impacts have transformed its natural landscape and strongly decreased its biodiversity (Laurance et al., 2009). The industrialization and agricultural expansion are considered to be the main causes of AF landscape fragmentation (Scarano and Ceotto, 2015). Currently, the AF covers <12% of its original area, mostly comprising fragmented and disconnected patches of <50 ha (Ribeiro et al., 2009). Nonetheless, the remaining AF hosts a larger number of endemic species and is considered one of the five major hotspots for conservation in the world (Myers et al., 2000; Visconti et al., 2011).

Two species of tortoise occur in the AF, the red-footed toirtoise (*C. carbonarius*) and the yellow-footed tortoise (*C. denticulatus*) (Fig. 1). Tortoises are popular hunting targets since they can be easily captured and kept alive for a long time. Thus, they have probably been used as food by humans for millennia. These species are known to rapidly disappear in overhunted areas (Peres and Nascimento, 2006), and it is likely that many tortoise populations went extinct in the AF after the Europeans arrived and occupied the Brazilian coast (Dean, 1996). Today, the conservation status of both tortoise species should be considered as critical in the AF, although many populations of both species still occur in the Amazon and the Cerrado (Fig. 1).

Ecological niche models

Ecological niche model (ENM) estimates associations between environmental variables and known species occurrences to infer the conditions under which the populations of a species can survive and then plot suitability values in areas where the species' occurrence is unknown (Franklin, 2009; Peterson et al., 2011).

We collected information on the occurrence of *C. carbonarius* and *C. denticulatus* in South America using four different methods: personal observations, online databases (GBIF – Global Biodiversity Information Facility; MCZBASE – The Database of the Zoological Collections, and records in iNaturalist and VertNet), news websites, thesis, academic papers, and management plans for protected areas. We only used information that contained locality or geographic positions, the observer name and the date (month or year) of the records. In total, we found 76 and 94 occurrence points for *C. denticulatus* and *C. carbonarius*, respectively (Fig. 1). After the search, we filtered these points to obtain a unique occurrence in each cell, using a grid of cells with 2.5 arc-minutes resolution (∼4.5 km × 4.5 km at the Equator). We used this cell size because all climate layers used in our study were available in this resolution and embraced all known occurrence points of these tortoise species.

We used the entire South American continent as a background for our modeling because we considered this region as being open/available to dispersal for our two studies in historical time and all known occurrence points are in this area, two crucial criteria for background selection (Barve et al., 2011). To characterize the environmental aspects of the background region, we downloaded all 19 bioclimatic variables available in the *WorldClim* database (www.worldclim.org; Hijmans et al., 2005). These variables are derived from temperature and precipitation data, and are thus likely to be correlated among them. To decrease the correlation rate, we performed a factorial analysis on the 19 the bioclimatic variables to select variables with low multicollinearity, using *Varimax* rotation (similar to the method used by Sobral-Souza et al., 2015). In the end, five variables remained: Annual Mean Temperature, Mean Diurnal Range, Isothermality, Precipitation of Wettest Quarter and Precipitation of Driest Quarter, which together explained 92% of background climate variation within our 2.5 arc-minutes cell size.

Currently, there are many different algorithms available to predict species distribution and the combined use of several of these algorithms is generally thought to increase the reliability of models by considering a wide range of distributional patterns (Barry and Elith, 2006; Araújo and New, 2007; Diniz-Filho et al., 2009). In this sense, we used five algorithms based on different modeling methods. The first three were presence-only methods: envelope score – Bioclim (Nix, 1986), and two distance methods – Mahalanobis Distance (Farber and Kadmon, 2003) and Domain (Gower distance; Carpenter et al., 1993). The last two were machine-learning methods based on presence-background records: Support Vector Machines (SVM) (Tax and Duin, 2004) and Maximum Entropy – MaxEnt (Phillips and Dudik, 2008). The algorithms were built in "dismo" and in "kernlab" R-packages (Karatzoglou et al., 2004; Hijmans et al., 2015).

We partitioned the occurrence points into two subsets, 75% and 25% for training and evaluate the models, respectively. As the training and testing points are subsets of the same occurrence points, we randomized the two subsets 20 times to minimize the spatial structure between the training and testing datasets, thus providing less biased evaluations. In this way, we built 20 models with each of the five algorithms, totaling of 100 models (20 times × 5 algorithms) for each tortoise species. Based on recommendations by Liu et al. (2013, 2016) about which threshold to use when presence-only data are available in niche modeling analysis, we used the maximum sensitivity and specificity threshold to transform the continuous maps into binary maps. With this threshold we evaluated the models using the True Skill Statistic (TSS) value, which ranges from −1 to 1. Negative or near-to-zero values indicate that predictions are not different from a randomly generated model, whereas predictions with values closer to 1 are considered to be excellent (Allouche et al., 2006).

To predict the final maps, we followed the ensemble forecast proposed by Araújo and New (2007). For this, we concatenated the 20 binary maps belonging to the same algorithm and obtained the final consensus map by computing frequencies from all algorithms.

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