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Rewiring of experimentally disturbed seed dispersal networks might lead to unexpected network configurations

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Abstract

The consequences of species extinctions in ecological communities may be buffered through the rearrangement (rewiring) of the interactions between the remaining species. The structural and functional consequences of such extinctions can be explored by means of computer simulations that try to predict secondary extinctions and the degradation of ecosystem services. However, to improve the accuracy of these simulations, it is pivotal to evaluate their performance in predicting changes observed in natural communities. In this study, we first described the avian seed dispersal networks in 17 sites throughout Portugal, and found that blackberry (*Rubus ulmifolius*) was the most dispersed species in 13 out of the 17 sites. Second, we performed a manipulative experiment to evaluate the effect of removing the most dispersed plant species and compared the observed outcome in the structure of the network with computer simulations with and without rewiring. Observed changes were consistent with some rapid network rewiring, with dispersers shifting to alternative fruit species. Although the observed network topology after the

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experimental removal was not accurately predicted, the extinction simulation with rewiring performed considerably better than that without rewiring. Individual species roles were even harder to predict than emergent network properties on both types of models. We show that incorporating rewiring rules can considerably increase the accuracy of species extinction models, however, the functional consequences of losing important resources might not be easily anticipated, and rewiring might occur in unexpected directions.

Keywords: Ecological networks; Frugivory; Passerines; *Rubus ulmifolius*

Introduction

The loss of any species from a community entails a concomitant loss of all its interactions with other species, whether they are prey, predators, hosts, parasites or mutualists (Bond 1994). In some cases, the extinction of these ecological interactions can lead to secondary species extinctions (Brodie et al. 2014), which are intrinsically hard to predict (Ives & Cardinale 2004; Brodie et al. 2014; Timóteo, Ramos, Vaughan, & Memmott 2016) as communities may undergo a structural rearrangement through the establishment of new interactions among the remaining species, i.e. rewiring (Brosi & Briggs 2013; Goldstein & Zych 2016; Timóteo et al. 2016; CaraDonna et al. 2017; Hallett, Mitchell, Chamberlain, & Karron 2017). Recently, the complex web of interactions that sustain long-term survival of co-occurring species has been visualised and analysed in the form of interaction networks, whose structure can be described by topological descriptors, such as connectance, nestedness, or specialization (Petanidou, Kallimanis, Tzanopoulos, Sgardelis, & Pantis 2008; Ramos-Jiliberto, Valdovinos, Moisset de Espanés, & Flores 2012; Poisot, Stouffer, & Gravel 2014; Trøjelsgaard, Jordano, Carstensen, & Olesen 2015).

Under the ongoing global biodiversity crisis, gaining predictive capacity regarding the consequences of species extinctions is arguably one of the most pressing needs in ecology (Isbell et al. 2017). Extinction simulations of species interaction networks can be particularly useful to predict consequences of species extinctions at the community level (Rumeu et al. 2017). Several studies have now shown that the extent of secondary extinctions is affected by the original structure of the networks, for example with more connected mutualistic communities being more robust to such perturbations (Thébault & Fontaine 2010). However, such simulations have been increasingly criticised for being too conservative regarding the establishment of new interactions (Blüthgen, 2010; Vieira & Almeida-Neto 2015). Although most studies to date do not allow network rewiring (i.e. the emergence of new interactions that compensate for lost ones) (Memmott, Waser, & Price 2004; Santamaría, Galeano, Pastor, & Méndez 2014; Correa et al. 2016), some began to incorporate different algorithms that allow some type of network rearrangement (Carvalheiro, Barbosa, & Memmott 2008; Kaiser-Bunbury et al. 2010; Ramos-Jiliberto et al. 2012; Schleuning et al. 2016). To prevent the virtual creation of interactions that are actually impossible due to morphological, temporal or spatial mismatches, i.e. forbidden links (Jordano 2016), some of these studies constrain rewiring to previously observed interactions (e.g. Kaiser-Bunbury et al. 2010; Timóteo et al. 2016). The incorporation of rewiring in extinction simulations showed ecological networks to be more robust to secondary extinctions than when no rewiring was accounted (Kaiser-Bunbury et al. 2010). Nevertheless, since the potential interactions considered in simulations with rewiring are often constrained by the locally observed interactions, these may be biased towards the most abundant interactions (Fründ, McCann, & Williams 2016; Plein, Morris, Moir, & Vesk 2017). Therefore, the potential of natural communities to originate new interactions that have not been previously recorded in the target network remains unclear, rendering most simulations highly speculative as they may not reflect the real consequences of species extinctions (Timóteo et al. 2016). To overcome this limitation and increasing the spectrum of potential interactions being established during rewiring simulations, one can incorporate information of interactions observed on other locations.

Given the ongoing threat that frugivores and their habitats are facing worldwide (Farwig & Berens 2012), experiments on how seed dispersal networks behave after the extinction of fleshy-fruited plant species are needed to evaluate the potential consequences for the remaining species in these networks, which ultimately may affect plant recruitment and long-term vegetation dynamics (Traveset, Heleno, & Nogales 2014; Bello et al. 2015; Rumeu et al. 2017). On the one hand, the typical generalist nature of frugivorous interactions (Fuentes 1995; Blüthgen, Menzel, Hovestadt, Fiala, & Blüthgen 2007) is likely to render dispersal networks more robust to species extinctions than predicted through constrained extinction simulations that do not allow the establishment of previously unobserved interactions (Rumeu et al. 2017). On the other hand, there are important morphological, temporal, and spatial limitations to the interactions between fruits and their bird dispersers (Olesen et al. 2011), and unconstrained rewiring might lead to a dangerous overestimation of network resistance to secondary extinctions (Ramos-Jiliberto et al. 2012; Rumeu et al. 2017). Therefore, identifying potential interactions is essential for meaningful extinction simulations.