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Predicting the impacts of co-extinctions on phylogenetic diversity in mutualistic networks



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ABSTRACT

An important bias in the estimations of threatened evolutionary history is that extinctions are considered as independent events. However, the extinction of a given species may affect the vulnerability of its partners and cause extinction cascades. Co-extinctions are likely not random in the tree of life and may cause the loss of large amounts of unique evolutionary history. Here, we propose a method to assess the consequences of co-extinctions for the loss of evolutionary history and to identify conservation priorities. We advise considering both the complexity of the interaction networks and the phylogenetic complementarities of extinction risks among species. Using this approach, we demonstrated how co-extinction events can prune the tree of life using various species loss scenarios. As a case study, we identified pollinators for which extinctions would greatly impact plant phylogenetic diversity within local pollination networks from Europe. We also identified species features that may result in the highest losses of phylogenetic diversity. Our approach highlights the consequences of co-extinctions on the loss of evolutionary history and may help address various conservation issues related to co-extinctions and their impacts on biodiversity.

1. Introduction

Phylogenetic Diversity (PD) is now considered to be a key measure for conservation. In addition to representing the heritage of Earth, PD may also capture feature diversity and future benefits to society (i.e., option values) (Forest et al., 2007; Faith et al., 2010). The impact of the 6th extinction crisis on PD could be dramatic, especially when extinctions tend to be clustered in the tree of life (thus threatening not only terminal branches but also deep branches shared by the species at risk) or when species descending from long and isolated branches are threatened (Veron et al., 2016). However, previous assessments of atrisk PD considered extinctions as independent events (Faith, 2008; Jono and Pavoine, 2012) and did not account for possible co-extinctions (Dunn et al., 2009). A co-extinction is the extinction of a species as a consequence of its dependence on another that has gone extinct or declined below some threshold abundance (Colwell et al., 2012). In a recent study, Veron et al. (2016) reviewed the global loss of evolutionary history due to species extinctions in taxa such as mammals, birds, squamates, amphibians, corals, plants and fish but none of the estimated loss considered co-extinctions. Similarly, conservation strategies based on evolutionary history at risk generally rely on species IUCN threat status but do not account for the dependence of species on each other to survive (e.g. May-Collado and Agnarsson, 2011; Gudde et al., 2013; Jetz et al., 2014; Veron et al., 2017). Co-extinctions could be the primary fuel for the extinction crisis and particularly affect mutualistic communities (Koh et al., 2004; Rezende et al., 2007; Dunn et al., 2009). Mutualistic networks used to exhibit remarkable persistence and stability. However, current threats, including climate change, nutrient enrichment, habitat fragmentation, overhunting and exotic species introduction, have decreased the resilience of mutualistic communities and precipitated local extinctions (Tylianakis et al., 2008; Dunn et al., 2009; Toby Kiers et al., 2010). Moreover, when conditions become more stressful, mutualist species may increasingly depend on each other. They may thus collapse simultaneously when a critical point in the driver of extinction has been reached (Dakos and Bascompte, 2014; Lever et al., 2014).

Plant-pollinator networks may be particularly vulnerable to such coextinction phenomena due to the global fall in pollinator populations (Potts et al., 2010, 2016). Declines in pollinator species have been documented in highly industrialized countries due to anthropogenic pressures, such as changes in land use, pesticides, management-induced pathogens, and invasive species (Potts et al., 2016). Pollinator decline

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may be interdependent with plant decline as a large proportion of plants depend on animal pollination for reproduction (Ollerton et al., 2011). For example, in Britain and the Netherlands, Biesmeijer et al. (2006) found evidence of a decline in bee diversity that corresponded to a parallel decline in plant abundance. Co-extinctions are expected to weaken the sustainability of mutualistic networks and cause loss of species richness (e.g., Memmott et al., 2004), functional diversity (Sellman et al., 2016) and evolutionary history (Dunn et al., 2009). However, the magnitude of losses in these three components of biodiversity may differ (Dunn et al., 2009; Cianciaruso et al., 2013; Sellman et al., 2016). Here, we focus on the impacts of co-extinctions on evolutionary history which have been poorly investigated so far.

It has been well established that the tree of life is vulnerable to coextinctions when interactions are evolutionarily conserved, i.e., when closely related species tend to share many interacting partners (Gómez et al., 2010; Elias et al., 2013; Fontaine and Thébault, 2015). First, some species interact with partners sharing similar traits, which may be related to a shared evolutionary history (Faith, 1992; Thompson, 2005; Santamaría and Rodríguez-Gironés, 2007; Junker et al., 2013; Chamberlain et al., 2014; but see Ives and Godfray, 2006; Fontaine et al., 2009). Consequently, the extinction of those species can increase the vulnerability of closely related partners. These extinctions may thus cause a fast decline in evolutionary history (Rezende et al., 2007; Cianciaruso et al., 2013; Vieira et al., 2013). Second, the phylogenies of interacting species may mirror each other, a hypothesis called "Fahrenholz's rule" (Fahrenholz, 1913). The extinction of related species may lead to the co-extinction of closely related interacting partners (Light and Hafner, 2008; Cruaud and Rasplus, 2016; but this still must be demonstrated in mutualistic networks).

Only a few studies have considered co-extinctions to estimate threatened evolutionary history, and the models used by these studies were too simplistic. For example, they assumed that a plant could go extinct only when all its interacting pollinators were lost (Rezende et al., 2007; Cianciaruso et al., 2013), or they did not account for the expected losses based on phylogenetic complementarities among species (Vieira et al., 2013; Vieira and Almeida-Neto, 2015). A complementarity approach based on extinction risks states that the probability that a deep branch will go extinct depends on the probability that all the species supported by the given branch go extinct (Faith, 2008). If complementarity is not accounted for, the risk of losing deep branches is incorrectly assessed, as is the risk of losing PD (Steel et al., 2007; Faith, 2008; Veron et al., 2016). Here, we propose a new method to fill this gap and to estimate potential extinction risks in a phylogenetic context that accounts for the probabilities of co-extinctions and phylogenetic complementarities among species. We assessed how much evolutionary history could be lost when consecutive co-extinctions occur. This approach enabled us to identify species for which extinction would cause a disproportionate loss of evolutionary history in their interacting partners. We then investigated how the timing of extinctions as well as plant and pollinator features related to mutualism may influence the risks of losing evolutionary history. We applied this approach to eight flower visitor networks in Europe. In spite of the previously mentioned benefits to use PD in conservation, concrete actions are scarce. The EDGE program (Isaac et al., 2007), the list of threatened fish in the U.S (Fay and Thomas, 1983), educational panels in the Australian museum of natural history (Faith, personal communication), are among the few practical examples we are aware of (Veron et al., 2016). This may be because of practical difficulties, such as the lack of phylogenies for some taxa or because the benefits to use evolutionary history in conservation are misunderstood (Winter et al., 2012). We demonstrated, thanks to our concrete case study, how evolutionary history and co-extinction can be incorporated in biodiversity loss assessments to enlighten conservation actions. Our method has thus the potential to be a new valuable contribution to design a framework for PD conservation.

2. Materials and methods

2.1. Expected loss of PD and species richness due to co-extinctions

The method we propose is based on the inclusion of probabilities of co-extinction in an index of expected loss of PD (ExpPDloss).

2.1.1. Expected loss of PD

The ExpPDloss index has been highly recommended for measuring the PD of a group threatened with extinction (plants in our case study). Indeed, this index accounts for the phylogenetic complementarities of extinction risks among species of a given group (Steel et al., 2007; Faith, 2008; Veron et al., 2016). Consider a phylogenetic tree, hereafter simply named 'tree', for the group of species of interest (plants in our case study). The tips of the tree represent species. Consider also a vector named 'proba' with the extinction probabilities of these same species. Expected loss of PD (ExpPDloss) can be calculated as follows:

$$ExpPDloss(tree, proba) = \sum_{b} L_{b} \prod_{k_{b}} p_{k_{b}}$$
(1)

where k_b designates the k^{th} descendant of branch *b* in tree, p_{k_b} is the extinction probability of the k^{th} descendant of branch *b*, and L_b is the length of branch *b* (Faith, 2008; Fig. 1).

We define the expected loss of species richness (ExpSRloss) as the sum of extinction probabilities:

$$ExpSRloss(proba) = \sum_{i} p_{i}$$
⁽²⁾

where *i* designates the *i*th species (plant species in our study) and p_i denotes its extinction probability.

In our model, we then used the probabilities of co-extinctions in Eqs. (1) and (2).

2.1.2. Probabilities of co-extinctions

We defined the probabilities of co-extinctions following Vieira et al. (2013):

$$P_{ij} = R_i d_{ij} \tag{3}$$

where P_{ij} accounts for the co-extinction probability of the affiliate species *i* following the loss of species *j*, R_i is the demographic dependence of species *i* on mutualism and d_{ij} is the dependence of species *i* on species *j*. In plant visitation networks, we estimated R_i for each plant species according to three reproduction traits: pollination vector, selfsterility and reproduction type. The qualitative data for those traits were derived from the BioFlor database (Klotz et al., 2002). We then converted the qualitative data for those three traits into discrete quantitative scores (Table 1). R_i was then assessed as the mean value of the three scores. We calculated d_{ij} as the proportion of interactions that species *i* loses when species *j* goes extinct out of all interactions involving species *i* (Bascompte et al., 2006). The vector of co-extinction probabilities due to the loss of pollinator *j* refers to the probabilities of co-extinctions of all the plants that interact with species *j* (Fig. 1).

2.2. Loss of plant evolutionary history due to pollinator extinctions

2.2.1. Consequences of pollinator extinctions for plant ExpPDloss and ExpSRloss

We used data from eight plant visitation networks sampled in Europe to estimate the possible consequences of pollinator extinctions for the plant evolutionary history under various scenarios of species loss. Full descriptions of networks can be found in the literature (Herrera, 1988; Elberling and Olesen, 1999; Memmott, 1999; Dicks et al., 2002; Bartomeus et al., 2008; Dupont and Olesen, 2009) as well as in the Web of Life database http://www.web-of-life.es. Four networks were binary, whereas the other four were quantified with visitation frequencies. The approach we developed allows for the Download English Version:

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