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Original research article

Does the role that frugivorous bird species play in seed dispersal networks influence the speed of evolutionary divergence?

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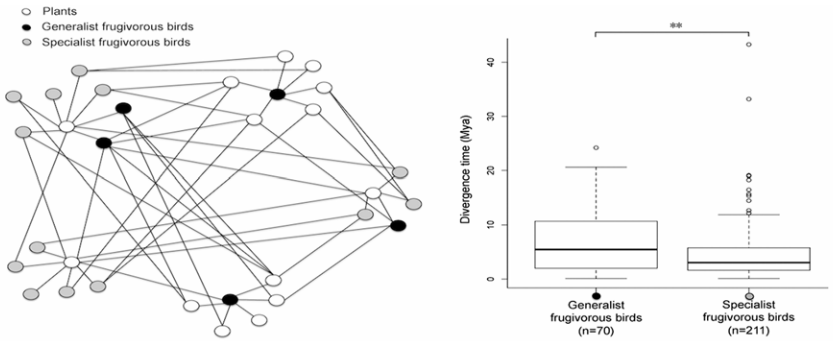
GRAPHICAL ABSTRACT



HIGHLIGHTS

- Do specialists in mutualistic networks diverge faster in evolutionary time?
- A phylogeny includes the divergence time of frugivorous birds from sister taxa.
- Species were classified as specialists or generalists in seed dispersal networks.
- Divergence times of specialists were smaller than those of generalists.

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ABSTRACT

Extensive work on plant–animal mutualistic networks has shown that species in such networks vary in their number of connections with other species, from highly connected species ('super-generalists') to those connected only to a few other species ('specialists'). How these species with different degrees of network specialization differ in their speciation

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rate remains largely unexplored. Here we hypothesize that having many interaction partners lowers the amount of leverage of any one partner, and slows coevolution. We then explored the speciation rate in frugivorous birds in a dataset of published seed dispersal networks, using a recent phylogeny that has a date for the divergence time of all bird species from their most closely related sister taxa. We found that generalist species' divergence time was longer than specialist species'. While there may be other correlated traits to specialization that could contribute to this result, specialists and generalists did not vary in the size of their global distributions, and thus specialists are not simply rarer, if the size of the distribution reflects the species' abundance. We discuss whether similar tests can be applied to other kinds of plant–animal interactions, and what level of taxonomy is appropriate to investigate to answer these sorts of questions.

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1. Introduction

In ecological and evolutionary studies, the introduction of network analysis has revolutionized our understanding of species interactions, including both trophic interactions and mutualisms (Proulx et al., 2005). Early work incorporating network approaches to mutualistic plant animals interactions (Jordano, 1987; Bascompte et al., 2003), focused on the topology of the network architecture. One pattern seen repeatedly in mutualistic networks is that species have skewed distribution of links per species, with some very connected species and many poorly connected ones (Vázquez et al., 2009). Poorly connected species are generally called "specialists", and better connected ones "generalists" or even "super-generalists"; however, because of the ambiguity in these words (Devictor et al., 2010), we hereafter refer to them "network specialists", "networks generalists". Networks are also generally nested (network generalist animals interact with network specialist plants, and visa versa), and show evidence for modularity (groups of species that interact closely with each other; Bascompte et al., 2003; Jordano et al., 2003; Bascompte et al., 2006; Olesen et al., 2007; Bascompte, 2009; Fontaine et al., 2011).

With the better understanding of mutualistic networks' structural properties and a large number of empirical network data available, researchers have also begun exploring how networks evolve over time and influence the evolution of the species that participate in them. For example, Rezende and colleagues found that phylogenetically related species tend to play the same roles (i.e., have similar number of interactions) in more than one third of the networks they studied, and interact with the very same subset of partners in nearly half of those networks (Rezende et al., 2007a), and this phylogenetic signal may ultimately contribute to nestedness (Rezende et al., 2007b). Guimarães et al. (2011) took a different tack, looking at issues such as the complementarity (characteristics that facilitate interaction) between interacting species and convergence (similar characteristics) among species at similar positions in the network, and finding that network super-generalist species intensified coevolution (a point that was also theoretically suggested by Thompson, 2005). However, a question that remains unanswered is whether network specialists and network generalists evolve at different rates.

The question of whether specialization influences the speed of evolution and speciation is a major focus of the field of evolutionary ecology. Previous studies on the evolution of ecological specialization mainly focus on one taxon or just a few taxa (Vrba, 1987, 1992; Fernández and Vrba, 2005; Cantalapiedra et al., 2011; Salisbury et al., 2012). Specialization is a bit of paradox in evolution as it has long been thought of as a dead-end, with specialized taxa vulnerable to extinction (Simpson, 1944; Moran, 1988). But theoretical work is conflicting: whereas Vrba (1980, 1987) suggested that generalist species have lower speciation and extinction than specialist species, Eldredge and Cracraft (1980), invoking competition, proposed generalist species might have a higher chance of extinction. Empirical evidence on the transition rates between the two states have also produced conflicting results, with some studies finding the transition towards specialization more prominent (e.g., wood beetles, Kelley and Farrell, 1998; walking sticks, Crespi and Sandoval, 2000; phytophagous insects, Nosil, 2002; mammals, Fernández and Vrba, 2005), and others finding the opposite trend (e.g., birds, Lanyon, 1992; bees, Muller, 1996 and Armbruster and Baldwin, 1998; butterflies, Janz et al., 2001; seed beetles, Morse and Farrell, 2005). The cumulative evidence from phylogenetic work, however, has shown that specialization is not necessarily an evolutionary "dead-end": generalists may become specialists over time, and the process may also go in reverse (Colles et al., 2009).

Importantly, the definition of specialization here in this literature is usually linked to foraging niche, habitat selection, or distributional range (e.g., in Devictor et al., 2010 categorization, "realized Grinnellian specialization"). Similar questions need to be asked for network specialization (which may be categorized by Devictor et al., 2010 as "realized Eltonian specialization"), and the recent wave of time-calibrated phylogenies may provide sufficient data for such investigations. We here conduct an exploratory analysis on how the network specialization of frugivorous birds in seed dispersal networks may have influenced their speciation rates and divergence times. For the evolutionary data, we used recent global time-calibrated phylogeny of birds, in which all known bird species are included (Jetz et al., 2012, 2014), and network data was obtained from previously published studies. We hypothesized that network specialist species are dependent on their few interacting partners and that this dependence might increase their chances of extinction, or the possibilities of speciation. In contrast, the many interactions of network generalists mean that the leverage of any one partner is less. We also test whether network generalists and specialists have differently sized distributional ranges, to see if network specialists might be generally rare, and such rarity might increase their extinction rates.

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