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Review paper

Making dispersal syndromes and networks useful in tropical conservation and restoration

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ABSTRACT

Dispersal syndromes and networks must be used cautiously in conserving and restoring seed-dispersal processes. In many tropical forests most tree and shrub species require dispersal by animals for local persistence and for migration in response to environmental change. The most important errors to avoid in practical use of both dispersal syndromes (suites of fruit and seed characteristics that attract different dispersal agents) and network modules (groups of interacting dispersal agents and plants bearing fruits or seeds that they eat) are: (1) assuming that use of fruit resources by fruit-eating animals implies effective seed dispersal; (2) assuming that superficially similar fruits imply equally effective dispersal by similar animals, and (3) assuming that fruit resources at issue support animal populations. This essay explores strengths and weaknesses of uses of dispersal syndromes and disperser networks modules in conservation and restoration. Examples include some that are consistent with expectations from syndrome categorization and some that are not. An unappreciated weakness in using either dispersal syndromes or network modules is that contingent foraging by animals in highly disturbed habitats, now comprising 60%–70% of tropical land biomes, may not resemble foraging choices or consequences in protected closed forests, where most research on tropical seed dispersal is done. General prescriptions for the future include maintaining or creating habitat heterogeneity in largely deforested landscapes where remnant closed forests still exist, and active restoration in landscapes where little heterogeneity remains. In both cases, adaptations of multiple frame-work tree approaches have the best chance of preserving or enhancing populations of animal-dispersed trees and their seed vectors, and in opening migration paths in response to climate change.

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1. Introduction

Changes in land use and climate affect and will continue to affect interactions among species. The range of phenomena is potentially huge, including competition, predation, herbivory, pollination, and the balance of mutualistic and harmful microbes in soil, roots and above-ground tissues of plants (e.g. Blois et al., 2013; Brodie et al., 2014; Mangan et al., 2010; Valiente-Banuet et al., 2015). Alteration of any of these could be limiting for some plant and animal species, but the class of interactions most at risk that affects both plant persistence in place and migration in response to global change is seed dispersal (Corlett, 2009; Howe, 2014; Martínez-Garza and Howe, 2003; McConkey et al., 2012). Insufficient attention is given to tree persistence and migration in the 60%–70% of the area of tropical forest biomes that have been substantially altered by deforestation, habitat fragmentation, agriculture or bushmeat hunting within the last century (e.g. Effiom et al., 2013; McConkey and Drake, 2006; Moran et al., 2009). This is troubling because residual forests provide valuable functions that deserve attention (Turner and Corlett, 1996; Hernández-Ruedas et al., 2014). For instance, 50 km^2 of a 96% deforested Mexican landscape still hold more tree species than all of Europe (Arroyo-Rodríguez et al., 2009; Latham and Ricklefs, 1993). To preserve biodiversity in place and to facilitate tree migration, far more attention must be paid to conserving and restoring seed-dispersal processes in fragmented and otherwise disturbed landscapes than is now the rule.

A potential tool is to use fruit and seed characteristics to predict dispersal processes as tools for conservation and restoration of tropical biodiversity. Plants produce fruits and seeds that are clearly adapted by morphology and nutritional content for dispersal, and animals have morphological, physiological and behavioral adaptations for finding and eating fruits (Table 1). Van der Pijl (1982) documents broad suites of fruit or seed characters as "dispersal syndromes" reflecting agents most likely to disperse seeds. Potential relevance of dispersal syndromes is more important than ever with development of theory of mutualist networks (e.g. Bascompte and Jordano, 2014). Network frameworks promise to quantify interactions among mutualists within entire communities, both to understand the contemporary structure of interactions as indicated by which animals eat fruits and potentially disperse seeds, and by identifying "modules" of plant species served by predictable guilds of dispersal agents (Table 2). Understanding modular structure helps forecast changes in network structure from anthropogenic disturbances. Modules are not synonymous with dispersal syndromes, but both frameworks use suites of fruit and seed characteristics to predict use by different groups of animals. A difference is that dispersal syndromes are general properties thought to reflect evolutionary history, while modules are derived from empirical results that indicate that the indicated interactions exist somewhere some of the time. Legitimate questions are "How predictive are syndromes and networks in radically changing landscapes?" and "Are these networks of mutualists?"

Definitions offered here are simplified for discussion (Table 2). For instance, "narrow sense" effective dispersal is in principle possible to measure, but is not operational because it is not feasible to follow fates of thousands to millions of individual seeds from dispersal to reproduction for trees that require decades to mature (Schupp and Jordano, 2011). It is feasible to document rates of survival and mortality in demographic stages (seeds, seedlings, saplings, sub-adults, adults) for many plant species in different environments. Probabilities of survival vary with environment, but their estimation is possible, making the idea of effective dispersal instructive. In another example, actual definition of network modules employs an algorithm based on empirical determination of links (interactions) between fruit- or seed-eating animals and plants that they disperse (Bascompte and Jordano, 2014, pp. 151–152). This means that a prospective dispersal syndrome that predicts interactions is retrospectively reflected by empirical determination of network modules at a given time