Network analyses have emerged as a new tool to study frugivory and seed dispersal (FSD) mutualisms because networks can model and simplify the complexity of multiple community-wide species interactions. Moreover, network theory suggests that structural properties, such as the presence of highly generalist species, are linked to the stability of mutualistic communities. However, we still lack empirical validation of network model predictions. Here we outline new research avenues to connect network models to FSD processes, and illustrate the challenges and opportunities of this tool with a field study. We hypothesized that generalist frugivores would be important for forest stability by dispersing seeds into deforested areas and initiating reforestation. We then constructed a network of plant–frugivore interactions using published data and identified the most generalist frugivores. To test the importance of generalists we measured: 1) the frequency with which frugivores moved between pasture and forest, 2) the bird-generated seed rain under perches in the pasture, and 3) the perching frequency of birds above seed traps. The generalist frugivores in the forest network were not important for seed dispersal into pastures, and thus for forest recovery, because the forest network excluded habitat heterogeneities, frugivore behavior, and movements. More research is needed to develop ways to incorporate relevant FSD processes into network models in order for these models to be more useful to community ecology and conservation. The network framework can serve to spark and renew interest in FSD and further our understanding of plant–animal communities.

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1. Introduction

Scientific progress depends on the existence of new analytical and conceptual models, as well as on shifts between old and new ones (Kuhn, 1962). In this paper, our goal is to advance a relatively new conceptual approach—mutualistic interactions from the perspective of the entire community—that has emerged since the seminal papers of Jordano (1987) and Jordano et al. (2003) introduced network theory to the study of mutualism. Here we identify the strengths, and most importantly, the opportunities that lay ahead with this analysis tool, along with a field study to illustrate these challenges and opportunities.

An appropriate approach for frugivory and seed dispersal (FSD) systems needs to be based on the consideration of multiple and simultaneous interactions between plants and frugivores. This is because FSD systems are characterized by plant species that are (or could be) dispersed by multiple frugivore species, which in turn disperse and/or depend on other plant species or foods (Herrera, 1985; Jordano et al., 2003, 2007). Furthermore, important pre- and post-dispersal processes exist, making the outcomes of plant–animal interactions highly contingent on local conditions (Herrera, 1985). Thus, we need a framework that not only considers multiple species, but also integrates this complexity with the context-dependence typical of FSD systems.

To explain interaction and coevolutionary patterns of plants and their mutualistic frugivores, a general model or “paradigm” was developed (Janzen, 1970; McKey, 1975; Howe and Estabrook, 1977). At the heart of this paradigm was a dichotomy between generalized and specialized coevolutionary plant and animal strategies (Howe, 1993). Under this paradigm there was a strong focus on coevolution, and thus, on interactions from the narrow perspective of a specific plant or frugivore (Herrera, 1985; Howe, 1993). Now, advances in network theory have enabled ecologists to examine plant–animal interactions at the level of whole communities, with the potential to begin linking FSD to plant community ecology and coevolutionary dynamics. Indeed, discussions about the importance and consequences of generalization and/or specialization in FSD and other symbiotic systems now take place in the context of network studies (e.g., Gómez et al., 2010).
1.1. Insights from plant–frugivore interactions networks

Networks are composed of nodes (i.e., species) and edges (i.e., relationships between nodes). For a plant–animal network, there are two types of nodes, the plant species and the animal species; these networks are bipartite (Fig. 1, Watts and Strogatz, 1998; Jordano et al., 2003; Bascompte and Jordano, 2007). With network analyses we can simplify the complex connectivity patterns between interacting species in plant–animal communities, and gain insight into ecological and evolutionary processes (Bascompte and Jordano, 2007; Ings et al., 2009; Bascompte, 2009). Network analyses are especially useful because they provide a way to quantitatively compare plant–animal interaction patterns across different communities by means of standard network measurements (Bascompte and Jordano, 2007). This tool represents a substantial advancement by allowing simple natural-history observations to include information beyond the mere presence and frequency of interactions collected in a variety of ways – to be used quantitatively in network measurements (Jordano, 1987; Bascompte et al., 2003).

The major theoretical finding from network analyses is that properties (i.e., measurements) of mutualistic networks and their nodes are linked to the stability and functioning of these communities (Jordano et al., 2003; Bascompte and Jordano, 2007; Bascompte, 2009; Table 1). The presence of certain network properties in mutualistic communities may make networks more resistant to collapse from the extinction of species, correlating with community robustness to natural and anthropogenic disturbances (Fontaine et al., 2006; Jordano et al., 2006; Memmott et al., 2004; Bastolla et al., 2009). Most mutualistic networks have an overabundance of specialists (i.e., species that have few mutualists), and extremely few generalists (i.e., species with many mutualists). Because these highly generalist species have such a large contribution to the connectivity of a network, they are hypothesized to be critical for the stability of communities.

1.2. Challenges and opportunities

Given the prominence that mutualistic network models now have, we are now faced with the challenge of experimentally validating hypotheses from network models (Table 1). We are poised to progress beyond quantifying and comparing mutualistic network properties (e.g., Basilio et al., 2006; Jordano et al., 2003; Philipp et al., 2006), explaining interaction structure (e.g., Rezende et al., 2007; Santamaría and Rodríguez-Girones, 2007), or exploring the theoretical consequences of network structure in communities (e.g., Fortuna and Bascompte, 2006; Okuyama and Holland, 2008). We need explicit empirical tests of the relationship between structure and function in FSD networks (Table 1). At the most basic level, studies are needed to examine and validate how network and node properties predict ecological outcomes (Table 1). A network perspective thus has a large potential to inform conservation, management, and restoration practices in terrestrial ecosystems if important processes can indeed be inferred from network structural patterns (Bronstein et al., 2006; Rico-Gray and Oliveira, 2007; Tylianakis et al., 2010).

1.3. Establishing and testing the relationship between pattern and process in plant–frugivore mutualistic networks

In order for FSD networks to inform seed dispersal and community processes, we must expand conventional FSD network models to include information beyond the mere presence and frequency of frugivory events (e.g., see Vázquez et al., 2005). The appropriateness and accuracy of the data that goes into the network will directly affect the certainty of our interpretations regarding structure and process. For example, if the purpose is to use networks to depict the effect of frugivores on the plant community, then the presence/absence data on frugivore use of plants may not suffice. To bridge theoretical conclusions and biological interpretations, we must ensure that species (nodes) that are identified as important by network analyses are truly important species in communities and processes.

For example, independently of the frequency with which frugivores interact with fruiting plants, frugivores can display plant-specific variation in handling behavior, quantity of seed removal as related to frugivore size (Fig. 2), and effects of guts on seed germination (Moermond and Denslow, 1985; Wheelwright, 1991; Jordano and Schupp, 2000; Carlo et al., 2003; Levey and Martínez del Río, 2001). Furthermore, differences in the movement behavior of frugivores, including interactions with habitat heterogeneities and resource fluctuations, can further decouple node importance in networks from the actual dispersal process (Howe, 1993; Wang and Smith, 2002; Carlo and Morales, 2008; Genini et al., 2009). Studies have shown how dispersed seeds can experience different mortality rates when dispersed across a variety of habitats and microhabitats (Schupp and Fuentes, 1995; Levine, 2000). Species that appear to be important or keystone in a frugivory network graph may prove less important or unimportant when additional aspects of frugivore behavior and habitat heterogeneities are critical to FSD outcomes (e.g., Fig. 1).
A solution could be to weight edges in a way that depicts plant–frugivore relationships at each stage of the seed dispersal loop (Fig. 1A). For example, we can assign a weight to edges in a frugivory network according to the frequency of interaction between plants and frugivores, or by the quantity of seed removal (Figs. 1A and 2). An approach could be to first construct separate networks with weighted edges that incorporate different FSD processes, and then combine them to obtain the overall contribution of specific plant–frugivore interactions (edges) to the network (Fig. 1A). For example, to use networks to examine the community context of plant recruitment, information can be combined on frugivory rates, fruit-handling, seed removal, movement, seed deposition patterns, and recruitment. To examine the contribution of different frugivores to recruitment, we sum each frugivore’s edges into its weighted degree (Fig. 1B). The development of innovative indexes to use as FSD edge weights, as well as the ways to combine them is a fertile ground for future research.

### 1.4. Case study: identifying important seed dispersers (frugivory nodes) from a frugivory network

Here we will illustrate how ignoring FSD processes and context-dependence of networks can lead to misidentifying the nodes (species) that are most important for ecological outcomes. In our example, we will try to infer from a network the importance of species for the stability of a forest community. In this case, stability refers to the ability of a forest community to regenerate after deforestation. Seed dispersal into human-made pastures is the most critical process for tropical forest regeneration (Holl, 1999), thus we hypothesize that the most generalist frugivores — the nodes who interact with the greatest number of species, and have the greatest interaction frequency — are the most important agents of seed dispersal into pastures. For this we constructed a network of plant–frugivore interactions (Fig. 2) using the data from Carlo et al. (2003). Spindalis portoricensis, Vireo altiloquus, and Locustella portoricensis were the top three frugivore generalists in this network. The adjacency matrix was derived from observational frugivory data collected in four study sites, during an eight-month period, in mature Puerto Rican montane secondary forests. For further detail about the sampling we refer readers to Carlo et al. (2003).
1.5. Bird movement patterns and seed dispersal on pastures

To test the specific hypothesis generated from the network (Fig. 3), we measured the arrival of bird-dispersed seeds in pastures adjacent to forest habitats. We measured four parameters: 1) the frequency with which bird species moved from pastures to forest and vice versa, 2) the bird-generated seed rain under naturally occurring perches in the pasture, 3) the frequency of perching of birds on such natural perches, and 4) the presence and absence of species in both habitats. The study was conducted in Hacienda La Esperanza (HLE) nature reserve in the municipality of Manatí, in the northern coast of Puerto Rico (18°28’47.07”N, 66°31’31.93”W). The reserve has an area of 1005 ha, and is composed of pastures (formerly sugar cane), and fragments of mature subtropical humid forests. The transitions between pasture and forest habitats are abrupt around forest patches.

From February through July of 2009 we documented the movement patterns of seed-dispersing birds in three pastures at HLE that were adjacent to patches of forest. Observations were conducted for 1-h periods at three study sites (Site 1 = 18°28’36.44’’N, Site 2 = 18°28’36.54’’N, Site 3 = 18°28’36.11’’W; 18°28’47.04’’N, 66°31’33.30’’W). Observers worked in pairs, with one person watching and following the movements of individuals while the other person recorded data. Observations were recorded from bird species already known to consume fruit as a regular component of their diet (i.e., focal species), and to effectively disperse seeds (Carlo et al., 2003). Activity from granivorous finches, hummingbirds, and falcons was not recorded since such species do not eat fruit or disperse seeds. Once a frugivorous bird was located in the pasture, it was followed until lost from view, or for up to 10 min (whatever occurred first). The habitat transitions of birds were also recorded during observation periods. A habitat transition was counted when a bird that was perched on the pasture moved to a forest patch and vice versa. Observations were conducted on 14 different days, spending one hour between 7:00 and 11:00 am at each site on each sampling day, for a total of 42 observation hours. Once a month for six months we also conducted 10-min temporal measures (11 sampling days for each of three sites), compared for bird species using one-way ANOVA. Because there were repeated temporal measures (11 sampling days for each of three sites), we used the average number of transitions per bird species per site to conduct the ANOVA, which resulted in a (conservative) sample size of three.

2. Results and discussion

2.1. Avian-generated seed rain in pastures

The 50 seed traps placed under isolated trees at the three pasture locations captured a total of 3409 avian-dispersed seeds. These seeds belonged to 23 avian-dispersed plant species (44 seeds from two unidentifiable species), with traps having an average count of 23.5 ± 3.95 (S.E.). The most seeds belonged to trees (10 spp.), followed by shrubs (8 spp.) and lianas (5 spp.). Erythroxylum brevipes, Cordia polypephala, Cissampelos pareira, Casearia sylvestris, and Cissus verticillata accounted for 86.7% of seed counts. Of these, the tree E. brevipes and the shrub C. polypephala accounted for 54.3% of the total number of seeds and were the most widespread across seed traps. Seeds from 17 species were rare and represented by less than 100 seeds (avg. = 28 ± 7.0 S.E.).

In the forest fragments we found 17 of the 24 birds found by Carlo et al. (2003) in other forest fragments, and used to build the frugivory network (Fig. 3), but of the top three generalist species (ranked by degree) we recorded only 2 (S. portoricensis, the top species, and V. alitloquus, the third species). In addition, we recorded two species that were not present in the network: Crotaphaga ani and Icterus icterus. In pastures we found only C. ani, Mimus polyglottos, Myiarchus antilinarum, S. portoricensis, and Tyrannus portoricensis. In pastures we recorded a total of 952 frugivore movement and perching observations. Of these, 68.8% belonged to Tyrannus, 30.1% to Mimus, and the remaining 1.1% to three bird species (Coccyzus, Myiarchus, and Crotaphaga). Of all records, 545 were perching records at locations containing seed traps (Fig. 4A and B). When correlating the perching records for each frugivore species, we found a positive relationship between the quantity and species richness of seeds on seed traps, and the perching frequency of Tyrannus, which is an insectivore that occasionally eats fruit, above seed traps (Fig. 4A and B). There was no trend for the relationship between Mimus, which was the second...
most active bird species on pastures and is more frugivorous than *Tyrannus*, and the seed rain (Fig. 4A and B). When examining habitat crosses among bird species, we recorded a total of 155 habitat crosses, with *Tyrannus* being responsible for 70.3% of all crosses, *Mimus* for 27.1%, and all other avian species for 2.6%. Thus, forest–pasture crossing rates were significantly higher for *Tyrannus*, averaging about 4 crosses per hour across sites, and clearly outperforming all other bird species in connecting forest–pasture habitats (Fig. 4C).

Our results suggest that *Tyrannus dominicensis* was mainly responsible for the bulk of the copious and diverse ornithochorous seed rain arriving in the three pasture sites, although *Tyrannus* has little participation in the network. But their insect-dominated diet is precisely what makes them very abundant and active in open habitats such as pastures (Raffaele, 1989), where they can feed on insects using their characteristic "flycatching" behavior from perching locations. Their insect-dominated diet of *Tyrannus* also serves to disguise its importance as a frugivore in the original network. The frequent use of perches on pastures, combined with their frequent habitat crosses to exploit fruit resources in forest patches, have the potential added benefit of directing seeds to protected and shaded microhabitats (shrubs, trees) that should increase recruitment in pastures (Vieira et al., 1994; Slocum, 2001).

3. Concluding remarks

As shown by our case study, the capacity of a network analysis to inform frugivory and seed dispersal processes was highly dependent on the nature, detail, and context of the data used to construct the network. Our frugivory network was based solely on observations made in forested habitats, and not surprisingly, it failed to reveal the key species that are most important for the ability of these habitats to recover from severe perturbations. If important underlying heterogeneities are not considered (e.g., spatial, temporal, behavioral), a network could be unable to identify the agents important for seed dispersal, and thus fail to correctly assess community organization and dynamics. This limitation can be overcome by including the most appropriate measurements to represent the network edges. For example, in our case study we directly related frugivore activity to the seed dispersal process and rejected the hypothesis that the most generalist frugivores were responsible for bringing...
seeds into pasture recruitment sites. However, with this additional information we can improve our network model and make it more representative of the frugivore community's role in seed dispersal and forest regeneration in Puerto Rican pastures. Therefore, in addition to experimentally testing relationships between network measurements and ecological processes (Table 1), a network model could be made to include spatial and movement information in its edges in a multiplicative fashion (Fig. 1).

In conclusion, network theory provides ecologists with an important tool to examine complex interactions between multiple species of plants and animals, and has great potential to advance FSD research. Most of the emphasis so far has been placed on the theoretical study of network structure, and less attention has been given to the relationship between network structure and predictions about ecological processes (Table 1). We believe that the next stage for FSD will be to design and conduct studies that explicitly test network predictions that include different ecological processes. For this, new studies designed with network models in mind are needed because relevant tests cannot be conducted with most available plant–animal mutualistic data sets. Examining the role of species in communities is an especially important new focus, because node properties have been understudied in FSD networks (Table 1). More emphasis on node (i.e., species) properties has the potential to create a stronger connection between network theory and empirical FSD research. The network framework can thus serve to spark and renew interest in the gathering of new, community-wide natural-history data that will also serve in the testing and validation of network models and further our understanding of plant–animal communities.

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