

Transience and constancy of interactions in a plant-frugivore network

SUANN YANG,^{1,†} RÉKA ALBERT,² AND TOMÁS A. CARLO³

¹*Biology Department, Presbyterian College, Clinton, South Carolina 29325 USA*

²*Department of Physics and Department of Biology, Pennsylvania State University, University Park, Pennsylvania 16802 USA*

³*Department of Biology, Pennsylvania State University, University Park, Pennsylvania 16802 USA*

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Abstract. Plant-animal mutualistic interactions such as frugivory and seed dispersal display great variation in time due to fluctuations in fruit abundance, animal abundance, and behavior. In particular, some species participate in interactions with other species only transiently, while other species are active for longer periods of time. Species with a longer period of activity are able to interact with more species, and thus engage in constant participation in an interaction network. Species with high constancy would thus be expected to help maintain the biodiversity of a community; however, the manner in which constant species link to their partners may be critical to species coexistence. Because species that interact with many partners concurrently could create more competition compared to those species that interact sequentially with many partners, evaluating the concurrence in an interaction network sheds light on how the network can maintain biodiversity. In this study, we investigate how phenological patterns of fruit production and frugivore presence affect the temporal variation of a plant-frugivore network, and focus on the manner in which high degree species collect their interactions over time. We found a clear separation of activity periods: most species appeared only briefly and participated in relatively few interactions, or showed activity for longer time periods and participated in more interactions. Species that were active for longer time periods often shifted interactions, resulting in a sequential collection of their partners in time, rather than concurrence. For the seed dispersal mutualism in particular, sequential accumulation of partners may allow plant species more opportunities to disperse their seeds compared to concurrence. We suggest that for temporally and spatially heterogeneous landscapes, sequential accumulation of partners would serve to reduce competition and facilitate coexistence of species.

Key words: abundance; frugivory; mutualism; network; phenology; temporal dynamics.

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† **E-mail:** syang@presby.edu

INTRODUCTION

Network analyses of mutualistic plant-animal interactions reveal that certain network properties of these communities remain invariant, though interactions are inherently dynamic and change over time (Jordano et al. 2003, Basilio et al. 2006, Medan et al. 2006, Bascompte and

Jordano 2007, Olesen et al. 2008, Petanidou et al. 2008, Burkle and Alarcon 2011). Intra-annual temporal dynamics have been documented in several plant-pollinator networks (e.g., Basilio et al. 2006, Medan et al. 2006, Alarcón et al. 2008, Olesen et al. 2008) and a few plant-seed disperser networks (e.g., Carnicer et al. 2009, González-Castro et al. 2012). The dynamics of mutualistic

animal-plant interactions are in part driven by temporal changes in the abundances of animals and the plant resources they use, such as fruits for frugivores (e.g., Carnicer et al. 2009) and flowers for pollinators (e.g., Olesen et al. 2008). Availability of flowers and fruits, in turn, is largely controlled by species-specific phenological patterns and its interaction with supra-annual weather patterns. Phenology, by influencing patterns of interaction (i.e., edges) among species, can have a large role in determining the properties of networks as a whole.

Phenological drivers of the interactions between plant and animal species may also have implications for the stability of communities. Species that are highly abundant and/or active for longer periods of time have a greater opportunity to interact with many other species, and therefore should engage in a high number of mutualistic interactions relative to species that are transient and/or rare (Olesen et al. 2008, Olesen et al. 2010). For example, newly active species interact with partners that already have many partners over the course of a year (Olesen et al. 2008); thus some mutualistic networks appear to grow by preferential attachment (Barabási and Albert 1999). If species of greater constancy support many other species (i.e., act as generalists), then they would be expected to maintain the biodiversity of the community (Bascompte and Jordano 2007).

The realization of this expectation, however, could depend on how interactions between species are formed over time. Interactions of a generalist species that are concurrent may have different ecological consequences from those interactions occurring in a non-overlapping fashion. Specifically, how the partners of generalist species are accumulated over time could translate into different regimes of inter- and intraspecific competition. For example, generalist frugivores could interact with the majority of fruiting species available at any moment, or the occurrence of pairwise interactions could be affected by competition and facilitation between fruiting species (Carlo 2005, Carlo et al. 2007). How competition takes place within the network is important to evaluate because classic theoretical models (May 1973, Pimm 1979) and field experiments (e.g., Tilman 1996) predict that population dynamics of individual species in a

community become progressively unstable as the number of competing species increases. Interspecific competition, however, could be reduced if interactions between species are structured in certain ways. For example, theory suggests that competition between species is minimized if they share generalist mutualistic partners; this reduced competition increases the number of species that can coexist in the community (Bastolla et al. 2009). In other words, the benefit from sharing a mutualistic partner can counteract competition for other resources (e.g., soil nutrients for plants). An assessment of how species interact with their mutualistic partners throughout the entire season, specifically how those partners are accumulated over time, could be critical to our understanding of how interaction networks affect biodiversity, particularly for dispersal-limited plant species (e.g., Howe and Miriti 2004).

In this study, we first assess the temporal variability in interactions between species in a plant-frugivore community. We then focus on the extent to which interactions are constant vs. transient in the network of interactions, as well as how concurrent vs. sequential are interactions that involve generalist species. We explore the role of phenological abundance in driving patterns of constancy and concurrence, and discuss the implications of constancy and concurrence for the dispersal of plant species and the stability of communities.

METHODS

The plant-frugivore network

In a plant-frugivore network, plant and bird species are the nodes, and a frugivorous interaction between a bird-plant pair constitutes an edge. We analyzed the plant-frugivore interaction data in Carlo et al. (2003) focusing on the Cialitos study site, a continuous 9-ha area composed of a near even mixture of rustic shade coffee (*sensu* Moguel and Toledo 1999) and 50-year old secondary forest patches. Here we will briefly describe the methodology, but for full details we refer readers to the original paper. Fruiting plant phenology in Cialitos was recorded once a month from February to September of 1998 from a sample of 190 trees belonging to 29 species of plant that included fleshy-fruited

epiphytes, parasites (mistletoes), shrubs, and trees. Plants were visited in a monthly schedule and the number of ripe fruit estimated using abundance categories that increased quasi-logarithmically. We used the average of the ripe fruit abundance categories' midpoints as our estimator of fruit abundance for each species within sites. We multiplied each of these species' ripe fruit mean estimates by the corresponding plant species density/ ha at each site to obtain an estimate of ripe fruit/ha for each fruiting plant species per month. The density of fruiting plant species was obtained by surveying 24 independent circular vegetation plots (11 m radius) evenly spaced throughout the plot. Bird abundance was also recorded once a month (always in the same week when fruits were counted) using nine permanent point count stations. Bird foraging observations were conducted for 5 hours each day, twice per week. Observations started each morning in a randomly selected area of the site, a point from which observers moved, following the nearest bird foraging activity. Observations (edges) were strictly independent from one another, and individual birds were observed until a feeding bout took place, a point at which a different individual was followed. For logistical reasons, a few plant species, such as the similar mistletoes *Phoradendron piperoides* and *Phoradendron hexastichum*, were not distinguished in the field, and thus are considered a single node (e.g., *Phoradendron* spp.).

These observation methods produced data of a high enough resolution to detect the preferences of frugivores for fruiting plants of both short (<1 month) and long (≥ 8 months) periods (Carlo et al. 2003). In addition, our separate assessment of species abundance allows us to estimate the reliability of our network representation of the true community. We estimated our network's reliability by first counting the frequency of co-occurrence of species for which edges are possible (an edge exists during any of the observation periods). We then examined our set of observations for mismatches of no edges when an edge is possible. We assumed that the absence of an edge when the abundance of both species was relatively high is a true zero. The remaining cases, when one or both species' abundances are lower than the lowest abundance in which an edge was observed, constitute 18 out of the 216

possible edges (8% of cases), and for these we may have lacked power to detect rare interactions.

Temporal measures of network structure

We initially analyzed our network with conventional network measures that are adjusted to include a temporal perspective. We then developed several measures to encapsulate constancy and concurrence of species and their interactions within our community. Except where noted, these measures use unweighted edges, thus capturing interaction diversity among species rather than interaction frequency. In addition, we define the number of different partners of a node (i.e., degree) as the amount of participation of a species in the network, rather than the level of generalization of a species. For birds, 'generalists' could be either frugivores that eat many fruiting plant species, or omnivores (dietary generalists that eat more than fruit). This distinction reduces the potential for confusion (Blüthgen et al. 2008).

Network-level measures.—To adjust conventional network measures to include temporal dynamics, we first constructed momentary subgraphs (Morris and Kretzschmar 1995); also called 'time-specific sequential webs' (Basilio et al. 2006) or 'temporal networks' (Kaiser-Bunbury et al. 2010), for each month of the frugivore network (Fig. 1b–i; Appendix). Note that we chose monthly momentary subgraphs, because Carlo et al. (2003) was able to detect frugivore preferences (i.e., important determinants of edges) using this time interval. We then compared these momentary subgraphs to the fully compiled graph of the entire season (full graph; Fig. 1a; Appendix). Each momentary subgraph includes only the edges observed during each monthly sampling period. Networks were visualized with the *plotweb* function and conventional measures calculated with the *networklevel* function in the *bipartite* package in R (Dormann et al. 2008, R Development Core Team 2013). Excluding inactive nodes (i.e., those that do not participate in an edge), we calculated for each subgraph several standard network properties, and then compared subgraph properties to those obtained from an analysis of the full graph for: degree (k , number of edges per node), edge weight (frequency of interactions between two

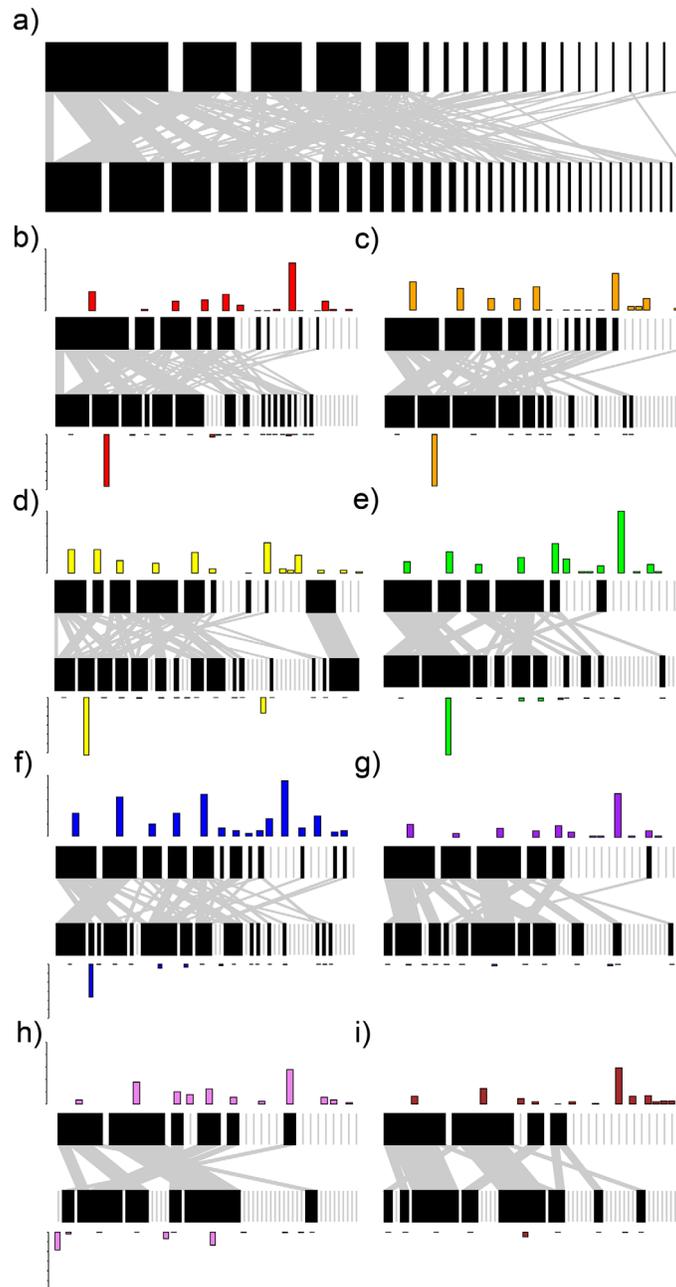


Fig. 1. (a) Full and (b-i) momentary network representations of the plant-frugivorous bird community are dissimilar. Birds are represented in the upper row and plants in the lower row of each network, in the same order as the full network. For (b) February, (c) March, (d) April, (e) May, (f) June, (g) July, (h) August, and (i) September momentary graphs, the relative abundance of birds is plotted above each bird node, and the fruit abundance below each plant node. All species from the full graph are included in each momentary graph. Species that participate in an interaction are drawn in black; those that do not participate in an interaction are drawn in grey (note that these inactive species are not considered in the calculations of network and node properties). For each network graph, the size of each species' box is proportional to that species' contribution to the interactions occurring in the network, and the width of each interaction is proportional to the frequency that this interaction was observed.

Table 1. Metrics to quantify temporal variation in ecological networks.

Temporal metric	Applicable network component	Definition	Values	Interpretation
Momentary degree, mk_i (Morris and Kretschmar 1995)	nodes	Number of partners that species i interacts with during a specific time interval	$mk_i \geq 1$	Larger values mean greater participation in the network of interactions during a specific time interval
Average proportional momentary degree, $\langle mk_i \rangle / k_i$	nodes	Average proportion of partners that species i interacts with during a specific time interval out of the total number of partners that species i has over the entire season	$0 \leq \langle mk_i \rangle / k_i \leq 1$	Smaller values correspond to species whose participation in the network is sequential rather than concurrent
Momentary weight, me_{ij}	edges	Frequency of interactions between species i and j during a specific time interval	$me_{ij} \geq 1$	More common interactions have larger values during a specific time interval
Relative momentary weight, me_{ij}^*	edges	How frequently the interaction between species i and j occurs relative to the average me_{ij} , i.e., $me_{ij} - \langle me_{ij} \rangle / \langle me_{ij} \rangle$	negative to positive values possible	Values closer to 0 mean that interactions occur consistently throughout their periods of occurrence
Duration (Russo et al. 2013)	nodes, edges	Number of time intervals in which species i interacts with any other species, or in which edge e_{ij} occurs	duration ≥ 1	Distribution of duration values shows the temporal variability in interactions throughout a community
Fidelity	nodes	Average edge duration of species i , divided by the duration of species i	fidelity > 0	Larger values correspond to species who participate reliably in the same interactions

nodes), connectance (proportion of realized edges in the network, Jordano 1987), number of connected components (isolated clusters of nodes, also called compartments), and nestedness (hierarchical structure, Bascompte et al. 2003). Although several nestedness metrics are currently available, we chose to use *NODF*, because it has been demonstrated to be robust to network size and thus allowed us to make comparisons between networks (Almeida-Neto et al. 2008). Nestedness may arise from specific species behavior or simply from random interactions between synchronously active species (Bascompte et al. 2003). The *occosimu* function in the *vegan* package (Oksanen et al. 2012) was used to test whether the nestedness in the observed network was random or not. We constructed 200 random replicates of each network using the quasiswap simulation method (nonsequential swaps only within rows or columns, Miklós and Podani 2004). Then, as an additional comparison across networks, we calculated relative *NODF* nestedness for each network as $NODF^* = (NODF - \langle NODF_R \rangle) / \langle NODF_R \rangle$, where $\langle NODF_R \rangle$ is the mean *NODF* for the 200 random replicates of the network (see Bascompte et al. 2003). For additional network properties and other information about the sub-

and full graphs, see the Appendix.

Node and edge measures.—The following measures (summarized in Table 1) quantify the temporal patterns of nodes and edges:

1. *Momentary degree, mk_i .*—A node’s momentary degree is the number of interactions that this node participates in during a particular momentary subgraph (Morris and Kretschmar 1995). In a plant-frugivore network, larger values denote greater participation in the network of interactions during a specific time interval. Average momentary degree of a node is calculated over all subgraphs (of the 8 possible in our case) in which the node was active. The average proportional momentary degree of species i , $\langle mk_i \rangle / k_i$, equals its average momentary degree divided by the total number of partners that species i has over the entire season. Species of smaller average proportional momentary degree are species whose participation in the network is sequential rather than concurrent.

2. *Momentary weight, me_{ij} .*—Edge weight is the frequency of observing an edge between two nodes; an edge’s momentary weight is then the frequency of observing this edge during a particular subgraph. More common interactions have larger values during a specific time interval. The average momentary weight $\langle me_{ij} \rangle$ is calcu-

lated over all subgraphs in which the edge was observed (i.e., its frequency is non-zero). Relative momentary weight, me_{ij}^* , shows how frequently the interaction between species i and j occurs relative to the average me_{ij} , i.e., $me_{ij}^* = (me_{ij} - \langle me_{ij} \rangle) / \langle me_{ij} \rangle$. Values closer to zero mean that interactions occur consistently throughout their periods of occurrence.

3. *Duration*.—We defined duration as the total number of subgraphs in which a node is active or an edge is observed (i.e., sum of occurrences; Russo et al. 2013). Like the distribution of node degree, which encapsulates the participation of nodes in an ecological network, the distribution of node durations reflects the overall phenology within the network. Although related, node duration differs from phenophase (Olesen et al. 2008), in that node duration includes only the time periods in which the focal node participates in an interaction, whereas phenophase encompasses the entire interval between the initiation and cessation of plant resource availability or animal visitation (Olesen et al. 2008). The distinction between duration and phenophase is important, because when frugivores exhibit strong preferences for a transiently fruiting plant species, they can cease interacting with less desirable, yet still available, fruiting plants (Carlo et al. 2003). Similarly, omnivorous animals may not always eat fruit (Herrera 1982, Wheelwright 1988, Carnicer et al. 2009). Furthermore, duration may not be continuous. To distinguish between continuous and interrupted duration, we plotted the longest continuous length of occurrence against the total number of segments of occurrence. For example, two nodes with duration of 5 months may differ in continuity. The first node, continually active for 5 sequential months, would be plotted at (5, 1). The second node, active for two separate segments of 2 months and 3 months, would be plotted at (3, 2). Note that discontinuity in duration may also be a result of insufficient sampling of rare interactions, rather than a true cessation of activity. Incomplete sampling is unlikely to be the cause of discontinuity in node duration in our dataset because all instances of discontinuous node duration occurred for highly abundant species.

4. *Node fidelity*.—Some nodes may more reliably participate in the same edges (interactions). We defined the fidelity of a node to its partners as

the average edge duration of species i , divided by the duration of species i . Larger values correspond to increasing participation in the same interactions over the entire season, or greater fidelity.

Species availability and interaction structure

Fruiting phenology can strongly influence the preferences of birds for certain fruiting plant species (Carlo et al. 2003), and can explain whether birds forage for fruit or invertebrates (Carnicer et al. 2009). We used general linear models to examine how temporal patterns in species abundance affect node properties and when edges are observed. We conducted separate analyses for birds and plants. For each model, the response variable was the species' average momentary degree, species full degree, proportional momentary degree, species duration, or node fidelity. The independent variable for each model was the relative abundance of species (number of individuals of a species/total number of individuals of all species). To model the presence or absence of edges, the model included bird abundance, plant abundance, and the bird \times plant abundance interaction as factors. These tests were conducted using the *glm.nb* function in R, with the exception of the *glm* function with binomial errors for proportional momentary degree and edge presence, and the *lm* function for arcsine-transformed node fidelity (R Development Core Team 2013). The best-fit models were chosen using AIC (Akaike 1974).

We hypothesized that species with longer durations would also have higher degree, because they have more opportunity to interact with other species throughout the season, compared to species with shorter durations. We classified nodes into four groups: high duration and high participation, high duration and low participation, low duration and high participation, and low duration and low participation. We defined high or low participation of nodes with respect to the average node degree of the network, $k^* = (k - \langle k \rangle) / \langle k \rangle$, such that $k^* > 0.1$ for high participation nodes, and $k^* < -0.1$ for low participation nodes. Likewise, high or low duration was determined with $\text{duration}^* = (\text{duration} - \langle \text{duration} \rangle) / \langle \text{duration} \rangle$, such that $\text{duration}^* > 0.1$ for high duration nodes and $\text{duration}^* < -0.1$ for low duration nodes.

Concurrent vs. sequential interactions in species with high degree

In plant-pollinator networks, species with high degree appear to accumulate partners throughout a season (Olesen et al. 2008). However, the extent to which interactions are concurrent and/or sequential is less known. Thus, we counted the number of partners gained, continued, and lost from one momentary subgraph to the next for the three plants and three birds of highest full graph degree (plants: *Schefflera morototoni*, *Cecropia schreberiana*, and *Phoradendron* spp.; birds: *Nesospingus speculiferus*, *Spindalis portoricensis*, and *Loxogilla portoricensis*).

RESULTS

Cumulative addition of species and interactions increases the size of the full network over time. The latest bird species, the mainly insectivorous *Todus mexicanus*, is added in July, whereas the latest plant species, the small vine *Momordica charantia*, is added in September, the final month of the study. In general, edges varied across the momentary subgraphs, and later momentary subgraphs had fewer active nodes than earlier ones (Fig. 1).

Temporal changes in network structure

As the season progressed, species tended to interact with fewer partners in each momentary subgraph (i.e., momentary degree decreased; Fig. 2a), and maximum edge weights declined over time (Fig. 2b). Because we consider only the active nodes in our calculations, connectance was higher for each momentary subgraph (except for June, month 6) than for the full graph (Fig. 2c). The number of connected components for the momentary subgraphs (active nodes only) also varied, with fewer components than the full graph earlier in the season, and more components than the full graph later on (Fig. 2d). Nestedness decreased with time, with earlier momentary subgraphs having greater nestedness than the full graph compared to later momentary graphs (Fig. 2e). None of the subgraphs or full graph had statistically significantly more nestedness than the randomly simulated networks (Fig. 2f); however, June had statistically significantly less nestedness than the random simulated networks ($p = 0.05$).

The duration of the 54 species in this network varied from only one month to the full length of the season, 8 months (no plants, only birds: *Euphonia musica*, *S. portoricensis*, *Vireo altiloquous*), though intermediate durations appeared to be lacking (Fig. 3a, b). The most frequent duration is one month only, especially for plants (Fig. 3a). The continuity of active participation in network also varied (Fig. 3c, d). Most of the species were continuously active (68% of plants and 75% of birds); however, several species participated in the network in two or more separate time segments (32% of plants and 25% of birds; Fig. 3c, d). With the exception of species with degree of $k = 1$ (in the full network), *Vireo flavirostris* (bird, $k = 2$), *Buchenavia capitata* (plant, $k = 2$), and *Dendroica tigrina* (bird, $k = 3$), species did not participate in the same interactions over time, as shown by node fidelity (Fig. 3e, f). Furthermore, there is a decrease in interaction concurrence, as shown by the average proportional node degree ($\langle mk_i/k_i \rangle$), with increased duration (Fig. 3g, h).

Most of the 81 edges in this network had very low momentary weight (Fig. 4a), that is, a particular interaction was observed infrequently during each month. About half of the edges (85/175) occurred at a frequency equal to their average momentary edge weights (i.e., $me_{ij}^* = 0$; Fig. 4b). However, edges that occurred during only one month comprise the majority of the edges where $me_{ij}^* = 0$, and only 15% of edges (27/175) occur consistently throughout durations of longer than one month. Although a third of the observed interactions (58/175) occurred only during one month, a few, such as that between *E. musica* and *Phoradendron*, *L. portoricensis*-*Guarea guidonia*, and *S. portoricensis*-*Ficus* (7 months) were present for longer time periods (Fig. 4c). The edge duration continuity for the edges revealed some discontinuity (Fig. 4d), like for the nodes (Fig. 3c, d). For example, the *E. musica*-*Phoradendron* and *S. portoricensis*-*C. schreberiana* interactions were in two segments.

The highest momentary edge weights belonged to the edges of longest duration, with the exception of the 2-month interaction between *S. portoricensis* and *Cordia sulcata* (Fig. 5a). In addition, species' average momentary edge weight does not appear to have a strong relationship with full graph degree (Fig. 5b); thus, the contribution of high-degree species to

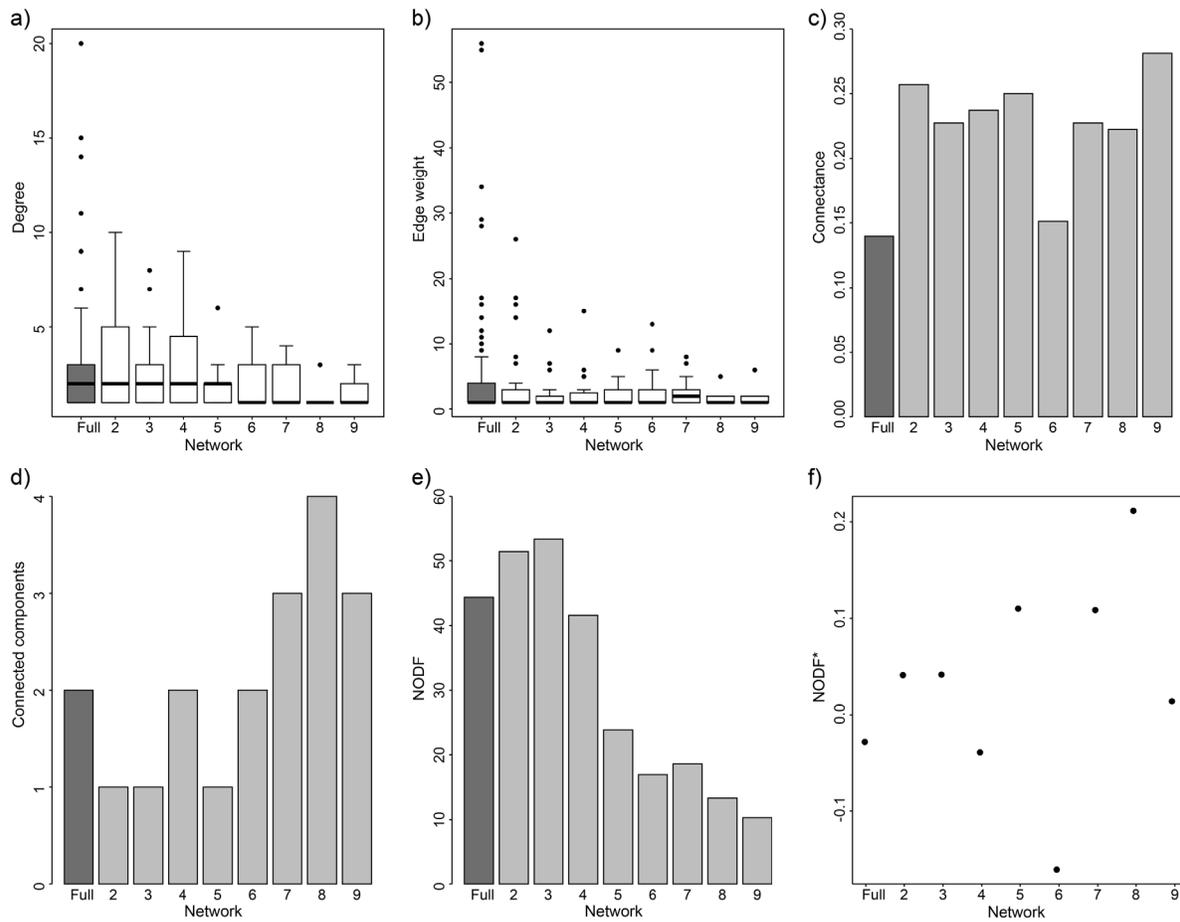


Fig. 2. Conventional network properties, with dark gray corresponding to the full graph, and light gray denoting the value of each property for each month (momentary graph). (a) Species degree, (b) edge weight, (c) connectance, (d) number of connected components, and (e) nestedness of momentary graphs do not always match that of full graphs. With the exception of June (6), whose nestedness was significantly less than the randomly simulated networks, nestedness was no different from the random expectation (f).

an interaction network is not necessarily via consistently frequent interactions with the same partners.

Species availability and interaction structure

We expected phenological differences between plant species to have an influence on network structure, as fruiting plant phenology affects frugivore foraging behavior (Carlo et al. 2003, Carnicer et al. 2009, González-Castro et al. 2012). The relative abundance of species was constant for some nodes, but highly variable for other nodes (Fig. 1). Relative abundance was not a significant predictor of proportional node degree (birds, $p = 0.593$; plants, $p = 0.612$). However,

higher relative abundance did correspond to higher average momentary degree (birds: $p = 0.00219$, plants: 0.0124), higher full degree (birds: $p = 0.0003$; plants: $p = 0.0006$), and to higher node duration (birds: $p = 0.001$; plants: $p = 0.027$). Edges were more likely to be observed when plant abundance was high ($p = 0.001$) and bird abundance was high ($p = 0.002$), though there was also a bird \times plant abundance statistical interaction ($p = 0.04$). Higher relative abundance corresponded to lower node fidelity for plants but not for birds (bird \times plant abundance, $p = 0.011$).

When we assessed node degree and duration simultaneously (Fig. 6), we found that most

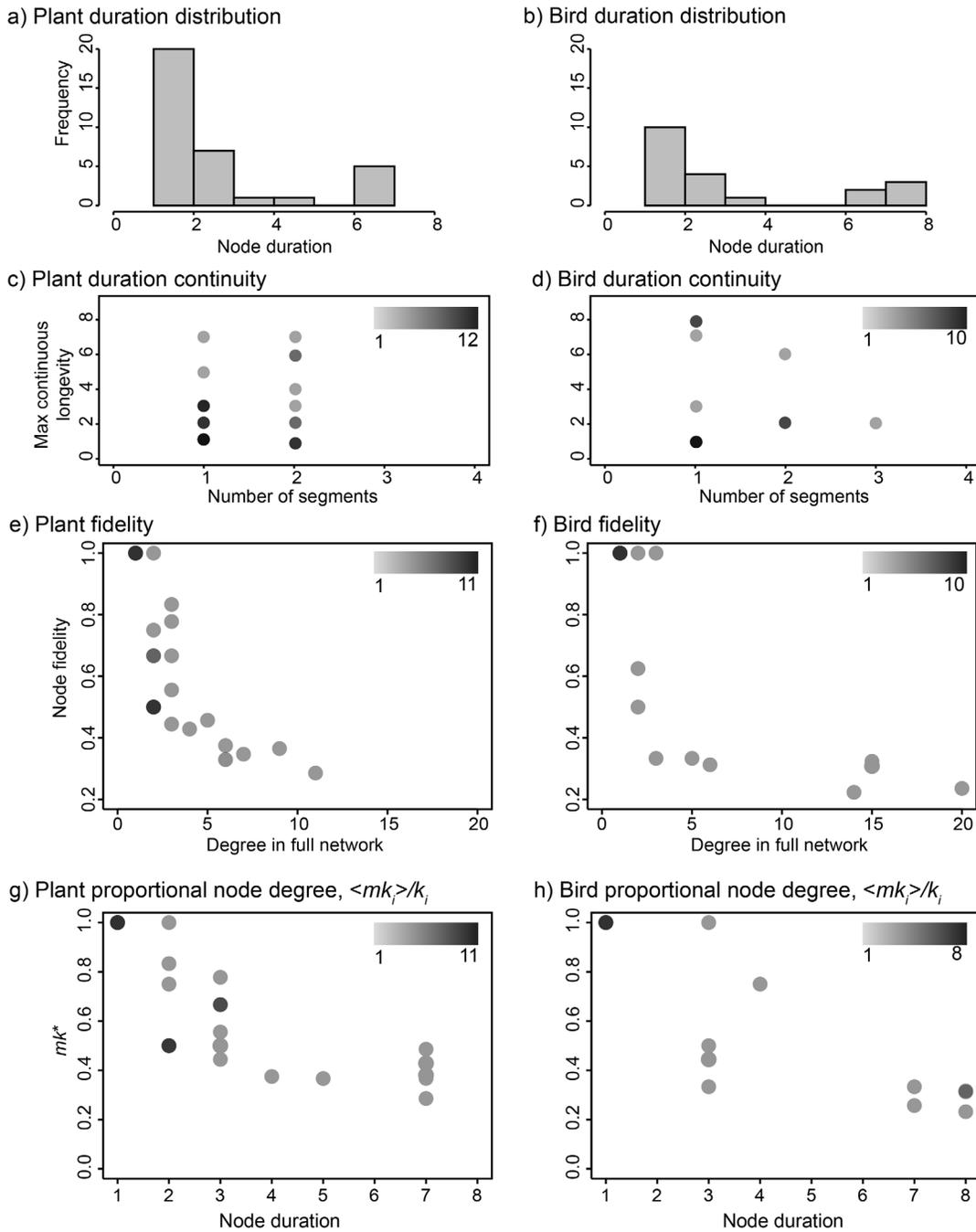


Fig. 3. Plant (left) and bird (right) temporal node measures: Node duration in this network tend to be either low or high, with few intermediate values (a, b). Node durations are primarily continuous, though several nodes do have interrupted activity periods (c, d). The color of each data point corresponds to the number of overlapping data points. The prevalence of low node fidelity reveals that nodes in this network do not participate in the same interactions over time (e, f). Average proportional momentary node degree decreases with node duration, because species with longer periods of activity switch partners frequently (g, h). For c–h, the color of each data point corresponds to the number of overlapping data points.

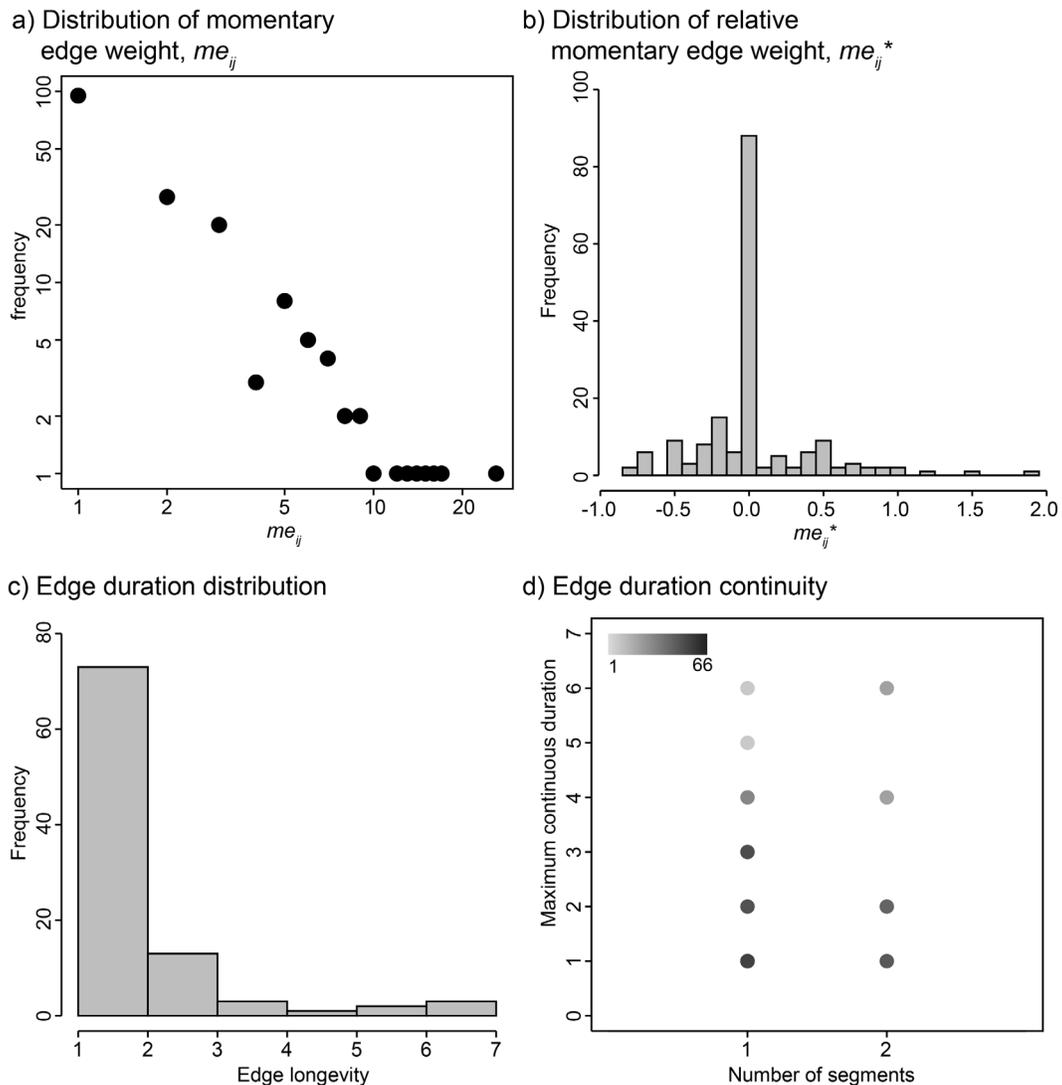


Fig. 4. Distributions of temporal edge measures: The distribution of momentary edge weights in this network shows that most interactions occur infrequently (a). Not all interactions occur consistently over time (b). Edge duration varies from 1 to 7 months, though most interactions are transient (c). Edge duration is primarily continuous, with a few occurring in multiple time intervals (d). The color of each data point corresponds to the number of overlapping data points.

species were categorized as low duration and low participation (13 birds and 19 plants), followed by high duration and high participation (5 birds and 11 plants), and only a few species exhibited high duration and low participation (1 bird: *Melanerpes portoricensis*; 3 plants: *Andira inermis*, *Anthurium scandens*, and *Syzygium jambos*) or low duration and high participation (1 bird: *Margarops fuscatus* and 1 plant: *Musa acuminata*).

Concurrent vs. sequential interactions in species with high degree

The highest full degree (k_i) plants and birds gained, continued, and lost interactions in nearly equal amounts from month to month (Fig. 7). A few interactions were maintained from month to month, but each species' losses across the entire season approached or exceeded each species' full degree (season losses: *S. morototoni* 10, *C.*

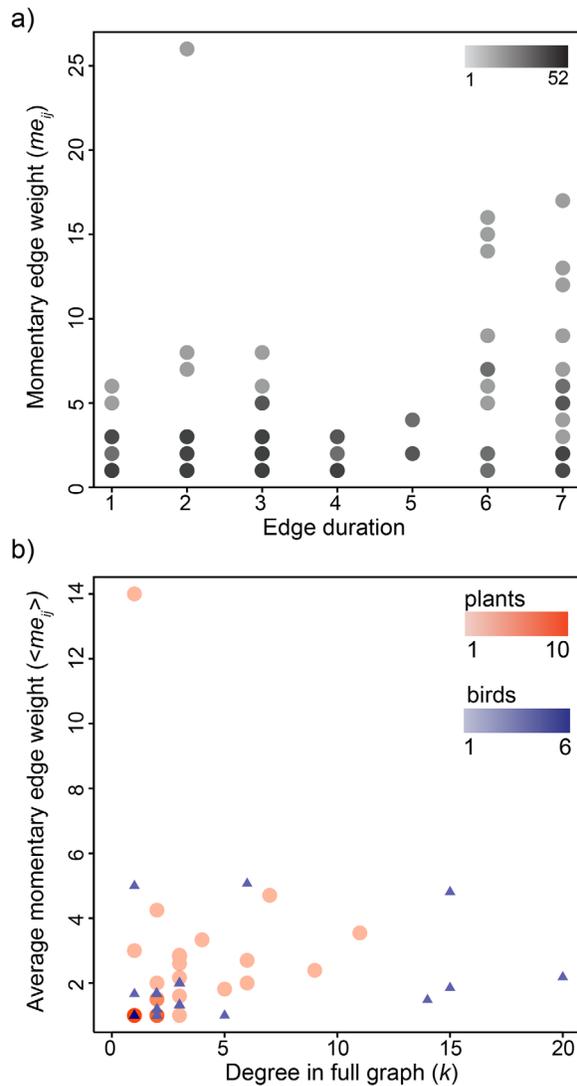


Fig. 5. The highest momentary edge weights appear somewhat more likely to be of long duration (a). A species' full graph degree does not necessarily predict its average momentary edge weight (b). For a–b, the color of each data point corresponds to the number of overlapping data points.

schreberiana 11, *Phoradendron* 8, *N. speculiferus* 19, *S. portoricensis* 17, *L. portoricensis* 15). Total losses can exceed full degree because of the discontinuity of edge duration. These six species have the lowest values of average proportional node degree ($\langle mk_i \rangle / k_i$, see Fig. 3g, h) because they regularly gain and lose many interactions with other species each month.

DISCUSSION

The activity period of the species, as well as the interactions that these species participate in, range from transient to constant. The combination of transience and constancy is reflected in the fluctuations we found in the structural properties of our interaction network over the season. Species that were active for a longer period of time and participated in relatively more interactions did not necessarily participate in the same interactions for their entire active period. Changes in the presence and relative abundance of fruits and frugivores explained the number of interactions of both plants and birds, as well as the length of their active period, but not whether interactions were concurrent or sequential. The group of species with the highest degrees (k) did maintain a number of concurrent interactions from month to month, but also displayed a substantial turnover in interactions. We first discuss the causes of temporal variability in our network, and then identify the consequences of sequential accumulation of interactions for plant-frugivore communities.

Causes of temporal variability

In general, most of the observed temporal variation in network interactions is primarily driven by the diverse phenological patterns of fruiting plant species in Cialitos, which is typical of most fruiting plant communities. Plant species can show striking differences in their patterns of producing and ripening fruit, especially in tropical regions (Frankie et al. 1974). Plant species like *C. sulcata* fruit synchronously in one month, which limits the number of partners it can have, while others like *C. schreberiana* bear ripe fruit for more than 7 months (Carlo et al. 2003), and thus has more opportunity to interact with more partners. To add complexity to this scenario, species with extended fruiting seasons can vary in how prolonged fruiting is accomplished, with some species having a single extended peak preceded by a single flowering event (e.g., *S. morototoni*), while others have several, smaller fruiting peaks that are the product of multiple consecutive flowering episodes (e.g., *G. guidonia*). Thus, the presence of fruit resources at different times within the sampling period serves as a primary filter for

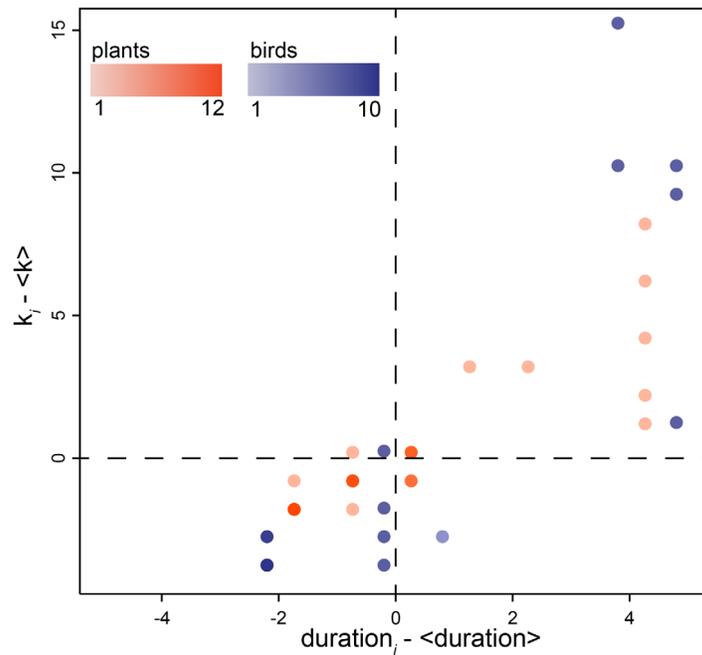


Fig. 6. Most species in this network were of low duration and low participation, or high duration and high participation. Upper left quadrant: low node duration, high participation. Upper right quadrant: high node duration, high participation. Lower left quadrant: low node duration, low participation. Lower right: high node duration, low participation. See *Methods* for calculation of relative k (k^*) and relative duration ($duration^*$). The color of each data point corresponds to the number of overlapping data points.

the presence or absence of edges in temporal networks.

In turn, patterns of frugivory are commonly conditioned by both the relative abundance of fruiting species, and by preferences and physiology of frugivores due to differences in nutritional

qualities of fruit among species (Herrera 1982, Moermond and Denslow 1983, Martínez del Rio et al. 1988). For example, frugivory rates can show type III functional responses (sensu Holling 1959) to the abundance of different fruiting species at any one time, resulting in frugivores

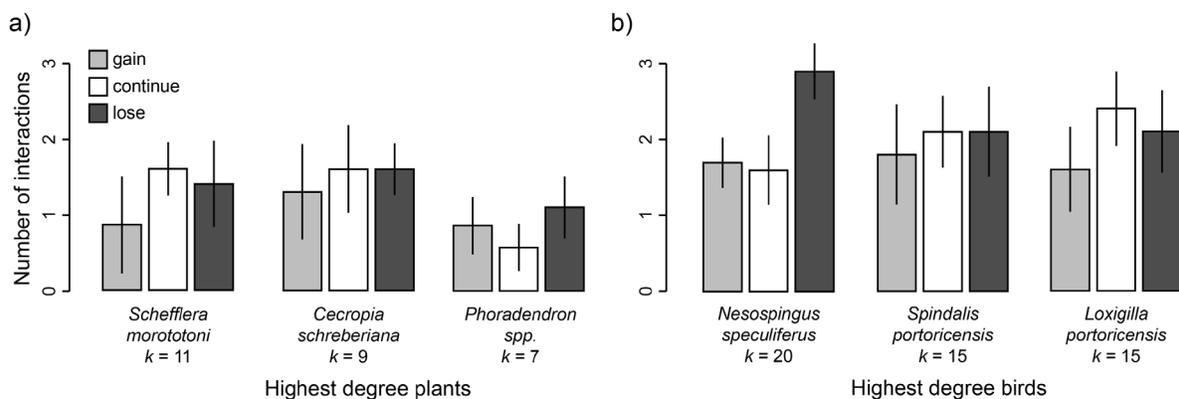


Fig. 7. The highest full degree (k_i) plants (a) and birds (b) continued interactions from month to month, but also exhibited turnover in the identity of their interactions.

temporally specializing on the most abundant species. This type of foraging response may also explain why most edges are of short duration. However, the occurrence and duration of some edges appear independent of relative fruit abundances (e.g., *E. musica*–*Phoradendron*, *L. portoricensis*–*G. guidonia*), which could be explained by the existence of hierarchical choices governing frugivory. Hierarchical choices of frugivores can also explain why nodes (species) show different fidelities, duration, and continuity even when present at similar abundances and/or for similar lengths of time. Indeed, in the analyses we found that a high-degree frugivore continually shifts its foraging focus among different fruit resources (Fig. 7).

Further, the temporal variation of frugivore participation in the network can be influenced by factors other than fluctuations in fruit abundances and hierarchical interactions among fruiting species. For example, diets of omnivores can shift away from fruit when entering breeding and/or migratory seasons, thus reducing their seasonal involvement in the frugivory network (Herrera 1982, Wheelwright 1988). Fig. 6 shows that the most omnivorous species (e.g., *Tyrannus dominicensis*, *Dendroica tigrina*) tend to participate with low duration and also low participation in the network (see also Fig. 1). Interestingly, other omnivores (i.e., *M. portoricensis*) may also have low network participation but show high duration. These differences in omnivory could signify different roles in the community. For example, some omnivores in this community (e.g., *T. dominicensis*) have been shown to be more effective than heavily frugivorous species (e.g., *S. portoricensis*, *L. portoricensis*) in dispersing seeds into deforested habitats (Carlo and Yang 2011).

Interaction concurrence and outcomes of mutualism

The temporal pattern by which high degree species become “generalists” has been described as an accumulation of partners (Olesen et al. 2008) or “preferential attachment” (Barabási and Albert 1999), but these terms incompletely describe the dynamics in our system. The high-degree species in our network do gain a substantial number of interactions each month, but they also maintain a relatively low fraction of

concurrent interactions and lose interactions each month (i.e., they participate in both concurrent and sequential interactions). In these species, specialization is thus possible over the scale of a few months, which is analogous to the observation that species specialize locally but are generalists when considered across biogeographical scales (Thompson 1999).

We propose that this dual (partly concurrent, partly sequential) network growth has consequences for how species of high degree contribute to ecological outcomes in temporally variable networks. In our system, species of high duration and network participation connect the subgraphs into the full season-long graph through the constancy of their activity; however, they do not necessarily participate in the same interactions continuously. In temporally variable networks, “generalists” can serve as the “backbone of the community” (Jordano et al. 2003, Bascompte and Jordano 2007) through their long durations or phenophases (see also Olesen et al. 2008, Olesen et al. 2010), and not through maintaining specific stabilizing interactions. Indeed, if high degree species do not substantially differ from lower degree species with respect to their average momentary edge weight (Fig. 5b), what is the role of these generalist species during shorter time scales? In the context of seed dispersal, seed predation and recruitment commonly vary over a season, and therefore the set of interactions that exists at one point in time could lead to different demographic outcomes compared to another point in time (Fig. 1). These consequences may or may not be captured in the temporally correspondent structure of the interactions (Fig. 2). Thus, we suggest that the importance of generalists vs. specialists during short time scales needs more attention. It may be that for seed dispersal outcomes, the distribution of interactions in a community is more important than the number of interactions that a particular species participates in (Berlow et al. 1999, Bascompte and Jordano 2007, Kaartinen and Roslin 2012).

In Cialitos, we found lower concurrence of interactions in species that had longer duration (periods of activity). Generalists that accumulate their interactions concurrently, rather than sequentially, may create situations of high competition, specifically if mutualistic partners are a

limited resource. For example, if fruiting plants must compete for the services of generalist frugivores, fewer seeds are dispersed from each species at any one moment. If this competition is very fierce, plants risk wasting resources in fruit production. Generalist frugivores with sequentially acquired interactions, on the other hand, arise if plants produce fruits asynchronously, rather than synchronously. With this time partitioning, competition for generalist frugivores is reduced and the likelihood of occurrence of seed dispersal events for each plant species is increased. From the plant point of view, those that sequentially acquire their frugivorous partners over a long time period would perhaps have fewer seed dispersal events at any one point in time compared to plants that maintain interactions with many partners simultaneously over a short time period. This strategy, however, would be expected to be more advantageous in unpredictable, heterogeneous landscapes because seed dispersal events have an opportunity to occur during a favorable time interval or into appropriate locations for establishment. Indeed, when many seeds are dispersed over a short time span, they disperse to fewer locations, which has consequences for the pattern of spatial spread and destination of seeds (Carlo et al. 2013, Morales et al. 2013). Overall, even in the absence of network nestedness (see Bastolla et al. 2009), a pattern of sequential, not concurrent, accumulation of interactions by generalists could create stability through reducing competition at any single point in time, as well as through facilitating the successful establishment of future generations of their partners.

Conclusion

Although many species in an interaction network may be present only transiently, other species participate with greater constancy. High duration species do not necessarily interact continuously with the same partners, and instead may switch their partners as the season progresses. The occurrence of sequential, rather than concurrent, interactions creates the possibility of generalists whose importance for network stability is context-dependent. Functionally, generalist species that accumulate interactions sequentially may play a different role in the community than species that maintain a similar number of

partners concurrently. The patterns of how species connect to other species in an interaction network can also have potential implications for the stability of communities. The concurrence of interactions within a network may reflect the inherent temporal and spatial heterogeneity of the landscape, and translate to how members of a community adjust to accommodate for competition for limited resources.

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SUPPLEMENTAL MATERIAL

APPENDIX

Detailed information for the full and momentary networks

An alternative, matrix representation of Fig. 1 is provided here. Matrix representations of full and momentary subgraphs (Figs. A1–A9) were drawn using the *visweb* function in the *bipartite* package (Dormann et al. 2008) of R (R Development Core Team 2013). Each cell contains the frequency of interactions between a plant (rows)

and a bird (columns).

Full graph and momentary subgraph properties are summarized in Table A1. Metrics were calculated using R (R Development Core Team 2013). All metrics except number of edges, mean edge weight, maximum edge weight, and frequency of edge weight = 1 were calculated with the *networklevel* function (Dormann et al. 2009) of the *bipartite* package (Dormann et al. 2008).

Table A1. Summary of full graph and momentary subgraphs.

Network	Full	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
Size (number of active nodes)	54	25	23	24	16	28	17	12	12
Number of active birds	20	9	12	9	6	12	6	6	4
Number of active plants	34	16	11	15	10	16	11	6	8
Number of edges (interaction links)	95	37	30	32	15	29	15	8	9
Mean edge weight (interaction frequency)	6.62	3.76	2.30	2.44	2.40	2.41	2.87	1.75	2.22
Maximum edge weight	56	26	12	15	9	13	8	5	6
Frequency of edge weight = 1 (singletons)	40	18	17	16	8	19	5	5	6
Connectance	0.14	0.26	0.23	0.24	0.25	0.15	0.23	0.22	0.28
Average unweighted degree, $\langle k \rangle$	1.76	1.48	1.30	1.33	0.94	1.04	0.88	0.67	0.75
Number of compartments	2	1	1	2	1	2	3	4	3
<i>NODF</i> nestedness	44.39	51.42	53.32	41.58	23.89	16.94	18.57	13.33	10.29
Web asymmetry	-0.26	-0.28	0.04	-0.25	-0.25	-0.14	-0.29	0.00	-0.33
Linkage density	5.03	3.59	3.59	3.24	2.12	2.61	2.05	1.52	1.53
Shannon diversity	3.66	2.97	3.02	3.09	2.40	2.93	2.47	1.87	1.85
Interaction evenness	0.56	0.60	0.62	0.63	0.59	0.56	0.59	0.52	0.53
Dependence asymmetry	-0.09	-0.11	-0.09	-0.08	-0.01	-0.05	-0.38	0.00	-0.04
Specialization asymmetry	0.22	0.18	0.09	0.08	0.09	0.05	0.18	0.00	0.20
Bird niche overlap	0.18	0.27	0.38	0.15	0.11	0.21	0.08	0.12	0.02
Plant niche overlap	0.27	0.35	0.28	0.26	0.25	0.15	0.16	0.12	0.21
Togetheriness	0.06	0.11	0.20	0.11	0.06	0.08	0.07	0.08	0.04
C-score†	0.54	0.39	0.30	0.53	0.76	0.68	0.81	0.80	0.89

† Mean checkerboard combinations across all birds.

