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Research

Temporal flexibility in the structure of plant–pollinator interaction networks

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Ecological communities consist of species that are joined in complex networks of interspecific interaction. These interactions often form and dissolve rapidly, but this temporal variation is not well integrated into our understanding of the causes and consequences of network structure. If interspecific interactions exhibit temporal flexibility across time periods over which organisms co-occur, then the emergent structure of the corresponding network may also be flexible, something that a temporally-static perspective will miss. Here, we use an empirical plant–pollinator system to examine short-term (week-to-week) flexibility in network structure (connectance, nestedness and specialization) and in the individual species interactions that contribute to that structure across three summer growing seasons in a subalpine ecosystem. We then compared the properties of weekly networks to the properties of cumulative networks that aggregate field observations over each full summer season. As a test of the potential robustness of networks to perturbation, we also simulated the random loss of species from weekly networks. A week-to-week view reveals considerable flexibility in the interactions of individual species and their contributions to network structure. For example, species that would be considered relatively generalized across their entire activity period may be much more specialized at certain times, and at no point as generalized as the cumulative network may suggest. Furthermore, a week-to-week view reveals corresponding flexibility in network structure and potential robustness throughout each summer growing season. We conclude that short-term flexibility in species interactions leads to short-term variation in network properties, and that a cumulative, season-long perspective may miss important aspects of the way in which species interact, with implications for understanding their ecology, evolution and conservation.

Keywords: connectance, interaction turnover, nestedness, robustness, seasonality, specialization, subalpine, temporal ecology

Introduction

Ecological communities are characterized not only by the identities and relative abundances of their component species, but also by the interactions among these species.

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These interspecific interactions often change perceptibly through time, as organisms transition through stages of their life histories and as seasons progress. As Charles Elton (1927, p. 96) observed, 'Since the biological environment is constantly shifting with the passage of the seasons, it follows that the food habits of animals often change accordingly'.

One common way to characterize interactions within communities is to cast them into an interaction network, whose topological structure may then be related to patterns of biodiversity, evolution of component species, and community function (Bascompte et al. 2006, Bastolla et al. 2009, Thébault and Fontaine 2010, Rohr et al. 2014, Schleuning et al. 2015). To date, the most common perspective on ecological networks is one that in effect assigns fixed values to interactions and to aspects of structure over relatively long time scales (Bascompte and Stouffer 2009, Burkle and Alarcón 2011, Blonder et al. 2012, McMeans et al. 2015, Poisot et al. 2015, Trøjelsgaard and Olesen 2016). Such a temporally-static perspective offers many insights into ecological communities. However, it also stands to overlook more rapid time scales at which interactions form and dissolve in many systems, as organisms (or their life stages that interact) appear and disappear, and as interactions among those present at the same time shift and rewire (i.e. temporal interaction flexibility; Elton 1927, CaraDonna et al. 2017, McMeans et al. 2019). In other words, if interspecific interactions exhibit temporal flexibility across time periods over which organisms co-occur, then the emergent structure of the corresponding networks may also be temporally flexible, something that a static perspective is likely to miss.

Temporal variation in the structure of interaction networks has indeed been documented at multiple scales, from days, to weeks, to months, years and beyond (Winemiller 1990, Alarcón et al. 2008, Olesen et al. 2008, Dupont et al. 2009, Burkle and Alarcón 2011, Trøjelsgaard and Olesen 2016). For example, considerable turnover of species and their interactions can occur across virtually all time scales (e.g. within a day, Fründ et al. 2011; across 120 years, Burkle et al. 2013). Such turnover may lead to greater variation in the structural properties of networks across finer time scales than across longer time scales (reviewed by Trøjelsgaard and Olesen 2016). Additionally, the few studies that have examined the potential consequences of short-term temporal variation in network structure suggest that it is an important component of community dynamics and species coexistence (Saavedra et al. 2016a, b, 2017). Yet, overall, it remains unclear what information is gained from different temporal perspectives, and whether the structural properties of networks are temporally consistent (Trøjelsgaard and Olesen 2016, Schwarz et al. 2020).

Here, we explore the magnitude and consistency of short-term (week-to-week) temporal variation in plant–pollinator networks in a subalpine ecosystem. Because species and their interactions turn over rapidly in this system (i.e. from one week to the next; CaraDonna et al. 2017), we focus on weekly time periods when species are known to co-occur and have the opportunity to interact. We also investigate temporal variation in the interactions of individual species (e.g. relative specialization) as well as their contribution to overall network structure in each week. To these ends, we use nearly 29 000 observations of pollinators visiting flowers recorded across three successive summer growing seasons. These observations yield 42 pollination networks resolved at the scale of single weeks, for each of which we quantified aspects of network structure and species' roles within these networks. With these data we 1) quantify temporal variation in network properties from week to week across the growing season; 2) explore how network properties calculated at finer, biologically-relevant time scales compare to those calculated from cumulative, season-long networks; and 3) ask whether weekly networks exhibit temporal variation in their potential robustness to the simulated loss of species. Our analyses shed light on some aspects of temporal consistency – and inconsistency – of network properties, and suggest how the temporal flexibility of interactions of individual species contributes to the emergent structural properties of networks containing those species.

Material and methods

Study site and system

We worked at The Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado, USA (38°57′5″N, 106°59′3″W, 2900 m a.s.l.) over the summers of 2013, 2014 and 2015. The RMBL is a mosaic of wet and dry subalpine meadows intermixed with aspen and conifer forest. This subalpine system is exemplified by temporal change (CaraDonna et al. 2017). It is highly seasonal, with long winters devoid of most biological activity and a short summer growing season of 3–5 months (CaraDonna et al. 2014). Within the summers a series of plant species flower in succession, and insect and hummingbird pollinators enter the system via eclosion and immigration and leave it via death, diapause and emigration.

Plant–pollinator observations

We observed interactions between flowers and insect and hummingbird pollinators at weekly intervals for the majority of all of the three summers (n = 12 weeks in 2013, 15 in 2014, 15 in 2015). Plant and pollinator species, as well as their interactions, can turn over rapidly across the summer growing season in this subalpine ecosystem (Fig. 1, CaraDonna et al. 2017). Our investigation of plant–pollinator interactions on a week to week basis reasonably captures this temporal variation and also provides us with sufficient information to construct meaningful interaction networks.

All observations took place in two adjacent dry meadows that cover ca 2800 and 3015 m^2 and are separated by ca 100 m of aspen forest, and began ca one week after snowmelt in each summer, coinciding with first emergence of flowers

and pollinators. We divided each meadow into four sampling quadrants. Floral abundance was measured once per week within a 25 × 1 m transect in each quadrant of each meadow, by counting all open flowers or flowering heads (for species with small clustered flowers, such as Asteraceae) within the transect (CaraDonna et al. 2017). Within each week, we also conducted 32 15-min observations of pollinators, for a total of 8 h per week. Each 15-min observation period occurred within a single meadow quadrant. We first randomly selected one of the two meadow sites; then we observed the four meadow quadrants within this meadow in random order; and then we repeated this process in the other meadow. During each 15-min period a researcher walked around the focal meadow quadrant and recorded all observed interactions between plants and pollinators. We defined an interaction as a visitor of any species unambiguously contacting the reproductive structures of a flower; we refer to floral visitors as pollinators while recognizing that their quality as mutualists may vary widely.

The number of observation periods during which a given pollinator species was observed during a single week was used as an estimate of its relative abundance (CaraDonna et al. 2017). Interaction rarefaction curves and abundance-based richness estimators indicated that our sampling effort sufficed to detect most (on average 85–93%) of the pairwise interactions that occurred in each week (see CaraDonna et al. 2017 for details). Each complete weekly census took place over 2–3 consecutive days and was separated from the start of the next census by 3–5 days.

A single plant–pollinator interaction network was constructed from the observations of each week. A cumulative plant–pollinator network was constructed by aggregating all weekly observations across each entire summer growing season. All flowering plants were identified to species, and all pollinators to species or to the finest taxonomic level possible under field conditions (for simplicity, we refer to all taxonomic levels as 'species' in what follows). Pollinators were not collected during observations to prevent artefacts of destructive sampling.

Structure of pollination networks

For all 42 weekly networks and for all three cumulative, season-long networks, we investigated temporal variation (i.e. temporal flexibility) in three metrics that describe different aspects of the structure of interactions: 1) connectance; 2) network-level specialization; and 3) network nestedness. For network connectance and nestedness, we calculated both binary (unweighted) and frequency-based (weighted) metrics (network specialization is already a frequency-based metric). Because overall patterns of week-to-week variation were the same when we calculated either binary or frequency-based metrics for connectance and nestedness, for brevity we mostly discuss binary metrics in the main text (details and values for frequency-based metrics are given in the Supplementary material Appendix 1 Table A1).

Connectance describes a basic component of network complexity (Bascompte and Jordano 2014) and is calculated as the proportion of observed links out of all possible links in the network (values range from 0 to 1). Observed connectance values are frequently correlated with network size (i.e. the number of species in the network), so we additionally calculated an estimate of connectance adjusted for size. To do this, we extracted the residuals from a regression of network size by connectance, which effectively removes any variation due to size. Values greater or less than zero respectively indicate that the network is more or less connected than expected after accounting for its size.

Network-level specialization, H_2', is a frequency-based metric that characterizes the level of interaction specialization within a bipartite network (Blüthgen et al. 2006). If we consider interactions as a feature of the ecological niche, network-level specialization describes the extent of niche partitioning across plants and pollinators in their use of mutualistic partners. Values of H_2' are based upon the degree to which the observed interactions in the network deviate from those that would be expected if they occurred at random (holding marginal sums constant). Values range from 0 to 1 with higher values indicating greater specialization, and therefore less niche overlap. H_2' effectively accounts for sources of variation related to network size and connectance, and can be considered a scale-independent metric that characterizes network specialization; it is appropriate for across-network comparison (Blüthgen et al. 2006).

Network nestedness describes the extent to which specialist species (those with few links) interact with generalists (those with many links; Bascompte et al. 2003). We calculated nestedness following the *NODF* (nestedness metric based on overlap and decreasing fill) algorithm of Almeida-Neto et al. (2008). Values range from 0 to 100, where 100 theoretically indicates a perfectly nested network. However, the actual maximum nestedness of a given network is often less than this theoretical maximum, which complicates the comparison of values across networks (Song et al. 2017). Furthermore, nestedness can be influenced by the size of the network and its connectance (Song et al. 2017). To account for these three issues we followed the methods developed by Song et al. (2017, 2019) and Simmons et al. (2019) to calculate the combined nestedness statistic. In brief, this is done by first calculating the maximum nestedness of each network using a simulated annealing algorithm; then a normalized value of nestedness is calculated by dividing the observed nestedness value by the maximum value; lastly, the normalized value is divided by the product of network connectance and network size which yields the combined nestedness statistic. This combined metric provides an estimate of nestedness that can be appropriately compared across networks of different sizes and observed connectance.

In addition to examining week-to-week variation, we compared the mean value of each network metric averaged across all weeks in each summer growing season to the value from the single cumulative network for that summer, using

one-sample t-tests. For both network specialization (H_2') and nestedness (*NODF*), we examined the extent to which the observed values for weekly and cumulative networks deviated from those generated at random using a null model with the following constraints: 1) the number of links within each network (i.e. observed connectance) was held constant, and 2) links were then randomized under the constraint that interactions for each pair of plant *i* and pollinator *j* occurred in proportion to the product of their interaction degrees (for binary webs; Bascompte et al. 2003), or in proportion to the frequency of visits between them (for frequency-based webs; Vázquez et al. 2007). We compared observed values to those generated from 100 simulated interaction matrices.

Species contributions to network structure

We explored temporal variation (i.e. temporal flexibility) in three measures of how interactions of individual species contribute to structure of their networks: 1) the number of links per species; 2) species-level interaction specialization; and 3) species nestedness contribution. We included only species that were present over two or more weeks in at least one of three summers. Links per species (i.e. species interaction degree) is simply the number of mutualistic partners a species interacts with. Because the number of links may be influenced by the number of available partners (i.e. resources), we additionally calculated normalized degree, which is the proportion of realized links for a given species. Species interaction specialization, d', is a measure of interaction niche breadth of a given species (Blüthgen et al. 2006). As with network-level specialization (H_2'), d' is based upon how strongly the interactions of a species deviate from those occurring at random among its available mutualistic partners, and accounts for sources of variation related to network size. Values range from 0 to 1 with higher values indicating greater specialization, and therefore narrower interaction niche breadth and smaller niche overlap between species. The relative contribution of a given species to overall nestedness (*NODF*) is calculated as the extent to which the nested structure of the network changes with the randomization of the interactions of the focal species (following Saavedra et al. 2011). Individual values are z-scores, which can range from positive to negative, indicating that a species has a positive or negative effect, respectively, on the network nestedness.

Network robustness to simulated species extinction

As a heuristic approach to explore potential network robustness to cascading extinctions, we simulated the random loss of species from both weekly and season-long networks (Memmott et al. 2004). We use the term 'potential' here in recognition that secondary extinctions are likely to play out more slowly than week-to-week. The simulations tabulated secondary species extinctions as a consequence of the sequential loss of 1) plant species, 2) pollinators or 3) both plants and pollinators simultaneously. Simulations removed species from networks in random order; when remaining species lost all interaction partners they were counted as secondary extinctions. We calculated network robustness as the area underneath the extinction curve (Memmott et al. 2004, Burgos et al. 2007); resulting values range from 0 to 1, where 0 indicates that all species become secondarily extinct after the first removal of a species (zero robustness), and 1 indicates that no species become secondarily extinct (complete robustness). Each simulation scenario was run 100 times for each network and robustness values were averaged across these runs. This method for assessing robustness treats the links within each network as unchanging, except when they are lost altogether. Although more complex methods are available, this simple approach serves our purpose, which is to raise the possibility that there are consequences of short-term temporal variation in network structure.

Effects of network size and species abundance

Because metrics can be sensitive to network size (Vázquez et al. 2009), we examined the relationship between each metric from each week and species richness of the network for that week. We also examined the relationship between the estimated abundance of each plant and pollinator species in each week and the metrics that describe its ecological role within the network in that week, using Pearson product–moment correlations.

Data analysis

All analyses where conducted in the R statistical computing environment (<www.r-project.org>). All network-level and species-level analyses, as well as secondary extinction simulations, were conducted using the R package 'bipartite' (Dormann et al. 2008, 2009, Dormann 2011).

Results

In total we analyzed 45 interaction networks (42 weekly and 3 cumulative, season-long networks), comprising 28 959 individual visitation events representing 547 unique links between 46 plant and 93 pollinator species. The mean parameter estimates and ranges of values for the weekly networks were largely consistent across all three summers, as were the structural properties of the three cumulative networks (Table 1; see Supplementary material Appendix 1 Table A2 for additional details on plant, pollinator and interaction richness for weekly and cumulative networks).

Structure of cumulative pollination networks

The 2013, 2014 and 2015 cumulative networks exhibited structural properties similar to those reported for many other mutualistic networks (Jordano 1987, Vázquez et al. 2009, Thébault and Fontaine 2010, Bascompte and Jordano 2014, Valdovinos 2019). Across all three summers, cumulative networks had relatively low values of connectance, a small

Table 1. Summary of the structural properties of cumulative, season-long networks and weekly networks. Cumulative values represent network metrics calculated from single point estimates from cumulative, season-long networks in each year of study. Weekly values represent the mean and variation in network metrics calculated from each of the weekly networks in each year.

Network parameter	Year	Cumulative value	Mean of weekly values	Range of weekly values	Cumulative versus weekly comparison	
					t	p
Connectance	2013	0.131	0.279	0.16–0.47	5.35	< 0.001
	2014	0.132	0.255	0.15–0.51	4.49	< 0.001
	2015	0.156	0.246	0.16–0.52	3.17	0.006
Connectance residuals (network size-adjusted)	2013	0.049	−0.004	−0.10–0.18	−2.15	0.055
	2014	0.059	−0.004	−0.11–0.23	−2.56	0.023
	2015	0.122	−0.008	−0.10–0.21	−6.17	< 0.0001
Nestedness (*NODF*)	2013	30.8	43.4	20.9–68.8	2.45	0.032
	2014	41.1	41.4	15.6–63.7	0.08	0.941
	2015	42.9	47.6	34.1–65.0	1.85	0.086
Combined nestedness statistic (size and connectance adjusted *NODF*)	2013	1.75	2.39	1.51–3.51	3.58	0.007
	2014	2.16	2.47	1.86–3.77	2.18	0.050
	2015	1.75	2.47	1.84–3.36	5.93	< 0.0001
Network specialization (H_2')	2013	0.464	0.446	0.13–0.80	−0.27	0.793
	2014	0.327	0.495	0.14–0.91	2.49	0.026
	2015	0.471	0.501	0.36–0.75	0.98	0.356
Robustness to plant extinction	2013	0.745	0.634	0.59–0.72	−8.85	< 0.0001
	2014	0.751	0.631	0.53–0.72	−9.82	< 0.0001
	2015	0.785	0.653	0.60–0.70	−15.62	< 0.0001
Robustness to pollinator extinction	2013	0.751	0.703	0.61–0.81	−3.15	0.009
	2014	0.767	0.725	0.59–0.86	−2.25	0.041
	2015	0.832	0.739	0.64–0.82	−8.24	< 0.0001
Robustness to plant + pollinator extinction	2013	0.481	0.372	0.30–0.44	−9.70	< 0.0001
	2014	0.480	0.379	0.27–0.42	−8.97	< 0.0001
	2015	0.517	0.382	0.25–0.43	−10.90	< 0.0001

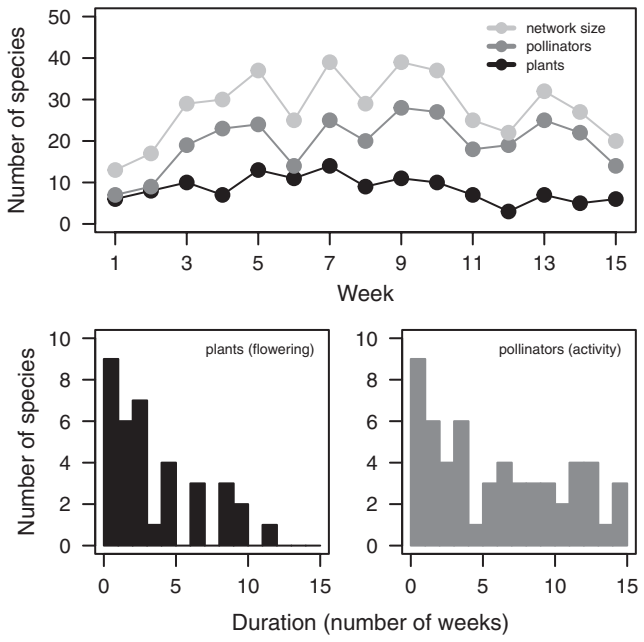

Figure 1. Temporal variation in species richness of plants and pollinators (top panel), and the flowering duration of plants (lower left panel) and the activity duration of pollinators (lower right panel). Data for 2014 are shown as an example; additional details on plant, pollinator and interaction richness for all three summers are shown in Supplementary material Appendix 1 Table A2.

average number of links per species (2.5–4.0), intermediate nested structure, and intermediate network-level specialization (Table 1).

Structure of weekly pollination networks

The structural properties of weekly networks were highly variable within each of the three summers (Fig. 1, 2, Supplementary material Appendix 1 Fig. A1). This within-season variation was consistent across the summers (Table 1, Supplementary material Appendix 1 Table A1, A2). For all metrics, weekly values spanned a wide range that was not reflected by the corresponding cumulative estimate (Table 1, Fig. 2). Cumulative connectance was much lower than mean weekly connectance; however, after accounting for network size, this relationship was reversed in that size-adjusted cumulative connectance was generally greater than weekly connectance (Table 1, Fig. 2). Cumulative network-level specialization (H_2') tended to be similar to mean weekly specialization, with the exception of one summer (2014) in which the cumulative value was lower. Cumulative nestedness (*NODF*) tended to be lower than mean weekly nestedness, although this pattern varied from summer to summer, whereas nestedness adjusted for size and connectance was more consistently lower for cumulative compared to weekly networks. All patterns were qualitatively similar for frequency-based metrics (Supplementary material Appendix 1 Table A1, Fig. A2–A4).

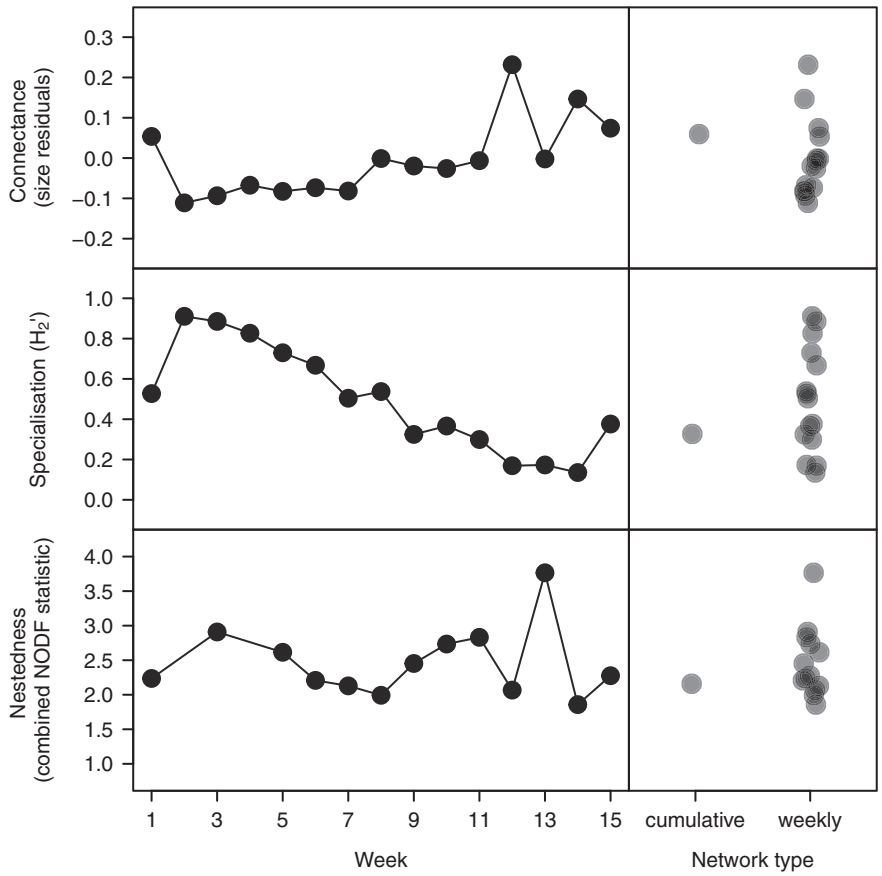

Figure 2. Temporal variation in the structure of plant–pollinator networks from week to week across the 2014 growing season (left panels) and comparison of cumulative, season-long network metrics with weekly metrics (right panels). Data for 2014 are shown as an example; data from the other two summers are shown in Supplementary material Appendix 1 Fig. A2, A3. Missing values for the combined nestedness statistic represent cases where calculations were not possible because there were fewer links in the network than the number of species.

The observed values of network specialization (H_2') for all three cumulative networks and all but one of the 42 weekly networks were significantly different from the values generated under our null model (Supplementary material Appendix 1 Table A3). Similarly, for nestedness (*NODF*), all three cumulative networks, and all but one of the 42 weekly networks were significantly nested. For weighted nestedness (weighted *NODF*), all networks were non-nested (i.e. anti-nested), a pattern that is consistent with many other mutualistic networks (whereby binary networks exhibit significant nestedness and weighted networks exhibit anti-nestedness; Staniczenko et al. 2013; Supplementary material Appendix 1 Table A3).

Species contributions to cumulative network structure

By being present over two or more weeks in at least one of three summer growing seasons, 72 pollinator species and 33 plant species met our criteria to be included in species-level analyses of their interactions and contributions to network structure. Few plants and pollinators were active for the entire summer growing season (Fig. 1; plant flowering duration: mean across seasons = 3.9 weeks, range = 1–12 weeks; pollinator activity duration: mean across seasons = 6.01, range = 1–15). The cumulative, season-long number of links (species degree) across plants species varied from 2 to 37 (mean = 9.8 links) and across pollinator species from 2 to 22 (mean = 6.0). Cumulative, species-level interaction specialization (d') was on average moderate (plant mean = 0.43; pollinator mean = 0.33), but values ranged from 0.10 to 0.84 across plant species and from zero to 0.85 across pollinator species. The contribution of individual species to the nested structure of cumulative networks was on average positive but ranged across species from positive to negative for both plants (z-score mean = 0.72; range −4.00 to +4.07) and pollinators (z-score mean = 0.85; range −2.17 to +2.72).

Species contributions to weekly network structure

Species-level interaction metrics within weekly networks spanned a wide range of parameter values that were not always similar to values from cumulative networks (Fig. 3, 4; Supplementary material Appendix 1 Fig. A5–A8). Averaging

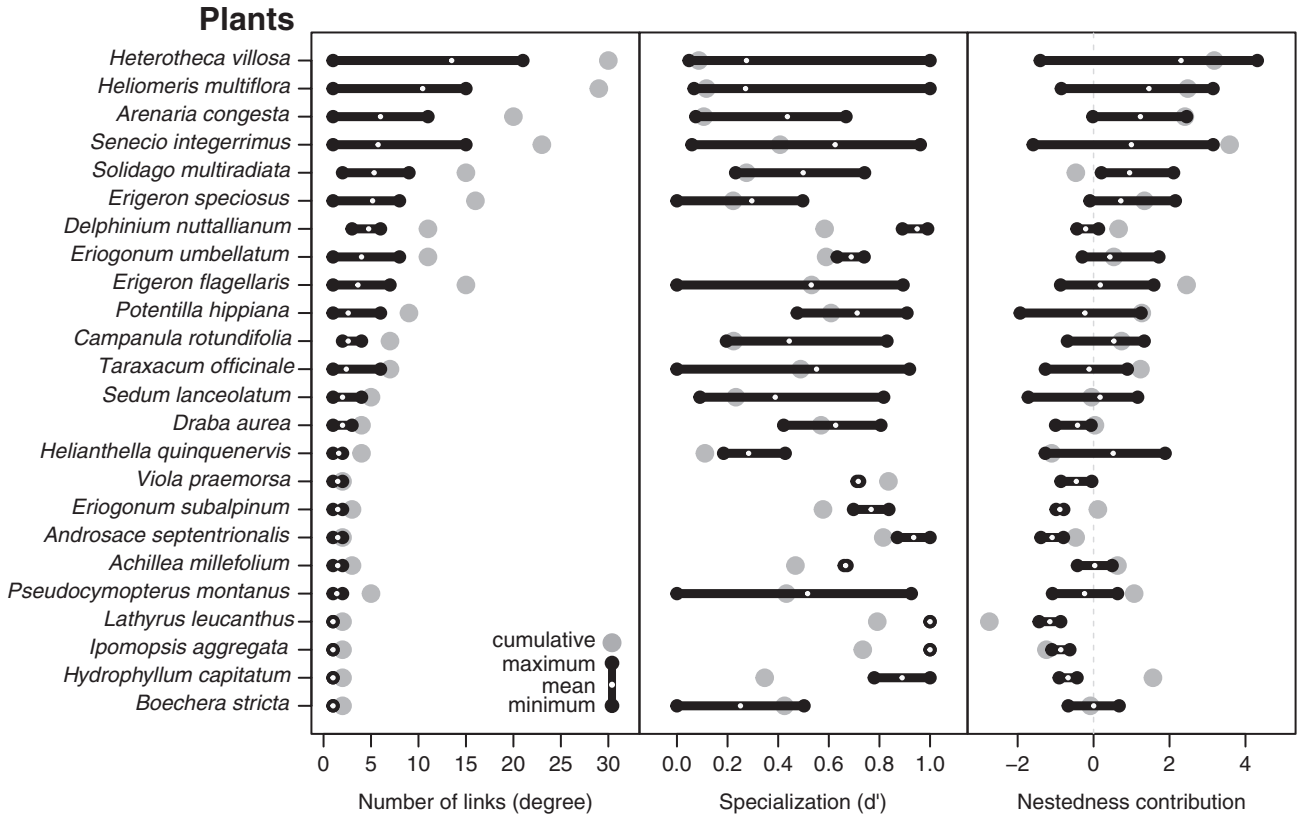

Figure 3. Temporal variation in plant species network roles: the number of links per plant species (left panel), interaction specialization (middle panel) and contribution to nestedness (right panel). Data for 2014 are shown as an example; data from the other two summers are shown in Supplementary material Appendix 1 Fig. A5, A6. Black dots and lines represent the range of weekly values; small white dots represent the mean of weekly values; and large grey dots represent cumulative values. Nestedness contribution values are z-scores generated from each network; if values overlap with zero this indicates that a species' contribution ranges from positive to negative; it is not to be interpreted as having an overall neutral effect.

across the three summers, the cumulative number of links per species (i.e. degree) for plants and pollinators tended to be greater than the range of weekly values: for plants, 84% of the cumulative numbers of links per species were greater than the maximum weekly value, and for pollinators, 88% of cumulative values were greater than the maximum weekly value (in all cases, the cumulative value was at least as great as the maximum weekly value). However, when accounting for the number of available resources (i.e. normalized degree), for plants, 28.4% of the cumulative values fell outside the range of the weekly values, and for pollinators, 42.6% of cumulative values did so. For neither plants nor pollinators was there a clear direction in the difference between cumulative interaction specialization (d') values and weekly values; for plant interaction specialization (d'), 39.5% of cumulative values fell outside the range of weekly values, whereas for pollinators 32.7% of cumulative values did so. The cumulative nestedness contribution for both individual plant and pollinator species tended to be greater than the mean of their weekly values; for plants, 49.4% of cumulative values fell outside the range of weekly values, whereas for pollinators only 64.5% of cumulative values did so.

Network robustness to simulated species extinction

Potential robustness to secondary extinctions for cumulative networks was similar when we removed either plants or pollinators in random order, but was lower when we simultaneously removed both plants and pollinators; these patterns were similar across the three growing seasons (Table 1, Fig. 5; Supplementary material Appendix 1 Fig. A9, A10). Our measure of potential robustness varied across weekly networks, and mean values across weeks tended to fall below the value for the corresponding cumulative network for all three extinction scenarios (removal of plants, pollinators or both; Fig. 5).

Effects of network size and species abundance

The relationship between network size and interaction structure depended on the network metric being considered (Supplementary material Appendix 1 Table A1). Connectance in each week was consistently negatively correlated with network size in all three summers. Network-level specialization (H_2') was not related to network size in any summer

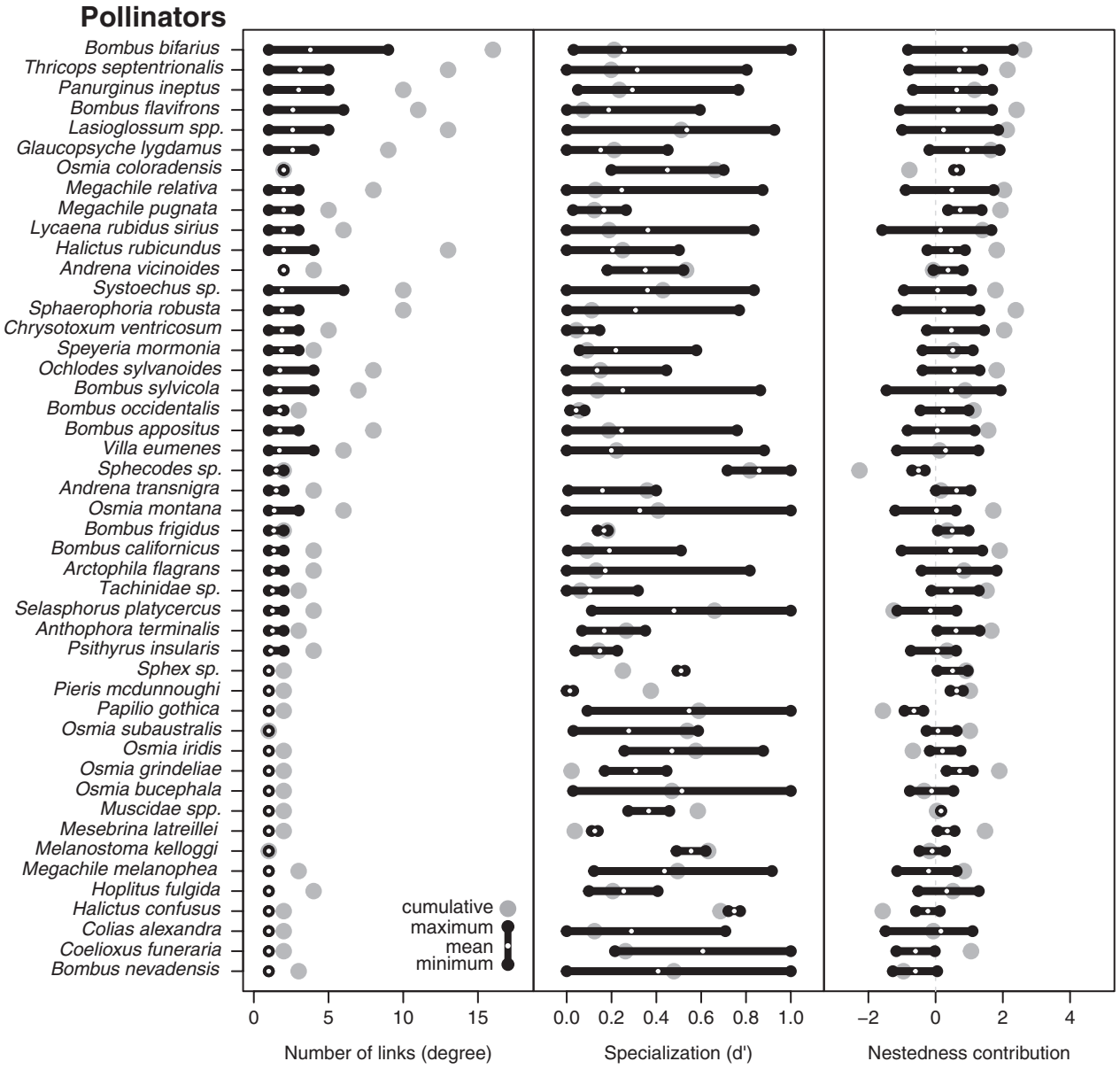

Figure 4. Temporal variation in pollinator species interaction roles within networks: the number of links per pollinator species (left panel), interaction specialization (middle panel) and contribution to nestedness (right panel). Data for 2014 are shown as an example; data from the other two summers are shown in Supplementary material Appendix 1 Fig. A7, A8. Other conventions follow Fig. 3.

(as expected; Blüthgen et al. 2006). Nestedness and network size were negatively correlated, although the strength of this relationship varied across summers. These patterns were qualitatively similar for unweighted and weighted networks (Supplementary material Appendix 1 Table A1). Network size tended to be weakly correlated with network robustness, and the direction of this correlation was inconsistent (Supplementary material Appendix 1 Table A1).

The numbers of links per species (species-level degree) tended to be moderately positively correlated with the estimated abundance of each species in each week (mean across species and years, $r = 0.55$). Species-level specialization (d') was not related to species abundance for most species in any summer ($r = -0.06$). Species-level nestedness contribution was consistently weakly correlated with species abundance in each week ($r = -0.24$). All species-specific correlation coefficients for each metric are included in the Supplementary material Appendix 1 Table A4.

Discussion

Our findings highlight considerable fine-scale temporal variability in network structure. The way in which species interact within networks varies substantially from week-to-week, and this flexibility of interactions, over time periods when species

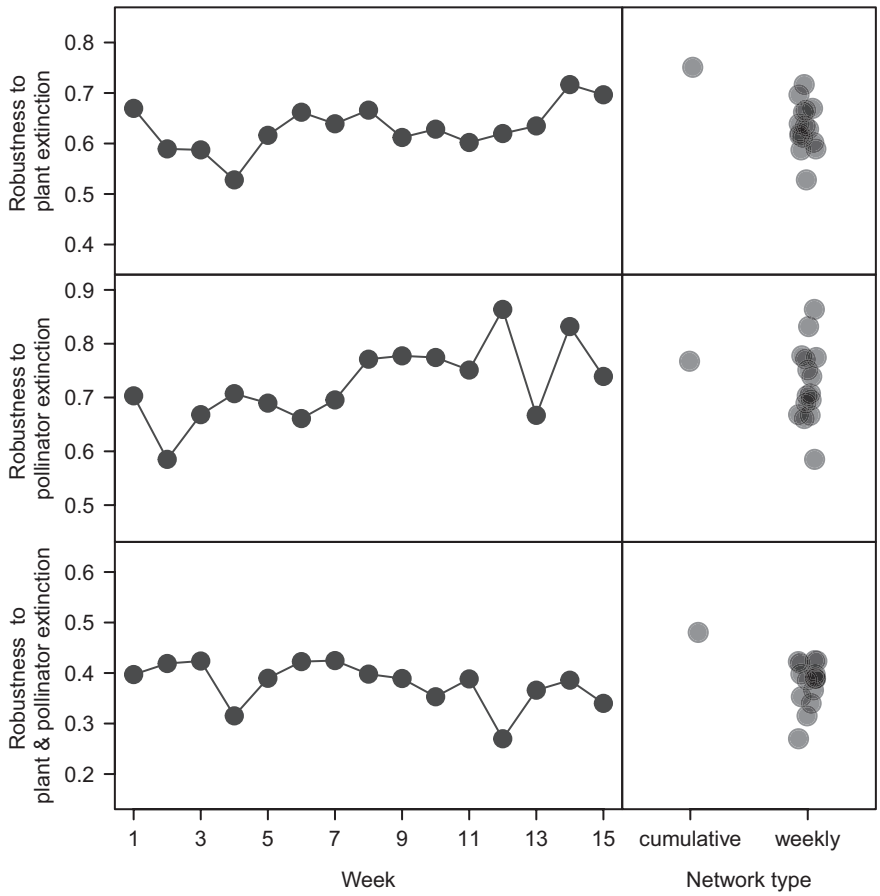

Figure 5. Potential network robustness to simulated random extinction of plants, pollinators, and plants and pollinators. Potential robustness values represent the area underneath the extinction simulation curve where 0 indicates a network that collapses via secondary extinction after the first primary extinction and 1 indicates a network that is completely robust to primary extinctions (i.e. no secondary extinctions even after all primary extinctions). Data for 2014 are shown as an example; data from the other two summers are shown in Supplementary material Appendix 1 Fig. A9, A10.

actually co-occur in the subalpine meadows, leads to constant change in network structure throughout the summer growing season. In contrast, this biologically-relevant variation is hidden in our cumulative, season-long networks. Furthermore, cumulative networks may not recover structural patterns that resemble even the averages from networks depicted on finer time scales (Fig. 2). For example, weekly networks were consistently more sparsely connected than cumulative networks, after accounting for variation in network size. This pattern reflects the fact that the species themselves have fewer interactions in any given week than they do across their entire activity periods, so that weekly networks are never as richly connected as a cumulative network might suggest. Weekly networks also tended to exhibit overall greater binary nestedness than cumulative networks, after accounting for network size and connectance. This is consistent with our finding that on average, across both plants and pollinators, individual species' contributions to nestedness tended to be positive from week to week – that is, their interactions with other species fostered a more nested network. Network specialization exhibited the greatest range of week-to-week variation. The mean of weekly values for this metric tended to more closely resemble cumulative network specialization; at the same time its substantial weekly variation indicates that the partitioning of plant and pollinator interaction niches can be highly changeable across the growing season.

The temporally-variable structure of our weekly networks is ultimately driven by the species that make up these networks and that are constantly modifying their interactions as the season progresses. To illustrate, *Erigeron speciosus* (tall fleabane daisy) received visits from individuals of 16 different pollinator species across its 7-week flowering period but in any given week was visited by 1–8 species, and on average was visited by 5; its interaction niche was overall moderately generalized, but ranged from being highly generalized to moderately specialized within any given week (Fig. 3). Similarly, *Bombus bifarius* (two-form bumble bee) visited 15 different plant species across its entire 15-week activity period but in any given week visited 1–9 species, and on average visited 4; its interaction niche was overall generalized, but ranged from being highly generalized to highly specialized (Fig. 4). These two examples represent a relatively common plant and

a common pollinator in a single summer (2014), but analogous patterns emerge for other plants and pollinators, and in other summers. Thus, species that would be considered relatively generalized in their interactions across their entire activity period may be much more specialized at certain times, and at no point as generalized as the cumulative network may suggest. This species-level temporal variability also translates into how a given species contributes to the nested structure of the network. Overall, many plant and pollinator species contributed positively to network nestedness across their activity periods, but week-to-week contributions for many species ranged from positive to neutral to negative – another difference that derives from temporally-variable interactions. These patterns together illustrate that species have dynamic roles within the network that can change rapidly over the course of a season.

At a basic level, the reason for temporal variation in network structure is straightforward: the species present in a community, and how they interact with others, are both changing through time (Fig. 1, 3, 4). In many ecosystems species are active only for portions of longer seasons (Olesen et al. 2008, Petanidou et al. 2008, Carnicer et al. 2009). Within these periods of biological activity, individuals of the species may vary their interactions at fine-time scales in response to changing resource abundances and accessibility as well as the resource use of competing individuals. The pollinators we studied experience rapid changes in the identities (and thereby phenotypes) and abundances of flowers (CaraDonna et al. 2017). In such a system we expect flexibility and opportunism, conditioned by sensory and cognitive abilities or constraints, to dictate who visits whom on scales of seconds to minutes to hours (Pleasants 1981, Waser et al. 1996, 2018, Chittka and Thomson 2001). It is therefore unsurprising that the structural properties of networks fluctuate as the exact mixture of co-occurring species shifts, and as species differ in their patterns of interaction within this shifting community context.

The temporal variation in network structure that we observed suggests that our plant–pollinator communities may be more or less sensitive to perturbation at certain times of the season (Fig. 5). Short-term variation in our measure of potential robustness to simulated (random) extinction of species supports this view. A real example of a short-term perturbation in our system is a killing late spring frost, whereby many floral resources can be destroyed overnight (Inouye 2008, CaraDonna and Bain 2016, Iler et al. 2019). Were such an extreme event to occur when the network is less connected, less nested and more specialized, its consequences might be more severe. Short-term variation in network structure can also alter the range of conditions under which all species within the community can maintain positive abundances (i.e. community feasibility; Rohr et al. 2014, Cenci et al. 2018). For example, day-to-day temporal variation in an arctic pollination network contributes to a greater range of conditions under which species can maintain positive abundances, suggesting that short-term variation may be an important component of species co-existence and community persistence (Saavedra et al. 2016a, Song and Saavedra 2018). Therefore, cumulative networks may overlook a relevant temporal scale for understanding network robustness and other aspects of community dynamics. However, we stress again that many responses to disturbance are likely to play out over time scales longer than weeks. For example, local extirpation of a generalized pollinator might be expected to harm one or more specialized plant species that depend on that pollinator (Brosi and Briggs 2013); but a conclusion of absolute loss of pollination for such plants should require us to examine their pollinator faunas for as long as their entire flowering seasons, and even across several successive seasons for perennial species, rather than in shorter time scales (Burkle et al. 2013).

Networks that depict the accumulation of interactions across an entire season or year contain the most total information about the system, but also obscure information on variation that may be important to consider. We uncovered considerable temporal variability in network structure that is linked to flexible species interactions within these networks – all of which would be hidden with a focus only on cumulative networks. This hidden variation has important practical implications for the fitness of individuals, for population dynamics, and for species conservation. The reproduction of an individual plant will be sensitive to its immediate pollinator environment; likewise, the fitness of a given pollinator will depend on the floral resources immediately available for consumption. Assuming that a species is rigidly embedded within a cumulative, season-long network overlooks the specific biotic (and abiotic) conditions that should directly give rise to reproductive success or failure of individuals, ultimately influencing population dynamics and natural selection on traits that mediate interactions. From a conservation perspective, our results suggest that we should carefully consider the temporal variation in how species are linked within a network. For example, even though a species may be relatively generalized across its entire activity period, effective conservation may be contingent upon management at particular times in a season when individuals have limited access to resources and are perhaps most vulnerable. From a multispecies perspective, understanding temporal variation in network structure may similarly highlight parts of the season when numerous species – and therefore the entire community – are collectively most sensitive to disturbance.

Speculations

Accepting that ecological networks constructed on any timescale are ultimately abstractions of an ecological community, is there a timescale that yields the most 'true' representation of network structure? We think not, because appropriate temporal resolution will depend on how slowly or quickly systems change and on the questions being asked. As Stigler (2016) explains in tracing the history of aggregation in statistics, aggregation reveals central tendencies and other large patterns in data that otherwise are not apparent. But aggregation

can shift the focus away from underlying variation (Iler et al. 2013, Sajjad et al. 2017, Schwarz et al. 2020). As our results illustrate, temporal variation in structural properties of interaction networks is not recoverable from single cumulative estimates. Might this suggest that our current understanding of network structure overlooks a key dimension of the way in which many species interactions take place in nature? If an overarching goal of ecology is to understand the factors that govern the distribution of species and their abundances, then a central question is: what use and what temporal resolution of networks are best for improving our predictive understanding of the structure and dynamics of ecological communities?

Data availability statement

The primary data associated with this manuscript are available in the Environmental Data Initiative (EDI) digital repository: CaraDonna (2020) <https://doi.org/10.6073/pasta/27dc02fe1655e3896f20326fed5cb95f>.

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Supplementary material (available online as Appendix oik-07526 at <www.oikosjournal.org/appendix/oik-07526>). Appendix 1.