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Temporal scale-dependence of plant–pollinator networks

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The study of mutualistic interaction networks has led to valuable insights into ecological and evolutionary processes. However, our understanding of network structure may depend upon the temporal scale at which we sample and analyze network data. To date, we lack a comprehensive assessment of the temporal scale-dependence of network structure across a wide range of temporal scales and geographic locations. If network structure is temporally scale-dependent, networks constructed over different temporal scales may provide very different perspectives on the structure and composition of species interactions. Furthermore, it remains unclear how various factors – including species richness, species turnover, link rewiring and sampling effort – act in concert to shape network structure across different temporal scales. To address these issues, we used a large database of temporally-resolved plant–pollinator networks to investigate how temporal aggregation from the scale of one day to multiple years influences network structure. In addition, we used structural equation modeling to explore the direct and indirect effects of temporal scale, species richness, species turnover, link rewiring and sampling effort on network structural properties. We find that plant–pollinator

network structure is strongly temporally-scale dependent. This general pattern arises because the temporal scale determines the degree to which temporal dynamics (i.e. phenological turnover of species and links) are included in the network, in addition to how much sampling effort is put into constructing the network. Ultimately, the temporal scale-dependence of our plant–pollinator networks appears to be mostly driven by species richness, which increases with sampling effort, and species turnover, which increases with temporal extent. In other words, after accounting for variation in species richness, network structure is increasingly shaped by its underlying temporal dynamics. Our results suggest that considering multiple temporal scales may be necessary to fully appreciate the causes and consequences of interaction network structure.

Introduction

The study of plant–animal mutualistic networks has led to many valuable insights into the structure, function and evolution of these interspecific interactions (Bascompte and Jordano 2013). For example, plant–pollinator networks are typically observed to have low connectance and also tend to have nested or modular structures (Jordano 1987, Bascompte et al. 2003, Olesen et al. 2007). Critically, these structural patterns are hypothesized to be related to community stability (Bascompte et al. 2006, Thébault and Fontaine 2010) and ecosystem functioning (Schleuning et al. 2015).

All studies of ecological networks aggregate data at some temporal scale. Many networks are constructed from highly aggregated data, for instance daily field samples temporally aggregated across weeks or entire seasons prior to analysis (Petanidou et al. 2008, Trøjelsgaard and Olesen 2016, Sajjad et al. 2017). However, the ideal temporal scale at which we collect, summarize and analyze interaction networks depends on the specific ecological and evolutionary questions one aims to address (Wolkovich et al. 2014, Trøjelsgaard and Olesen 2016). In fact, network patterns derived from different temporal scales may provide different answers to the same question. For example, species in networks aggregated over narrow temporal scales, such as a single week, may appear to be specialists, while they may appear to be generalists in networks aggregated at broad temporal scales (e.g. one year) if they change interaction partners throughout the season (Waser et al. 1996, Petanidou et al. 2008). Consequently, to understand the structure and function of these interaction networks, we need to know how the temporal scale of aggregation influences the patterns we find in the data.

Both sampling effort and ecological temporal dynamics (e.g. species turnover and link rewiring) may be important drivers of the temporal scale-dependence of network structure. Temporal data aggregation necessarily increases cumulative sampling effort and consequently species and link detection probabilities. Such aggregation is often motivated by the pursuit to increase sampling completeness (Chacoff et al. 2012, Fründ et al. 2016, Vizentin-Bugoni et al. 2016). However, as the total number of species in a network tends to increase with temporal aggregation, sampling effort per potential interaction (i.e. link) may not increase in the same way, which potentially limits sampling completeness. Furthermore, when data are aggregated over broad temporal scales (e.g. several weeks or months), species with non-overlapping phenologies will be included in the same network (Basilio et al. 2006, Vázquez et al. 2009a), introducing temporally forbidden links (Olesen et al. 2011). Additionally, even temporally co-occurring species may switch interaction partners over time, thereby rewiring the links within the network (Poisot et al. 2012). Understanding the influence of temporal dynamics – such as species turnover and link rewiring – on network structure at multiple temporal scales might be particularly important considering various drivers that alter the timing of species interactions, such as climate change (Park and Mazer 2019), habitat modification (Burkle et al. 2013, Ponisio et al. 2017) and species invasions (Herron-Sweet et al. 2016, Arroyo-Correa et al. 2019).

Currently, we lack a comprehensive assessment of the temporal scale-dependence of network structure. Several studies have shown the pattern that network structural properties vary with temporal scale, for example, specialization is lower and nestedness is greater in networks aggregated over broader temporal scales (Rasmussen et al. 2013, Falcão et al. 2016, Sajjad et al. 2017, Souza et al. 2018). However, such studies have been conducted mostly at only one or a few locations, and each of them have used different and limited ranges of temporal scales; this calls for a more comprehensive assessment of the temporal scale-dependence of network structure across a wide range of temporal scales and geographic locations. Furthermore, while the role of sampling effort in driving temporal scale-dependence of network structure has been demonstrated (Rivera-Hutinel et al. 2012, Vizentin-Bugoni et al. 2016), our understanding of how species turnover and link rewiring contribute to the scale-dependence of network structure is still limited (but see Olesen et al. 2008, Morente-López et al. 2018). Particularly, it remains unclear how sampling effort, species turnover and link rewiring act in concert to shape network structure across different temporal scales. We hypothesize that in addition to sampling effort, temporal dynamics such as species turnover and link rewiring are important determinants of network structure, particularly at broader temporal scales, where many species and links occur at different times.

In this study, we assess the temporal scale-dependence of the structure of plant–pollinator networks and investigate

how this scale-dependence is driven by the interplay of sampling effort, species turnover and link rewiring. We addressed three specific questions: 1) to what extent are network structural attributes dependent on the temporal scale of data aggregation? 2) What is the relationship between the temporal scale of data aggregation and network sampling completeness? And 3) are temporal-scale dependences of network structure modulated by species richness, species turnover and link rewiring? Although these questions have been partly addressed by previous studies, here we offer a more comprehensive examination of these questions by using a global database consisting of 30 temporally explicit data sets of plant–pollinator interactions that allow data aggregation over a wide range of temporal scales. We aggregated quantitative networks at five temporal scales (days, weeks, months, years and multiple-years) and calculated six commonly used network indices representing the main structural properties of bipartite networks (connectance, nestedness, modularity, network specialization, pollinator generality and plant generality). Our results highlight that analyzing data at multiple temporal scales within and across studies allows for a deeper understanding of the ecological processes that shape network structure.

Methods

Compilation of plant–pollinator network data

We selected 30 individual data sets of plant–pollinator interaction networks from published or unpublished studies and compiled them into a single database. These studies were conducted across several sites in nine countries, ranging from tropical to arctic regions but with the majority of sites being located in temperate regions (Supplementary material Appendix 1). To be included, individual data sets had to contain information on the sampling date for each recorded interaction and at least one site per study had to be sampled repeatedly over time to allow data aggregation (Supplementary material Appendix 1 Fig. A2). In all data sets, species correspond to either taxonomic species or morphospecies, and each recorded interaction corresponds to an observation of an animal visiting a flower. We usually used the same sites that were described by the original studies except when the original sites represented relatively small observational plots or were observed for only part of a day. Specifically, we pooled the original sites if they were less than ~6 km apart from each other, harbored similar plant communities, and if a reasonably large proportion of them were sampled on each sampling day (Supplementary material Appendix 1 Table A1).

Temporal data aggregation

To characterize the temporal scale-dependence of network structure, we aggregated data at five temporal scales: day,

week, month, year and multiple years. These calendar units are commonly used in other studies on pollination networks (Petanidou et al. 2008, Simanonok and Burkle 2014, CaraDonna et al. 2017, Kaiser-Bunbury et al. 2017) as they correspond with the temporal scale of various biological events. We standardized southern hemisphere dates by adding 182 days to each sampling date for each site in the southern hemisphere (n = 17) to assure that the whole flowering season takes place within one single calendar year. Finally, for each site, all observed interactions within the same day, week, month, year or the total sampling extent, respectively, were used to construct a quantitative interaction matrix, with rows corresponding to plant species, columns to pollinator species, and cell entries to the number of floral visits by each pollinator species to each plant species. For each network at each temporal scale, we compiled information on sampling effort (number of sampling days), temporal extent (temporal distance, i.e. number of days, between first and last sampling day), the total number of species (species richness) as well as numbers of plant species, pollinator species and unique links.

To assure that we only included networks in our analyses that sufficiently represent the respective temporal scale in terms of sampling effort and temporal extent, we defined specific rules. Weekly networks had to be based on at least two sampling days, monthly networks on at least four sampling days covering a time span of at least 11 days, yearly networks on at least eight sampling days covering a time span of at least 60 days, and multiple-year networks on at least 16 sampling days covering a time span of at least 381 days. Considering limited data availability, these threshold values reflect a compromise between avoiding to discard too many networks and ensuring that networks assigned to one temporal scale clearly differed from networks of other temporal scales. For studies that sampled interactions for only a subset of the available plant species on a given sampling day, daily or weekly networks were deliberately incomplete and were thus excluded from our analyses (Supplementary material Appendix 1 Table A1). Finally, we only considered sites that provided data to aggregate networks at a minimum of two temporal scales. To limit the influence of differences between networks within the same temporal scale, we used temporal extent as a continuous predictor that likely better relates to the temporal dynamics in the community than the five coarse categories of temporal scale. We considered the number of sampling days per network to be a measure of time-based sampling effort (Nielsen and Bascompte 2007) as sampling methods were mostly comparable among different days within individual studies. For studies not suitable to construct daily or weekly networks, absolute observation time and number of simultaneous observers may have differed between sampling days in some cases. However, these differences are likely to level off at broader temporal scales.

The procedure of temporally aggregating data described here resulted in some interactions being represented in only a subset of the temporal scales as not all networks met our minimum inclusion criteria for their respective temporal

scales. For example, data from a week with only one sampling day would not qualify to construct a weekly network, but they might be included in a monthly network when pooled with data from other weeks. To confirm the robustness of our results to this inconsistent inclusion of studies at different temporal scales, we analyzed a reduced data set that used exactly the same data across all temporal scales possible for a specific site (Supplementary material Appendix 5).

Calculation of network indices

To describe network structure, we calculated six network indices using the 'bipartite' package ver. 2.13 in R (Dormann et al. 2009): connectance, nestedness (NODF), quantitative modularity Q, network specialization index H_2', pollinator generality and plant generality. To increase the relevance of our work for other studies, we focused on indices that represent the main structural properties of bipartite networks and were commonly used before.

Connectance reflects the realized proportion of possible links in the network and consequently ranges between 0 and 1. Nestedness was calculated using the NODF algorithm (Almeida-Neto et al. 2008), which scales between 0 and 100, indicating lack of nestedness and perfect nestedness, respectively. We used NODF nestedness as it has been widely considered by other studies. We also report results for a normalized nestedness index ($NODF_c$), which accounts for connectance and network size and thus is robust for network comparisons (Song et al. 2017) (Supplementary material Appendix 3). We calculated weighted quantitative modularity Q using the DIRTLPA+ algorithm (Beckett 2016). Modularity Q ranges from 0 (which means the network does not have more links within modules than expected by chance) to a maximum value of 1 (all links are within modules). The weighted quantitative network specialization index H_2' (Blüthgen et al. 2006) describes the degree of specialization among plants and pollinators across an entire network. It ranges between 0 and 1, indicating extreme generalization and specialization, respectively. Weighted quantitative generality was calculated for both pollinators and plants, which reflects the mean effective number of plants per pollinator and vice versa weighted by their marginal totals (Bersier et al. 2002). We did not a priori adjust for network size in the calculation of network indices as we expected network size to strongly depend on the temporal scale of data aggregation and thus to be an important component of the effect of temporal scale. However, we still accounted for the effect of network size by including species richness as a co-variable in some of our statistical models.

Quantification of species turnover and link rewiring

For all networks aggregated at a scale broader than a single day, we described the temporal dynamics as species turnover and link rewiring between all sampling days within the time span across which data were aggregated. Species turnover was assessed by taking the mean of the weighted

Jaccard dissimilarities (= Soergel distance) in species composition calculated for all possible pairwise combinations of daily networks within the focal time span. Link rewiring was assessed accordingly using the weighted Jaccard dissimilarities in links among shared species (Poisot et al. 2012). Values for these measures can range between 0 and 1, indicating either complete or zero overlap in species or links among all daily networks within a focal time span. As the assessment of temporal dynamics was based on dissimilarities between daily networks, we only considered studies suitable to construct daily networks for these analyses.

Estimating sampling completeness

To estimate sampling completeness of species and links, we used the Chao1 estimator of asymptotic richness, which corrects observed species richness taking into account the ratio of singletons to doubletons (Chao 1984). For each network, we first estimated the asymptotic numbers of plant species, pollinator species and links using the 'estimateR' function of the 'vegan' package ver. 2.5-6 (Oksanen et al. 2019). Secondly, we calculated sampling completeness as the proportion of observed species or link numbers of the estimated asymptotic numbers of species and links. The Chao1 estimator may underestimate total species or link numbers and thus should be considered as a lower bound for asymptotic richness (Fründ et al. 2016). As an additional aspect of sampling completeness, we also estimated sampling coverage (Chao and Jost 2012) at the level of plants, pollinators and links for each network. We consider sampling coverage as a weighted measure of sampling completeness, which can be interpreted as the proportion of all individuals or interaction events in the community that belongs to the species or links represented in the sample used to construct a network (Chao and Jost 2012). Thus, in contrast to (binary) sampling completeness, sampling coverage does not inform us about how many species or links we missed but allows us to estimate how well the individuals and interaction events in the community are represented by a network (Chao and Jost 2012).

Statistical analyses

For all analyses, we only used networks for which the calculation of all six network indices was possible (n = 2006). In this way we excluded very small networks that likely reflected very limited observations (n = 329). All analyses were conducted with R ver. 3.6.1 (<www.r-project.org>). We used linear mixed effects models to test for the effect of temporal scale of data aggregation on 1) the six network indices and 2) the two measures of sampling completeness. Models were fitted with Gaussian error and with site nested within study as random effects using the restricted maximum likelihood method (REML) in the 'lme4' package ver. 1.1-21 (Bates et al. 2015). Some network indices (connectance, pollinator generality and plant generality) were log-transformed to improve normality of residuals and homoscedasticity.

To analyze the effect of temporal scale, we used log-transformed temporal extent as continuous predictor and included it as single and quadratic term in the linear mixed models. We also carried out post hoc Tukey HSD tests using the 'emmeans' package ver. 1.4.2 (Lenth 2019) to compare the means of network indices between the five categories of temporal scale. To illustrate the role of species richness in driving the effect of temporal extent on network structure, we re-ran the linear mixed models testing the effect of temporal extent on the six network indices as described above but additionally included log-transformed species richness as a co-variable.

To explore the direct and indirect effects of temporal extent, sampling effort, species richness, species turnover and link rewiring on the six network indices, we fitted structural equation models (SEMs) using the 'piecewiseSEM' package ver. 2.1.0 (Lefcheck 2016). For these SEMs, we could only consider networks for which we had quantified species turnover and link rewiring (i.e. networks aggregated at a scale broader than a single day but only of studies that allowed for constructing daily networks; n = 484). As with the linear mixed models, some network indices (connectance, pollinator generality and plant generality) as well as sampling effort, temporal extent and species richness were log-transformed to improve normality of residuals and homoscedasticity. For SEMs all variables were scaled between 0 and 1, and models were fitted with site nested within study as random effects. Among the three mediators (species richness, species turnover and link rewiring), no causal relationships were assumed and the significant relationships between species turnover and link rewiring as well as between species richness and link rewiring were accounted for by including correlational errors in the SEMs. We also included the relationship between the number of sampling days and temporal extent as correlational error. The full models including all pathways were simplified by retaining only statistically significant pathways in the model (p < 0.05). To better understand how sampling completeness and sampling coverage are affected by the temporal scale of data aggregation, and in turn, how they contribute to the temporal scale-dependence of network structure, we performed additional SEMs with either link completeness or link coverage as co-variables (Supplementary material Appendix 4).

Results

Temporal scale of data aggregation and network structure

Overall, we analyzed 1307 daily, 380 weekly, 229 monthly, 71 yearly and 19 multiple-year networks that were constructed based on 124 708 interactions sampled within 30 studies across 159 sites and ninecountries (Supplementary material Appendix 1 Fig. A1). We found that all network indices except for network specialization H_2' were affected by temporal extent (Fig. 1, Table 1). All six indices were sensitive to the temporal scale of data aggregation in some

way (Supplementary material Appendix 2 Fig. A4, Table A2). Overall, the effects of temporal extent as a continuous predictor and of temporal scale as a categorical predictor resulted in the same patterns. From the narrowest (one day) to the broadest temporal scale (multiple years) connectance decreased by 66%, plant generality increased by 166% and pollinator generality increased by 207% (Fig. 1). For nestedness, modularity and network specialization H_2' we found only weak effects of temporal scale and no consistent trends of either an increase or decrease from days to several years (Fig. 1b–d). The nestedness of weekly and monthly networks was slightly higher compared to the nestedness of daily networks (9% and 15% respectively), while the modularity of yearly networks was slightly higher (12%) compared to the modularity of weekly networks (Fig. 1b–c). Network specialization H_2' differed only between daily and monthly networks with a slight decrease (11%) from daily to monthly networks (Fig. 1d). Temporal extent still affected five of the six indices after including species richness as a co-variable in the model, indicating that species richness may partly but not entirely explain the effects of temporal extent (Supplementary material Appendix 2 Fig. A6, Table A3). Performing the same analyses using a reduced data set revealed very similar patterns (Supplementary material Appendix 5).

Temporal scale of data aggregation and sampling completeness

Temporal extent as well as the temporal scale of data aggregation did not affect sampling completeness of plant and pollinator species nor sampling completeness of the links between them significantly (Fig. 2, Table 2). The numbers of observed plant and pollinator species as well as the number of observed links within a network increased with increasing temporal scale (Fig. 2a–c, Table 2). However, the estimated asymptotic numbers of species and links increased similarly and, thus, sampling completeness (expressed as the detected proportions of estimated species and link numbers) was relatively constant across temporal scales (Fig. 2d–f). Sampling coverage for plants, pollinators and links was relatively high at all temporal scales (median ≥ 96% for plants; 84% for pollinators; 70% for links), but increased with temporal extent as well as with temporal scale (Fig. 2g–i, Table 2). The analysis of the reduced data set resulted in quantitatively similar patterns (Supplementary material Appendix 5).

Effects of species richness, species turnover and link rewiring

Structural equation models revealed that the temporal scale of data aggregation affected the six network indices via various pathways, representing both biological processes as well as sampling artefacts (Fig. 3). Intuitively, increasing temporal scale closely corresponded to increases in both sampling effort (the number of sampling days) and temporal extent (the temporal distance between first and last sampling day) (Supplementary material Appendix 2 Fig. A3). In turn,
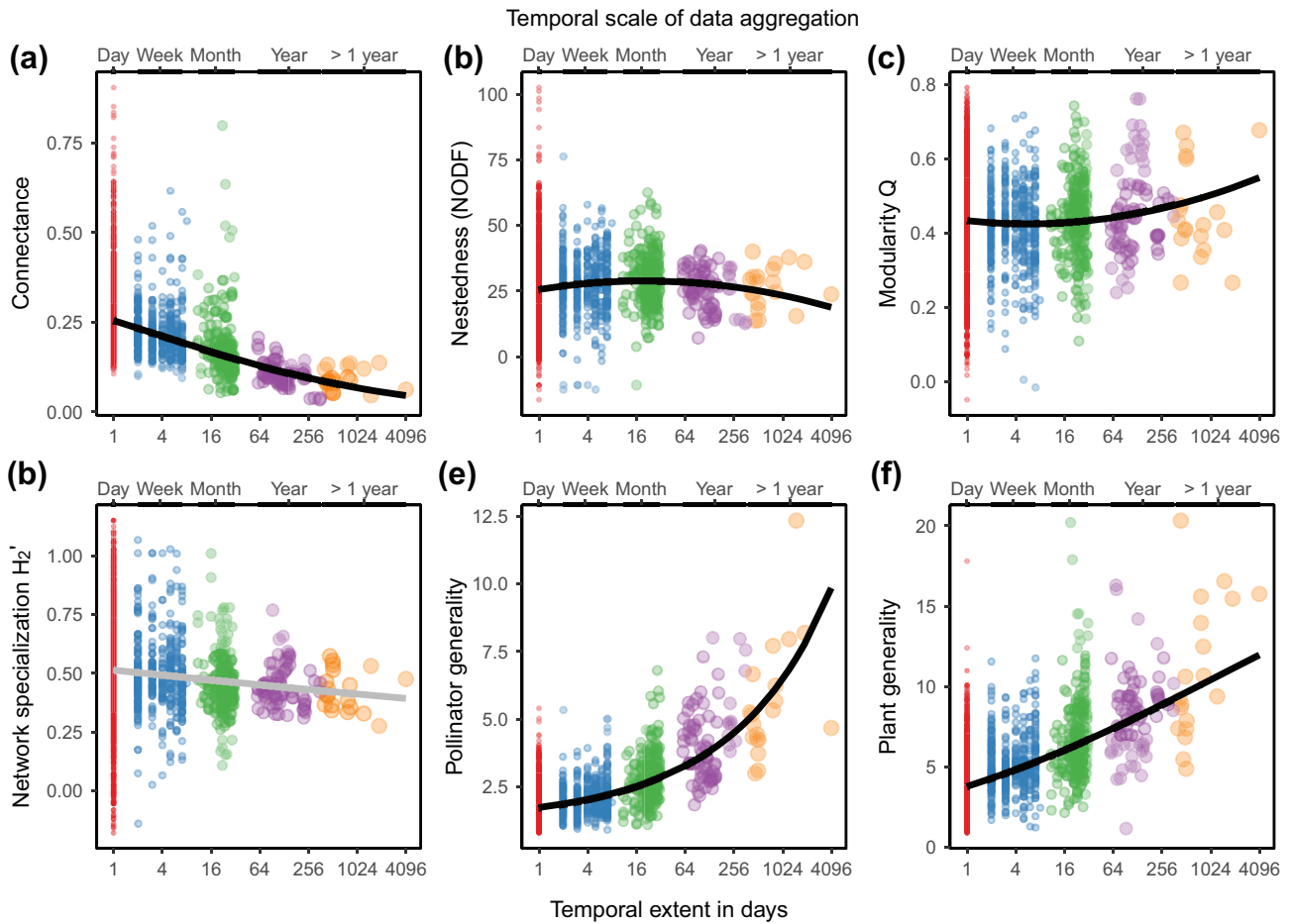
Figure 1. Effects of the temporal scale of data aggregation on (a) connectance, (b) nestedness (NODF), (c) modularity Q, (d) network specialization H_2', (e) pollinator generality and (f) plant generality. Trendlines are based on predictions of linear mixed models testing the effect of temporal extent as single and quadratic term. Black and gray trendlines indicate significant and no effects of temporal extent, respectively. Statistical fits for connectance, pollinator generality and plant generality are based on log-transformed data, whereas figure axes represent the scale of the original data. These partial residual plots correct for baseline differences among studies and sites (specified as random effects in linear mixed models), which occasionally leads to data points lying outside the range of the variable.

Table 1. Effects of the temporal scale of data aggregation on six commonly used indices to describe network structure. Statistics are based on linear mixed models testing the effect of temporal extent as single and quadratic term. Significant effects ($p < 0.05$) are reported in bold.

| Response	Sum sq	Mean sq	Num. df	Den. df	F-value	pr(>F)
log(Connectance)						
log(Temporal extent)	7.37	7.37	1	1858.05	59.40	**<0.001**
log(Temporal extent)^2	1.33	1.33	1	1848.77	10.73	**0.001**
Nestedness (NODF)						
log(Temporal extent)	2373.24	2373.24	1	1883.30	12.75	**<0.001**
log(Temporal extent)^2	1514.52	1514.52	1	1874.02	8.13	**0.004**
Modularity Q						
log(Temporal extent)	0.05	0.05	1	1871.88	3.01	0.083
log(Temporal extent)^2	0.10	0.10	1	1854.55	5.84	**0.016**
Network specialization H_2'						
log(Temporal extent)	0.12	0.12	1	1854.43	2.86	0.091
log(Temporal extent)^2	0.00	0.00	1	1857.99	0.00	0.955
log(Pollinator generality)						
log(Temporal extent)	4.84	4.84	1	1867.68	53.84	**<0.001**
log(Temporal extent)^2	2.13	2.13	1	1858.58	23.76	**<0.001**
log(Plant generality)						
log(Temporal extent)	17.32	17.32	1	1855.08	108.62	**<0.001**
log(Temporal extent)^2	0.36	0.36	1	1842.06	2.27	0.132
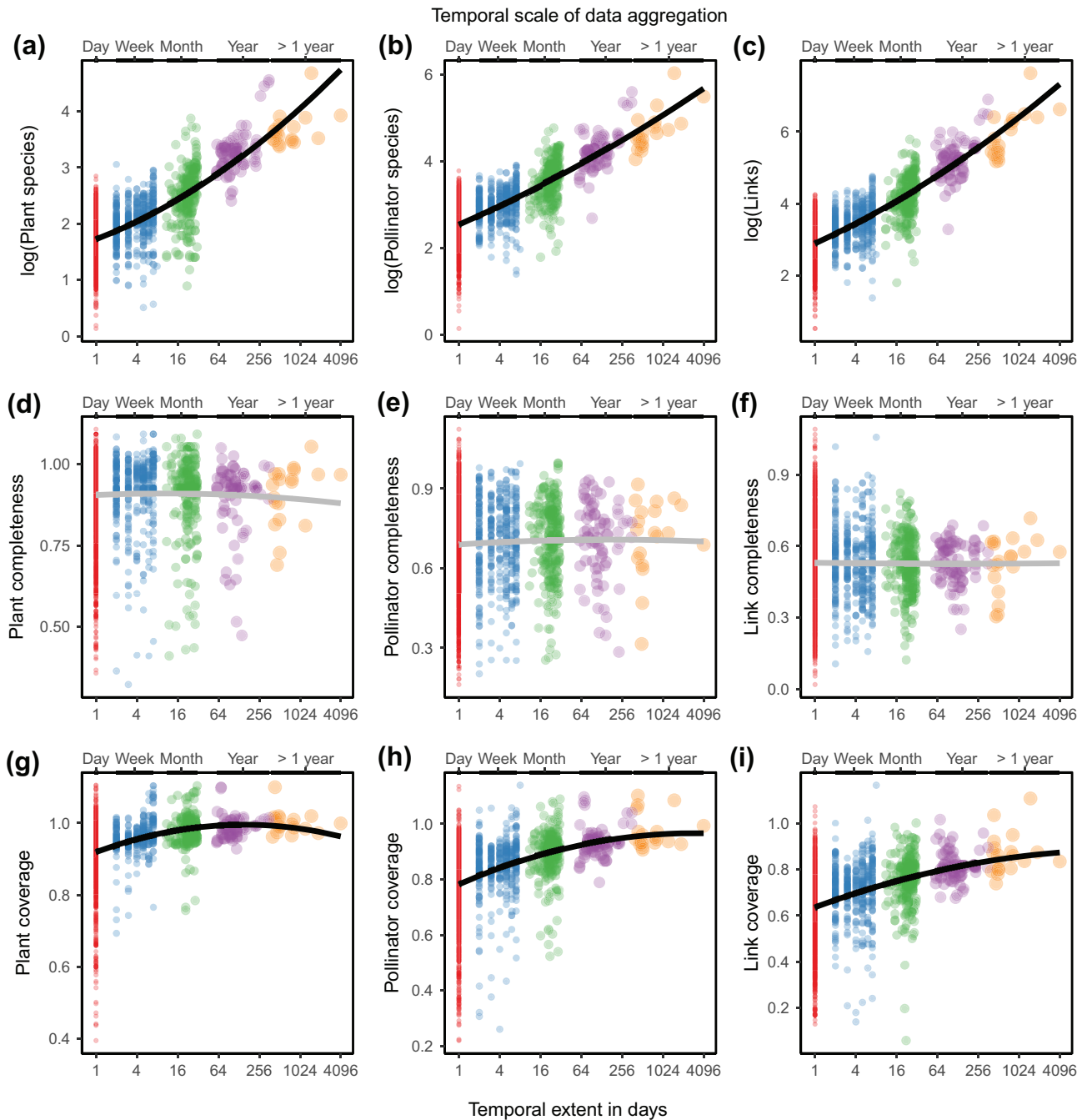
Figure 2. Effects of the temporal scale of data aggregation on network size, sampling completeness and sampling coverage. The nine panels show effects on the log-transformed numbers of (a) plant species, (b) pollinator species and (c) links, effects on sampling completeness of (d) plant species, (e) pollinator species and (f) links, as well as effects on sampling coverage at the level of (g) plants, (h) pollinators and (i) links. Trendlines are based on predictions of linear mixed models testing the effect of temporal extent as single and quadratic term. Black and gray trendlines indicate significant and no effects of temporal extent, respectively. Sampling completeness was quantified as the proportion of observed species or link numbers of the species and link numbers estimated by the Chao1 richness estimator. Sampling coverage is an estimation of the proportion of all individuals or interactions that belong to the observed species or links. These partial residual plots correct for baseline differences among studies and sites (specified as random effects in linear mixed models), which occasionally leads to data points lying outside the range of the variable.
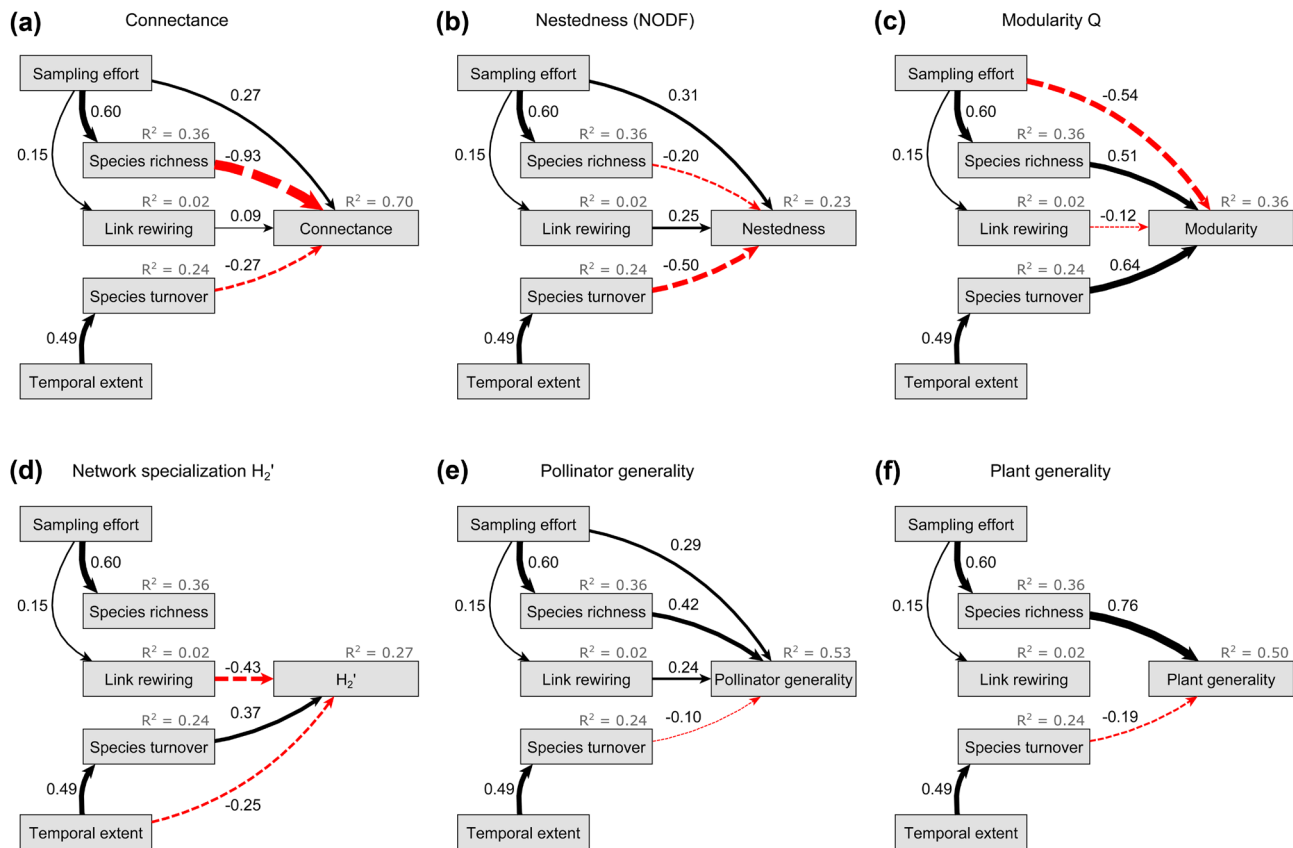
Figure 3. Structural equation models showing the effects of potential drivers of the temporal scale-dependence of (a) connectance, (b) nestedness (NODF), (c) modularity Q, (d) network specialization H_2', (e) pollinator generality and (f) plant generality. Standardized coefficients are presented as numbers on or below arrows. To indicate relative effect strengths, arrow widths are scaled to standardized coefficients. Red dashed and black solid arrows indicate negative and positive effects, respectively. Marginal R^2 values indicate the proportion of variance in the response variables explained by the fixed effects. See Supplementary material Appendix 2 for model fits. During model simplification only statistically significant pathways have been retained ($p < 0.05$). Correlations among variables are not shown. Note that the six models only differ in the network index used, explaining identical effects of sampling effort and temporal extent on species richness, link rewiring and species turnover in each model.

sampling effort and temporal extent affected network indices either directly or indirectly via increased species richness, link rewiring and species turnover (Fig. 3).

Sampling effort had a direct positive effect on connectance, nestedness and the generality of pollinators, and a direct negative effect on modularity (Fig. 3). The direct effects of sampling effort on connectance, nestedness and modularity were of opposite direction with respective to the indirect effects via species richness. Species richness was significantly and positively affected by sampling effort (36% of variance explained), in turn affecting five of the six network indices. Species richness was also the most important predictor for connectance, pollinator generality, and plant generality, and of intermediate importance for nestedness and modularity (Fig. 3). The effect of sampling effort on link rewiring was relatively weak (2% of variance explained). In turn, link rewiring had positive, albeit also relatively weak, effects on connectance, nestedness, and pollinator generality, and negative effects on modularity and network specialization H_2'. For H_2' link rewiring was the most important predictor (Fig. 3d).

Temporal extent had only a direct negative effect on H_2'. However, temporal extent positively affected species turnover (24% of variance explained). In turn, species turnover had negative effects on connectance, nestedness, pollinator generality, and plant generality, and positive effects on modularity and network specialization H_2'. Species turnover was the most important predictor for both modularity and nestedness (Fig. 3b–c).

Performing the structural equation models with either link completeness or link coverage as a co-variable (Supplementary material Appendix 4), and performing them for the reduced data set (Supplementary material Appendix 5), yielded overall qualitatively similar results, supporting the robustness of our findings.

Discussion

Our analysis of 30 data sets of temporally-resolved plant–pollinator interactions illustrates that the structure of interaction

Table 2. Effects of the temporal scale of data aggregation on network size (species and link richness), sampling completeness and sampling coverage. Statistics are based on linear mixed models testing the effect of temporal extent as single and quadratic term. Significant effects (p < 0.05) are reported in bold.

Response	Sum sq	Mean sq	Num. df	Den. df	F-value	pr(>F)
log(Plant richness)						
log(Temporal extent)	20.23	20.23	1	1852.57	115.54	**<0.001**
log(Temporal extent)^2	4.60	4.60	1	1845.20	26.29	**<0.001**
log(Pollinator richness)						
log(Temporal extent)	44.90	44.90	1	1865.65	207.35	**<0.001**
log(Temporal extent)^2	1.13	1.13	1	1856.04	5.21	**0.023**
log(Link richness)						
log(Temporal extent)	71.79	71.79	1	1864.79	242.37	**<0.001**
log(Temporal extent)^2	4.25	4.25	1	1856.41	14.35	**<0.001**
Plant completeness						
log(Temporal extent)	0.01	0.01	1	1881.31	0.52	0.472
log(Temporal extent)^2	0.01	0.01	1	1883.32	0.54	0.463
Pollinator completeness						
log(Temporal extent)	0.03	0.03	1	1901.59	0.90	0.343
log(Temporal extent)^2	0.01	0.01	1	1891.85	0.20	0.658
Link completeness						
log(Temporal extent)	0.00	0.00	1	1883.39	0.05	0.822
log(Temporal extent)^2	0.00	0.00	1	1863.65	0.01	0.912
Plant coverage						
log(Temporal extent)	0.44	0.44	1	1661.60	72.04	**<0.001**
log(Temporal extent)^2	0.10	0.10	1	1644.57	16.48	**<0.001**
Pollinator coverage						
log(Temporal extent)	1.08	1.08	1	1866.48	72.48	**<0.001**
log(Temporal extent)^2	0.10	0.10	1	1849.66	6.55	**0.011**
Link coverage						
log(Temporal extent)	1.12	1.12	1	1810.17	54.05	**<0.001**
log(Temporal extent)^2	0.06	0.06	1	1798.62	2.84	0.092

networks exhibits considerable change across temporal scales ranging from single days to multiple years. This temporal scale-dependence of network structure occurs because different temporal scales determine 1) the degree to which temporal dynamics (species turnover and link rewiring) are included in the network, and 2) how much sampling effort is put into constructing the network. Consequently, networks constructed at broader temporal scales are increasingly shaped by the temporal turnover of species and their interactions, as well as the interplay of these temporal dynamics with sampling effort.

These findings imply that the interpretation of network structural patterns differs among temporal scales. For example, a network constructed across the entire growing season will contain early-, mid- and late-season flowering plants as well as pollinators that occur only at certain times within the season; in contrast, a network constructed across a single week contains only species that are active at essentially the same time (Simanonok and Burkle 2014, Cuartas-Hernández and Medel 2015, CaraDonna et al. 2017). Thus, at broader temporal scales network structure includes its underlying temporal dynamics, whereas networks at narrow temporal scales essentially control for temporal dynamics. Therefore, studying interaction networks across a range of temporal scales may be necessary to fully understand the causes and consequences of their structure.

The effect of temporal dynamics on the temporal scale-dependence of network structure

Our structural equation models further highlight the important role of temporal dynamics (species turnover and link rewiring) in shaping network structure across temporal scales. In particular, species turnover, which increased with temporal extent, consistently influenced all six aspects of network structure, and was the most important predictor for nestedness and modularity. Owing to variation in species phenology, species turnover gives rise to temporally forbidden links – links that cannot form because species are not active at the same time (Olesen et al. 2011). These phenology-mediated forbidden links restrict the number of potential interaction partners for any given species, and can therefore ultimately influence the overall structure of the network (Vázquez et al. 2009a, b). High temporal turnover of species may therefore prevent the formation of a highly connected network core, thereby reducing network connectance and limiting overall network nestedness (Burkle et al. 2013). In contrast, the positive relationship between species turnover and modularity indicates that high temporal turnover of species can lead to the inclusion of additional modules into the network, a pattern that is consistent with other research (Martín González et al. 2012, Morente-López et al. 2018). If modules are mostly composed of temporally co-occurring

species, cross-module connections may be prevented due to phenological mismatches, while within-module connections are strengthened, thereby increasing overall network modularity. These strong effects of species turnover on nestedness and modularity suggest that the consideration of temporal dynamics could be critical in the study of how nestedness and modularity relate to network stability (Bascompte et al. 2006, Thébault and Fontaine 2010).

The observed effects of link rewiring on the temporal scale-dependence of network structure can be attributed to the fact that with increasing temporal scale, more links are realized among the same subsets of species. As a result, high rates of interaction rewiring led to greater pollinator generality, connectance and nestedness; and lower modularity and network specialization. We observed relatively weak effects of rewiring as compared to the effects of species turnover and sampling effort, which may be because rewiring defined as the dissimilarity in links among shared species does not capture all aspects of interaction flexibility, such as establishing links to partners only temporarily available (MacLeod et al. 2016). However, for network specialization (H_2'), which is robust to species richness differences and sampling effects (Blüthgen et al. 2006), rewiring was the most important predictor. Network specialization decreased with greater link rewiring and temporal extent, reflecting that species with longer phenophases accumulate more links over time, thereby reducing the specialization of the network. Nevertheless, the relationship between rewiring and network specialization did not lead to a consistent effect across temporal scales (Fig. 1d), as there was also a counteracting indirect effect of temporal extent via species turnover. High species turnover prevents many species from interacting, resulting in an apparently more specialized network pattern. Therefore, even for apparently scale-invariant network indices (such as H_2'), the interpretation of the underlying cause of network structure differs depending on temporal scale. Some of the observed specialization at narrow temporal scales may be due to short-term specialization, whereas at broad temporal scales, some of the observed specialization may be the result of temporal segregation.

The effect of sampling effort on the temporal scale-dependence of network structure

Sampling effort plays an important role in shaping network structure across different temporal scales, mainly due to its positive effect on species richness. Indeed, the effects of sampling effort and species richness have been explored in detail (Blüthgen et al. 2008, Dormann et al. 2009, Rivera-Hutinel et al. 2012), but what we show here is that these two factors are important, but not sufficient, to explain why network structure changes across temporal scales. The network indices that were most sensitive to the temporal scale of data aggregation were connectance, pollinator generality and plant generality, which were also the indices most strongly influenced by species richness. When sampling effort is held constant, species richness is negatively associated with

connectance, as the observation time per species decreases, and the likelihood of missing a link increases (Blüthgen et al. 2008, Vázquez et al. 2009b). The positive effects of species richness on plant and pollinator generality indicate that the number of interaction partners per species increases with increasing species richness despite the reduced observation time per species. Species richness also influenced modularity (positively) and nestedness (negatively) more weakly, and had no effect on network specialization (H_2'). Species richness effects on modularity and network specialization are in line with previous studies (Blüthgen et al. 2006, Olesen et al. 2007). However, whereas previous studies reported increasing nestedness with increasing species richness (Bascompte et al. 2003, Thébault and Fontaine 2010), we observed the opposite trend. Increased species richness reduces the observation time per species and thus may reduce overall nestedness as a result of a less complete detection of links among potential core species.

The direct effects of sampling effort on network structure likely stem from increased link detection. For example, increased link detection may lead to the discovery of a highly connected network core, explaining why nestedness increased with sampling effort. Similarly, network modularity may be greater with low sampling effort, if more sampling leads to the detection of new links that represent cross-module connections (Rivera-Hutinel et al. 2012). The effects of sampling on nestedness and modularity were of opposite direction to the effects of species turnover and may explain the non-linear effects of temporal scale on these two indices. For example, while the increase in nestedness from daily to weekly and monthly networks may reflect the effect of increased sampling effort, at broader temporal scales this effect seems to be counterbalanced by the effect of species turnover.

Temporal scale of data aggregation and sampling completeness

Temporal turnover of species also appears to be important for the effect of temporal data aggregation on sampling completeness. Our analyses show that the effect of increased sampling effort was counterbalanced by the strong effect of species turnover, which simultaneously increases the size of the species pool and the accumulation of links at broader temporal scales. While we found network structural properties to be sensitive to the temporal scale of data aggregation, estimated sampling completeness of species and their links remained constant independent of whether the data were aggregated within days, weeks, months, years or multiple years. This pattern persists despite the strong positive influence of temporal data aggregation on sampling effort and even though the number of detected species and links increased with broader temporal aggregation. In other words, unless sampling effort is drastically increased, temporally aggregated networks may be larger, but not necessarily more complete. This finding is consistent with the idea that the structure of mutualistic networks undergoes constant change, rather than simply building up to a single, cumulative structure (Burkle and Alarcón 2011).

In contrast to sampling completeness, sampling coverage increased with increasing temporal scale of data aggregation, suggesting that increasing aggregation leads to networks that better represent the most frequent links at the respective temporal scale. Thus, unobserved links may be quantitatively less important in a broadly aggregated network than in a short-term network. This pattern could also be driven by differences in phenophase length among species and links: the increased sampling effort due to temporal data aggregation is ineffective to increase detection probabilities of species (and links) with short phenophases, but likely increases detection probabilities of species (and links) with long phenophases. However, some of the difference between the estimators may also be because sampling completeness based on Chao1 can be an overestimate (Fründ et al. 2016). As both estimators assume that there is a true, static network to be sampled, future work could help to better understand the influence of temporal dynamics on the estimation of sampling completeness.

Guidance for the future study of ecological networks

Based on our findings about the temporal scale-dependence of network structure, we provide some guidance for the future study of ecological networks (Table 3).

First, as the temporal scale of data aggregation effectively determines which processes are giving rise to the observed network structure, the temporal scale needs to be representative of the processes relevant for the research question. For example, facilitative effects among species at the same trophic level that are mediated by common mutualistic partners may act independently of whether the species occur at the same time (Rasmussen et al. 2013). Thus, if the aim is to draw conclusions about facilitation, networks should be constructed on a relatively broad temporal scale. In contrast, for a study on how species partition their niche of mutualistic partners (Simmons et al. 2019), it may be informative to look at a narrower temporal scale to minimize other factors

Table 3. Strategies to deal with the temporal scale-dependence of network structure in the study of plant–pollinator networks. These strategies may serve as a guideline for single-network studies (S), cross-sectional studies (C), longitudinal studies (L) and meta-analyses (M).

	Study type				Issues	Strategies	Limitations
	S	C	L	M			
Study design and sampling considerations	×	×	×	×	Different temporal scales may provide different perspectives on network structure.	The temporal scale at which we sample and analyze networks has to fit to our research questions.	
		×	×		Networks need to be comparable in terms of sampling effort.	Standardize sampling effort per observation period, e.g. accounting for temporal distribution and total time of sampling events.	Seasonal/altitudinal/latitudinal differences between networks might require adjustments of sampling time and distribution.
Analysis considerations		×	×	×	Network comparisons can be biased due to differences in sampling effort and temporal extent.	If possible, compare only networks with similar sampling effort and temporal extent. Alternatively, correct for sampling effort, temporal extent, species richness or network size in the analyses (e.g. co-variables in statistical models, rarefaction or null-model analyses).	Correcting for species richness/network size might not remove the effect of temporal dynamics. Networks might differ in their underlying temporal dynamics despite similar extents.
	×	×	×	×	Important patterns can be overlooked when only one temporal scale is analyzed.	Compare several analyses at different temporal scales to clarify consistency or inconsistency in network patterns.	Data availability and logistical limitations could complicate such approaches.
Interpretations	×	×	×	×	Different processes influence network structure at different temporal scales.	Consider temporal scale and related factors (sampling effort as well as temporal dynamics) for improved interpretation of network structure.	Information on all aspects might not be available.
Publication considerations	×	×	×		Meta-analyses and other synthesizing studies depend on data.	Publish temporally (and spatially) explicit data instead of already aggregated data.	

(phenology, life history) that may be responsible for diet differences among species.

Second, studies comparing different networks (e.g. meta-analyses, cross-sectional studies and longitudinal studies) should use networks aggregated at similar temporal scales. Otherwise any observed patterns may be biased by differences in sampling effort and temporal extent across studies, sites or focal time intervals (Rivera-Hutinel et al. 2012, Falcão et al. 2016). Thus, sampling effort and its temporal distribution per network should be standardized within individual studies. For meta-analyses, the construction of appropriate networks will be facilitated if authors publish space- and time-explicit data, rather than already aggregated data (Knight et al. 2018). It is important to note that despite standardized sampling, networks can still differ in their underlying temporal dynamics: the same temporal extent may cover different proportions of the full flowering season depending on geographic position – even at the same locality, the same temporal extent may capture different levels of diversity depending on the season (Cuartas-Hernández and Medel 2015, Souza et al. 2018).

If no information on sampling effort and temporal extent is available, correcting for species richness and network size can go a long way in accounting for sampling biases, but ignores the effects of temporal dynamics. Possible correction methods include, for example, rarefaction analysis (e.g. downsampling networks to a common number of interactions; Gotelli and Colwell 2001), covariates in linear models and SEMs, or null models that explore if observed patterns can be explained by richness differences alone (Dormann et al. 2017, Pellissier et al. 2018).

Finally, we suggest that for a more complete understanding of how different processes determine network structure and function, future studies could consider multiple temporal scales in their analyses. For example, specialization of daily networks may represent short-term niche partitioning, whereas specialization of yearly networks includes the effects of phenological asynchrony. Such a multi-scale approach would be particularly informative for comparisons between networks that differ in their underlying temporal dynamics, e.g. networks from seasonal and aseasonal environments. In this vein, studying how the underlying temporal dynamics of networks vary along environmental gradients could bring new insights into why network structural properties vary along these gradients (Tylianakis and Morris 2017, Pellissier et al. 2018). For example, mean annual temperature might dictate not only which species potentially can interact but also the length and the synchrony of the periods in which these interactions are realized. This perspective may also help to predict the consequences of climate change (Park and Mazer 2019), species invasions (Herron-Sweet et al. 2016, Arroyo-Correa et al. 2019) or habitat degradation and restoration (Burkle et al. 2013, Ponisio et al. 2017).

Our analyses of a large global data set of quantitative and temporally explicit plant–pollinator networks shows that the depiction of network structure can vary considerably with the temporal scale of data aggregation. We emphasize that rigorous consideration of temporal dynamics of species interactions can considerably increase our understanding of the multi-scale temporal structure of networks.

Data availability statement

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