Phylogenetic diversity of flowering plants declines throughout the growing season across a subalpine elevational gradient

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Abstract

Co-flowering is a potential facilitative mechanism for plants to overcome pollinator declines and phenological mismatches by attracting more pollinators to a multi-species patch. Due to associated competition, facilitation is expected to be more beneficial among more distantly related plants that compete less, and more prevalent in stressful conditions where benefits outweigh potential costs. We test a novel set of predictions that follow from these hypotheses, including that modules of co-flowering species in montane plant communities will be associated with i) increased fitness, ii) phylogenetic overdispersion, and ii) higher elevations. We quantified flowering phenology and fitness of plants across an elevational gradient in the Colorado Rocky Mountains, identified co-flowering modules using a network approach, and analyzed the phylogenetic distribution of co-flowering modules. We found that fitness correlated positively with co-flowering across elevations, but the correlation was strongest at high-elevation sites. Phylogenetic dispersion increased with elevation but declined throughout the growing season. Late-season modules were more underdispersed at all elevations than early-season modules. By combining analyses of phenological timing, network structure, environmental stress, fitness, and phylogenetic patterns, our results reveal that plant communities may lose phylogenetic diversity as conditions become hotter and drier and climate change alters flowering phenology and pollination networks.

Key words: co-flowering, network analysis, Rocky Mountain Biological Laboratory, facilitation, phylogenetic diversity, elevational gradient

Introduction

Understanding the impacts of climate change on biodiversity is critical as global warming continues to accelerate [1]. Forecasts indicate that climate change could drive up to 54% of species towards extinction [2]. The loss of phylogenetic diversity—a key part of biodiversity—will likely follow in the wake of species loss, spurred by phylogenetically clustered extinction and extinction cascades [3–5]. When species losses are non-random across the tree of life, climate change will lead to a disproportionate loss of evolutionary history [6–8]. A critical determinant of how species declines will affect biodiversity will be the relationship between phylogenetic diversity and the biotic and abiotic interactions that render a species susceptible to extinction [9,10].

For nearly 90% of flowering plants, animal pollinators are essential to reproduction, and are likely to determine fitness and population persistence [11]. Worldwide pollinator declines are increasingly limiting pollination services to plants, however, disrupting plant-pollinator networks and driving declines in plant populations [12–14]. Therefore, understanding phylogenetic structure of flowering plant communities, and its relationship to pollinator services, will be essential for understanding and forecasting how plant biodiversity will respond to environmental changes.

An open question is how plant reproductive output is influenced by differences in flowering times within and between species in a plant community. Both facilitative and competitive interactions between plants have been studied in the context of pollination [15–17]. On the one hand, co-flowering of multiple species simultaneously is a potential mechanism by which plants might overcome pollinator limitation and attract more pollinators to a multi-species patch [18]. Indeed, some evidence suggests that co-flowering can be facilitative, increasing pollinator visitation rates and the fitness of participating species by increasing the rewards for pollinators [18–23]. For example, in a recent study at the Rocky Mountain Biological Laboratory (RMBL), the experimental removal of the dominant plant species, *Helianthella quinquenervis,* immediately lowered pollinator visitation rates and network robustness for remaining species [19]. These results have important implications for the consequences of climate change, because *H. quinquenervis* is known to die off during spring frosts, which are becoming more common [24]. On the other hand, sharing pollinators in time and space can lead to lower fitness through increased resource competition (due to niche overlap) and/or reproductive interference, particularly for closely related species [25,26]. A different recent study at RMBL found that co-flowering between *Linum lewisii* and *Potentilla pulcherrima* decreased *Linum lewisii*'s reproductive output [27], and other work with artificial flowers has shown that co-flowering increased pollinator visitation, but significantly decreased pollen purity [28].

Notably, little work on co-flowering has addressed the phylogenetic relationships of interacting species within plant communities (see [29,30]). Within and among groups of species that flower together (co-flowering modules), we can evaluate how phylogenetic diversity is distributed across a flowering season, and how phenological diversity patterns might be influenced by facilitative versus competitive interactions [31–34]. More distantly related species

with less similar traits are expected to compete less [35–37], and so we might expect facilitation via co-flowering to be more likely among more distantly related species [38], leading to more phylogenetic overdispersion in the community.

Here we test the hypotheses that i) co-flowering provides a fitness benefit to participating species, and ii) co-flowering species will be phylogenetically overdispersed to maximize fitness benefits. To do this, we present a novel phylogenetic analysis of co-flowering networks across multiple sites, ranging from montane to subalpine elevations in the Colorado Rocky Mountains. We selected sites that span an elevational gradient because co-flowering may also be affected by abiotic factors increasingly altered by climate change [27,39,40] low-elevation habitats will become less suitable for high-elevation species [41,42]. The Stress Gradient Hypothesis posits that facilitation will become more prevalent under more stressful conditions [20,43], which would typically occur at higher elevations [44,45]. A phylogenetic study of plant communities in the Rocky Mountains observed overdispersion at higher elevations [46]. Therefore we further hypothesize that iii) co-flowering modules will be more overdispersed and provide greater fitness benefits to plant species at higher elevations.

Our approach allows us to test a series of novel predictions: that the degree of co-flowering will correlate positively with species' fitness, that co-flowering modules will be overdispersed, and that these patterns should be more pronounced at higher elevations. Our analyses interrogate the interplay between phenological timing, network structure, environmental stress, fitness, and phylogenetic patterns in communities. By integrating across these often separate subfields, our goal is to shed light on how species may be affected by ongoing changes in climate and habitats.

Materials & Methods

Study Sites

We collected data at three sites in Washington Gulch near the Rocky Mountain Biological Laboratory (RMBL, Gothic, Colorado, USA) from June to August in 2021 and 2022. RMBL is located in the East River valley of the West Elk mountains, approximately 10 kilometers from Crested Butte, Colorado. The growing season lasts a relatively short 3-5 months, and snowmelt date is variable but arriving earlier on average with climate change [40,47]. Study sites were located at 2815 m (38°53'50"N, 106°58'43"W), 3165 m (38°57'38"N, 107°01'53"W), and 3380 m (38°58'10"N, 107°01'53"W) in elevation. These sites are part of a larger, long-term study of plant functional traits over an elevational gradient at RMBL established in 2003 [46,48]. All sites are approximately 50 m^2 and have similar slopes and aspects [48]. Using quadrats, we randomly defined five 1.2 m x 1.2 m plots within each site, then marked the plots with flags and strings. We removed these markings at the end of each summer, so exact plot locations shifted each year. The lowest and middle sites are in the montane vegetation zone, while the highest is subalpine [49]. We identified angiosperms in the plots using the *Flora of Colorado [49]* and specimens at the Rocky Mountain Biological Laboratory Herbarium (herbarium code RMBL).

Field Data Collection

Within the plots, we marked all newly open flowering units once per week from early June to mid-August for ten weeks of observation over each of the two summers. We counted flowering units as either a single flower (most species), a flowering head (Asteraceae), or an umbel (Apiaceae). We considered flowers open once the petals were separated and able to be counted. Each week, we tagged and recorded all new flowering units across species and sites with a unique color of yarn. We only counted flowering units once as they opened, so counts were not cumulative.

We quantified fitness as successful fruit and seed development at the end of the season. When flowers began to produce fruits, we counted the number of developed fruits produced by each flowering unit and recorded the week of flowering based on the yarn color. We opened one fruit per site for each species and flowering week to count the number of seeds inside. We recorded the number of flowering units with fruit, the number of fruits per unit, and the number of seeds per fruit. We could not count fruits and seeds for all species because they were consumed by herbivores too quickly, otherwise disappeared, or did not produce seeds during our field season (Supplementary material Table S1).

Co-flowering Networks

To quantify the duration and intensity of flowering overlap for each species pair, we calculated Schoener's Index (SI) of niche overlap [50] using the number of newly open flowers per week for each species. We also calculated fitness overlap as the SI for fruit produced from the flowers open each week. The formula is:

$$SI = 1 - 1/2\sum |Pik - Pjk|$$

where Pik and Pjk are the proportion of species i and j flowering in week k [51]. Values fall at or near 0 when there is no flowering overlap and close to or at 1 for near or complete overlap. We calculated SI in the R package spaa with the command niche.overlap() and method "schoener" [52].

Network analyses can define co-flowering species' modules within a community [29,31–33]. Using the SI values as a metric of co-flowering interaction strength, we constructed co-flowering networks for each site for 2021 and 2022 with SI values as edge weights [31–33]. We constructed networks using the igraph R package [53]. We calculated modularity using [54]'s algorithm via the cluster.louvain() command in igraph. We used weighted edges and a resolution of 1.0. We then generated null networks using the nullmodel() command and method "r2d" in bipartite and vegan R packages [55]. To determine the modularity significance, we calculated the modularity of the null models and then computed a z score for the observed modularity relative to the null distribution. Z-scores above 2 are considered significant [55]. We constructed all network visualizations in Gephi [56].

Phylogenetic Dispersion

We used the 'ALLMB.tre' angiosperm phylogeny from [57] to calculate all phylogenetic metrics. This phylogeny included all genera in our dataset and 49 of 56 species observed in our plots. If a species was missing from the phylogeny but was the only member of its genus in the plots, we replaced it with a closely related congener in the Smith and Brown phylogeny (Supplementary material Table S2). Only the genus *Senecio* had multiple species in the plots missing from the phylogeny. We replaced *Senecio integerrimus* Nutt. with sister species *S. triangularis* Hook. *[58]*. We removed *Senecio crassulus* A. Gray from all phylogenetic analyses because it has no available genetic or phylogenetic information.

We calculated Faith's PD [59], mean phylogenetic distance (MPD), and mean nearest taxon distance (MNTD) in geiger [60]. We calculated standard effect sizes (SES) for all three metrics in the picante R package [61]. We used each metric's "sample.pool" null model to draw species from the RMBL community with 5000 iterations randomly. Evidence of significant underdispersion was identified by a negative SES and low P value, and a positive SES and high P value identified overdispersion.

We analyzed all data in R version 4.2.3 [62].

Results

Flowering

We recorded data for 56 angiosperm species and 5,633 flowering units across all three sites and years (Fig. 1). We counted 3,660 flowering units in 2021 and 1,973 in 2022. Across both years, the lowest site had 31 species and 1,994 flowering units, the middle site had 27 species and 2,108 flowering units, and the highest site had 24 species and 1,531 flowering units. The 56 species spanned 24 families: 12 at the lowest site, 14 at the middle, and 16 at the highest. Five families (Asteraceae, Ranunculaceae, Rosaceae, Violaceae, Boraginaceae) occurred at all three sites. Five species occurred at all three sites: *Potentilla gracilis* Douglas ex Hook., *Viola nuttallii* Pursh, *Ranunculus inamoenus* Greene, *Mertensia brevistyla* S. Watson, and *Erigeron speciosus* DC.

Most species pairs had low or no overlap in their flowering phenology for all sites and years. Overall, 57.2% of pairs had a Schoener's Index of zero, and 67.4% were below 0.1. A small subset of species had high flowering overlap, with 5.4% above 0.7 (Fig. 2). We calculated fitness SI values for 788 of the 1262 species pairs. The correlation between species in fruiting success over time was positively related to the correlation in their flowering phenology, particularly at the high elevation site (Fig. 2). The strength of this relationship increased with elevation for both years (High site R^2=0.85 & 0.91, Low site R^2=0.43 & 0.72, for 2021 and 2022 respectively; $p<0.05$ for all).

Network Modularity

Network size ranged from 19 to 26 nodes per network and from 153 to 325 edges each (Fig. 3). All sites in both years were significantly modular (Q > 0.35 for all; Z-scores > 2 for all;

Table 1), but the highest site had the lowest modularity (2021: Q= 0.419, Z-score = 19.75; 2022: Q=0.357, Z-score=14.56) and the lowest site had higher modularity both years (2021: Q=0.44, Z-score = 24.37; 2022: Q=0.56, Z-score=43.12). All three sites had three modules each in 2021. In 2022, the high and middle sites again had three modules, while the lowest site had four. For all sites and years, modules corresponded with flowering at the beginning, middle, and end of the growing season. The low site in 2022 had two middle-season modules.

Phylogenetic Dispersion

At the community level, phylogenetic diversity (PD) and mean phylogenetic distance (MPD) and their standardized effect sizes (SES) indicated that the high site was more overdispersed than the low site in both years, and the overdispersion was higher in 2021 than 2022 (Table 1). This trend, however, was not true for MNTD, as MNTD SES values were similar at the high and low sites in 2021 and 2022 (High site MNTD SES=0.367, 0.015; Low site MNTD SES=0.417, 0.248). At all sites, Faith's PD and MPD showed higher levels of overdispersion than MNTD (Table 1). The middle site varied in its phylogenetic patterns depending on metric and year (Table 1).

At the module level, beginning-season modules were more overdispersed than end-season modules for all sites, years, and phylogenetic metrics (Fig. 4). The standard effect sizes for Faith's PD (0.227 to 1.809) and MPD (0.687 to 1.386) for beginning season modules were all greater than the standard effect sizes for Faith's PD (-0.89 to -3.54) and MPD (-0.894 to -4.94) for end season modules. The end-season modules for all sites were underdispersed by all metrics, with the most significant underdispersion in 2021 sites (Fig. 4; High SES: -3.05 to -4.29; Middle SES: -2.32 to -4.23; Low SES: -2.33 to -4.28). Across all sites and years, Faith's PD, MPD, and MNTD and their standard effect sizes decreased from beginning to end season co-flowering modules (Fig. 4).

Discussion

Despite the importance of flowering phenology for plant fitness and persistence during climate change [63,64], the distribution of phylogenetic diversity across flowering phenologies is largely unknown. Here, we find that plant communities are structured into groups of species that flower together and experience associated increases in fitness when co-flowering. These co-flowering modules are phylogenetically overdispersed early in the season and at higher elevations but become strongly underdispersed and depauperate in diversity at the end of the flowering season. Our results suggest that facilitation via co-flowering could contribute to community assembly in this system, and that interspecific interactions and/or abiotic conditions contribute to non-random phylogenetic patterns within co-flowering modules. If co-flowering drives community composition during different parts of the summer, individual species' declines and shifting phenologies could disproportionately affect the maintenance of phylogenetic diversity in these communities.

We observed a positive correlation between fitness overlap and flowering overlap for all sites and years. This suggests that co-flowering may be facilitative for at least some species and not harmful for most. Recent studies at RMBL have also found evidence for facilitation via co-flowering among species. Bain and colleagues (2022) experimentally removed *Helianthella quinquenervis*, the dominant flowering species in their sites, and found that pollinator visits to the patch immediately declined [19]. Arrowsmith and colleagues (2023) found that community members with similar floral shapes and sizes increased the seedset of *Delphinium barbeyi* [65]. In contrast, Faust and Iler (2022) found that co-flowering decreased the seedset of *Linum lewisii*, but only when the plants were relatively less drought-stressed, suggesting that abiotic factors mediate co-flowering interactions and may become more facilitative as environmental stresses increase [27].

Our analyses of phylogenetic diversity revealed that the high-elevation site as a whole was more overdispersed across both years by two of three diversity metrics (MPD & PD), and consistently more overdispersed than the low-elevation site. The low elevation site deviated little from null expectations and varied from weakly over- to underdispersed across metrics and years (Table 1). A previous study by Bryant et al. (2008) across this same elevational gradient also found that phylogenetic overdispersion increased with elevation, and that soil temperature, pH, and total nitrogen predicted this relationship [46]. Other studies have supported the idea that abiotic filtering drives underdispersion at high elevations, as only a subset of evolutionary lineages share adaptations to this environment [66–68]. However, multiple co-occurring processes likely impact community phylogenetic structure [69]. It is noteworthy that the overdispersion at our highest site was weaker in 2022, when the environment was more favorable (including later snowmelt and wetter and cooler conditions; [70,71]), suggesting that overdispersion was stronger in the more stressful 2021 season. Additionally, the stronger correlation between fitness and co-flowering at higher elevations aligns with previous findings about facilitation increasing with elevation worldwide [45]. The 'Stress Gradient Hypothesis' posits that facilitation should increase under more stressful environmental conditions [44]. However, we did not manipulate or isolate any environmental conditions. Many resources vary with elevation, so we do not know to what extent each of our elevational sites experiences resource limitation or other forms of stress.

Importantly, co-flowering at all three sites in both years was significantly modular, such that particular groups of species flowered together during the flowering season and likely interacted most strongly. The high-elevation site was less modular than the low-elevation site in both years. This could be due to a shorter growing season and condensed duration of opportunity to flower. However, our data do not show any significant differences in season length among the elevations included in this study (Supplementary material Fig. S1). Arceo-Gomez et al. (2018) suggested that modularity indicates multiple mechanisms affecting community assembly, and that no significant modularity may suggest random or single mechanism-driven assembly [31]. Given that we found significantly modular communities and different taxonomic compositions of

flowering modules, both biotic and abiotic factors likely impact the assembly of these communities.

The variation in taxonomic composition across co-flowering modules was associated with clear differences in the representation of regional phylogenetic diversity. In particular, species in the Asteraceae and, to a lesser extent, the Rosaceae dominated the modules at the end of the flowering season. To our knowledge, lower phylogenetic diversity of later flowering modules has not been previously reported. Earlier work in this plant community showed that later flowering species have not shifted their phenologies as significantly as earlier flowering species [40], suggesting that the composition of late flowering modules may have shifted less with climate change than earlier modules. In the same way that the Stress Gradient Hypothesis [44] proposes that facilitation will increase over stress gradients in space, facilitation could also increase with stress gradients in time, such as increased temperature and decreased water availability over the growing season.

At the module level, many biotic and abiotic factors vary across the flowering season and could contribute to lower phylogenetic diversity at the end of the season. Pollinators can structure plant communities [16,34], and may impact the changing diversity of our co-flowering modules directly or through their interactions with abiotic conditions. We counted pollinators throughout the summer of 2021 (Supplementary material Methods, Fig. S2). However, we found that abundance increased steadily over our data collection period (Supplementary material Fig. S2), which indicates that pollinators may not be more limiting over time and is consistent with prior findings [72,73].

Previous work has shown that pollen and pollinator limitation is often species-specific and/or context-dependent in RMBL plant communities [72,74,75], which suggests that the impact of co-flowering facilitation likely also depends on the context and individual species. Schiffer and colleagues (2023) found that early and middle-season species had higher fitness when they flowered separately from population peaks [72]. However, their late-season species, *Potentilla pulcherrima*, had the highest fitness when it flowered at its population peak. Like ours, these results highlight the potential importance of late-season facilitation and the need to clarify late-season flowering conditions further. Soil moisture also affects pollinator visitation rates [76], which may limit which species successfully flower at drier points in the season.

Abiotic conditions also change through the summer growing season, including declines in soil organic carbon, net ecosystem productivity, and soil respiration [48,77]. While each of these variables declines with decreasing plant diversity [78–80], we do not know of work suggesting that they would cause phylogenetic underdispersion. The relationship between abiotic conditions and phylogenetic diversity of co-flowering modules will be important to elucidate, as phylogenetic diversity promotes ecosystem stability and soil microbial diversity [81,82]. Low soil moisture may drive low phylogenetic diversity, as it causes declines in species richness and biomass production [83–86]. However, soil moisture is affected by snowmelt timing and precipitation from summer thunderstorms and has significant interannual variability [87–90], which would not explain our consistent results. In contrast, air temperature increases from June

to August at RMBL, and has been shown to impact flowering phenology, soil temperature, and pollinator behavior [47,91–93].

These potential drivers of low late-season flowering diversity will intensify with climate change and may contribute to a loss of phylogenetic diversity in these flowering communities. Snow is predicted to continue melting earlier with lower winter snowpack, and summer thunderstorm rains are predicted to become less consistent [93–95]. These changes will lead to drier conditions earlier in the summer and may decrease the taxonomic diversity of co-flowering communities earlier in the growing season. Both plant and pollinator phenology and availability are also changing [40,92,96,97] and creating phenological mismatches that could have widespread impacts on plant fitness as they shift the composition of co-flowering communities and alter potentially beneficial interactions between plant species.

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Data Accessibility

Raw phenology and fitness data are available on the Environmental Data Initiative (doi:10.6073/pasta/03029db50ae4a977c20267ebb13224ea [Package ID: edi.1478.1]) [98]. R code for analyses used here is available on GitHub: https://github.com/lveldhuisen/phd-chapter-1.

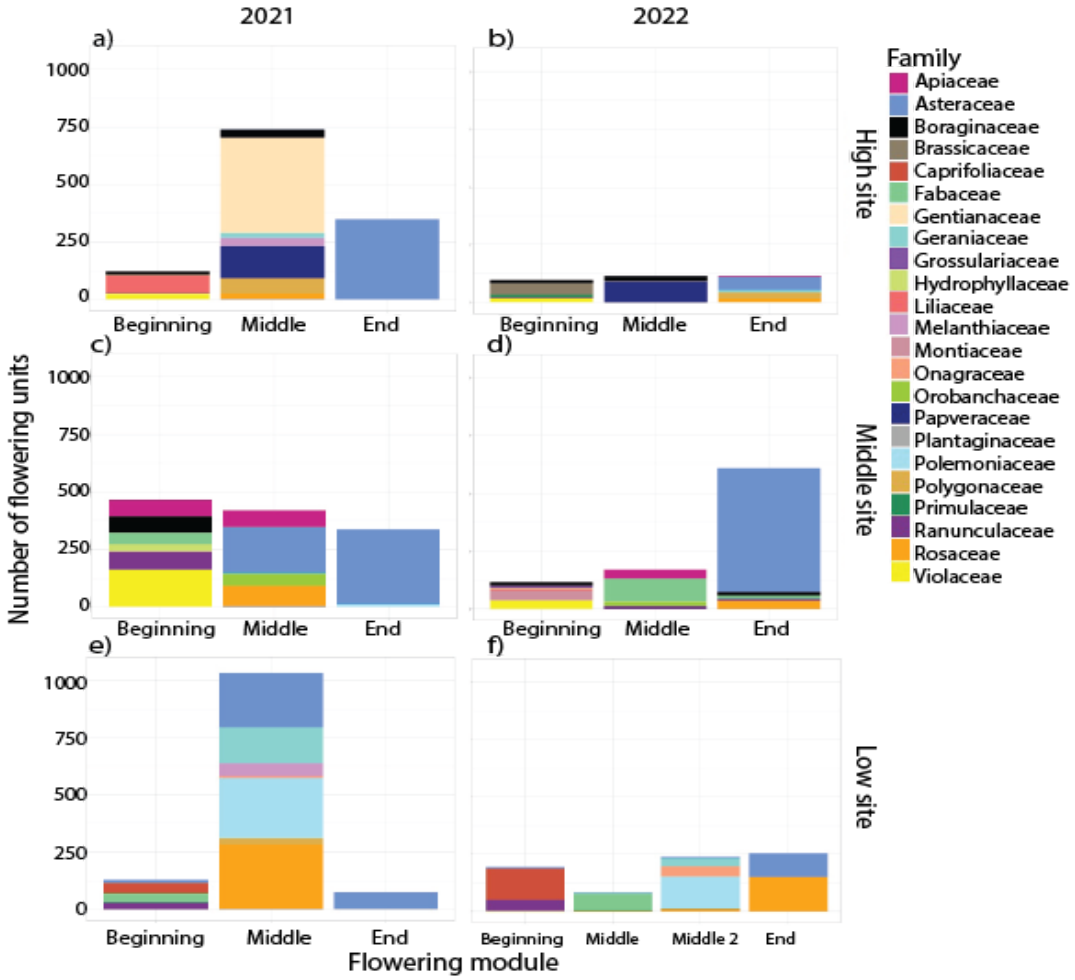

Fig. 1: Histograms of the number of flowering units color coded by family. Shown are panels for the High elevation site (3380 m; A-B), the Middle elevation site (3165 m; C-D) and the Low elevation site (2815 m; E-F) for 2021 (A,C,E) and 2022 (B, D, F) flowering seasons. Each season is partitioned into co-flowering modules (Beginning, Middle, and End). End season modules all show high proportions of Asteraceae and Rosaceae flowering, while Beginning and Middle modules have a greater number of families flowering.

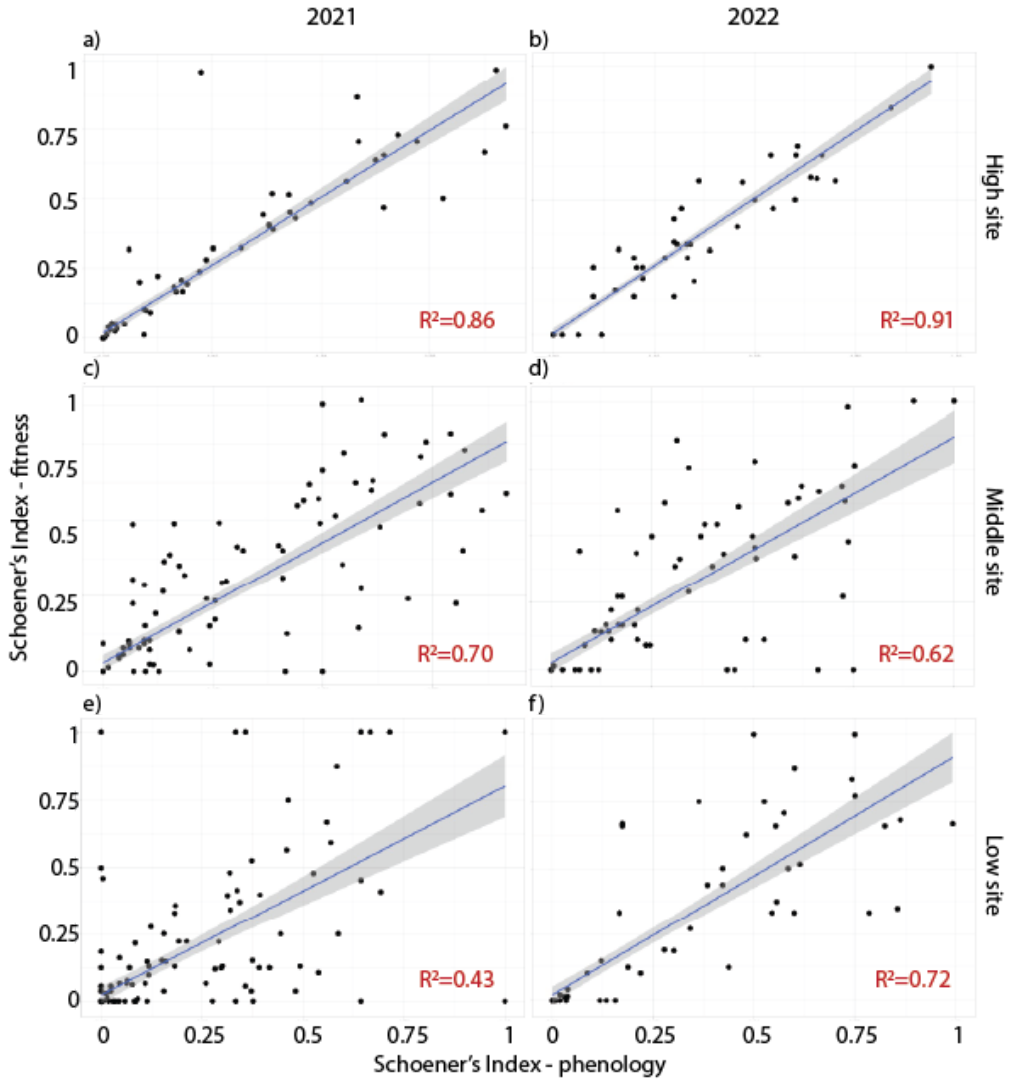

Fig. 2: Regressions of fitness overlap vs. co-flowering overlap for each site and year. Each data point reflects the Schoener's index of overlap for two species in terms of phenology (flowering units per week) and fitness resulting from flowering each week.

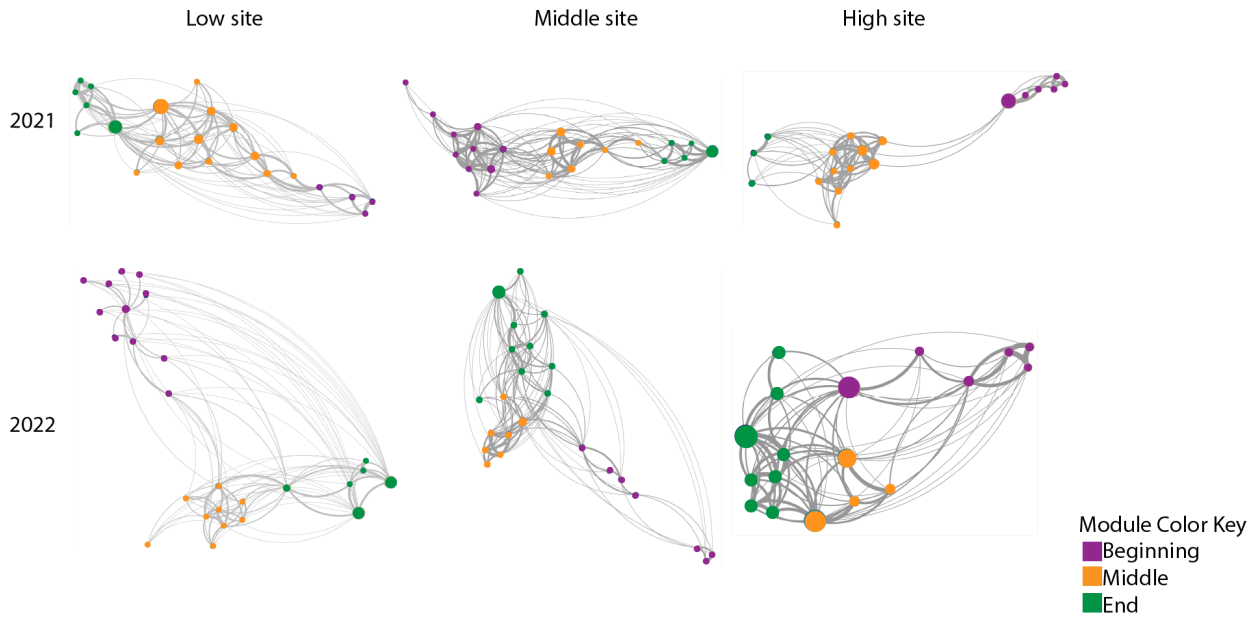

Fig. 3: Network analyses of flowering time for species at each site and year, with nodes color-coded according to the timing of flowering of the module of species flowering together. Species shown in purple flower earliest in the summer, followed by orange nodes in the middle of the summer and green nodes at the end of the summer. Node size represents betweenness centrality, with larger nodes co-flowering with more species. Edge weights are thicker with higher Schoener's Index (SI) values and thinner with lower SI values.

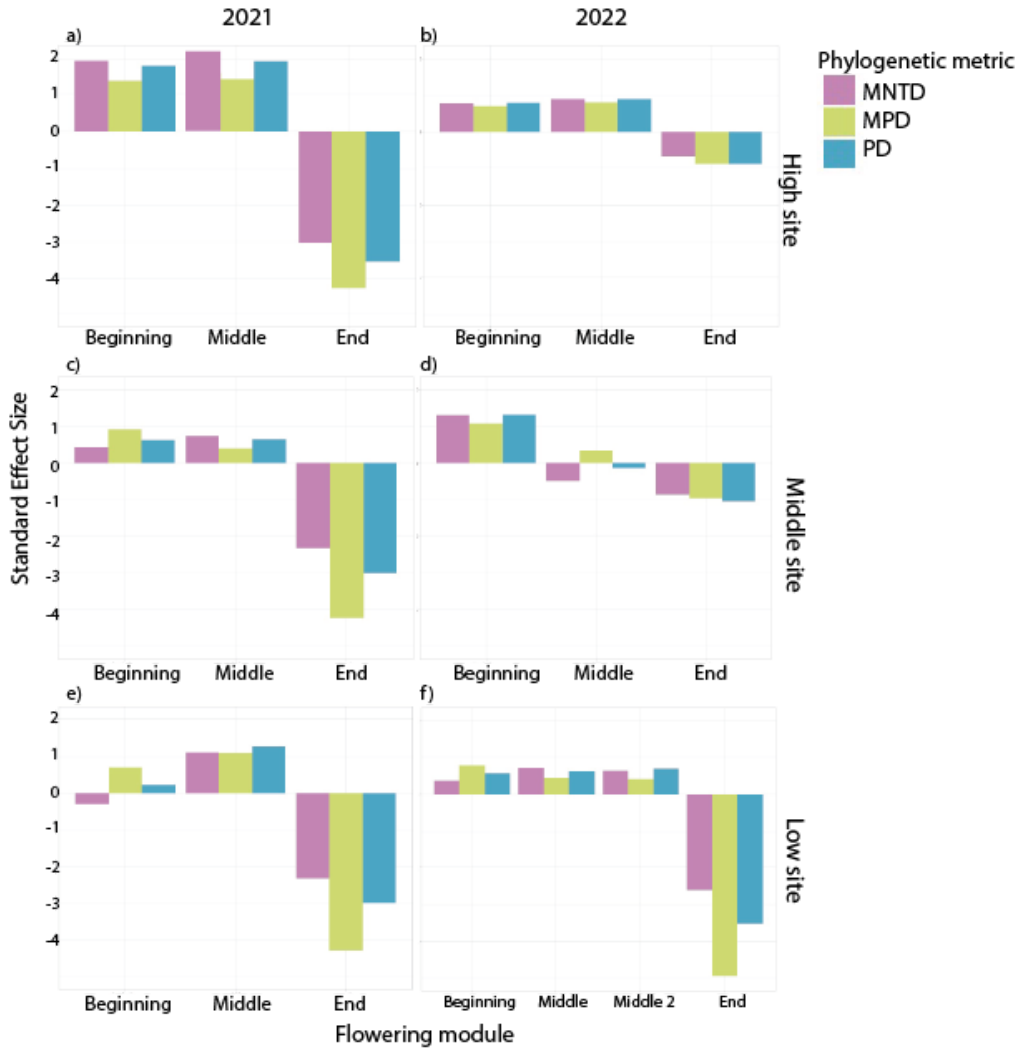

Fig. 4: Standard effect sizes for MNTD (mean nearest taxon distance; pink), MPD (mean phylogenetic distance; green), and PD (phylogenetic diversity; blue) for all sites and years. Shown are panels for the High elevation site (3380 m; A-B), the Middle elevation site (3165 m; C-D), and the Low elevation site (2815 M; E-F) for 2021 (A,C,E) and 2022 (B, D, F) flowering seasons. Within sites and years, panels show results for each co-flowering module from network analyses, including those flowering at the Beginning, Middle, and End of the season. The End season module is underdispersed across all sites and years, while the Beginning and Middle modules are comparatively overdispersed.

Table 1: Network and phylogenetic metrics, standard effect sizes (SES) and p values for each site and year.

Site	Elevation	Year	Modularity	Modularity Z score	Number of edges	Faith's PD	SES	SES p value	MPD	SES	SES p value	MNTD	SES	SES p value
PBM	high	2021	0.419315	19.75	171	1637.08	1.452	0.932	242.4298	1.859	0.993	131.769	0.367	0.635
Pfeiler	medium	2021	0.47698	28.22	231	1503.48	-0.8	0.211	221.7894	0.151	0.519	97.489	-1.397	0.082
Road	low	2021	0.440159	24.27	231	1720.712	0.325	0.627	220.2484	0.028	0.478	123.5657	0.417	0.653
PBM	high	2022	0.357483	14.56	153	1428.79	0.266	0.603	228.4453	0.322	0.578	126.61	0.015	0.499
Pfeiler	medium	2022	0.42668	26.86	276	1677.166	-0.085	0.466	232.5526	0.936	0.827	106.23	-0.591	0.276
Road	low	2022	0.558749	43.12	325	1841.51	-0.102	0.46	216.9188	-1.156	0.128	114.419	0.248	0.59

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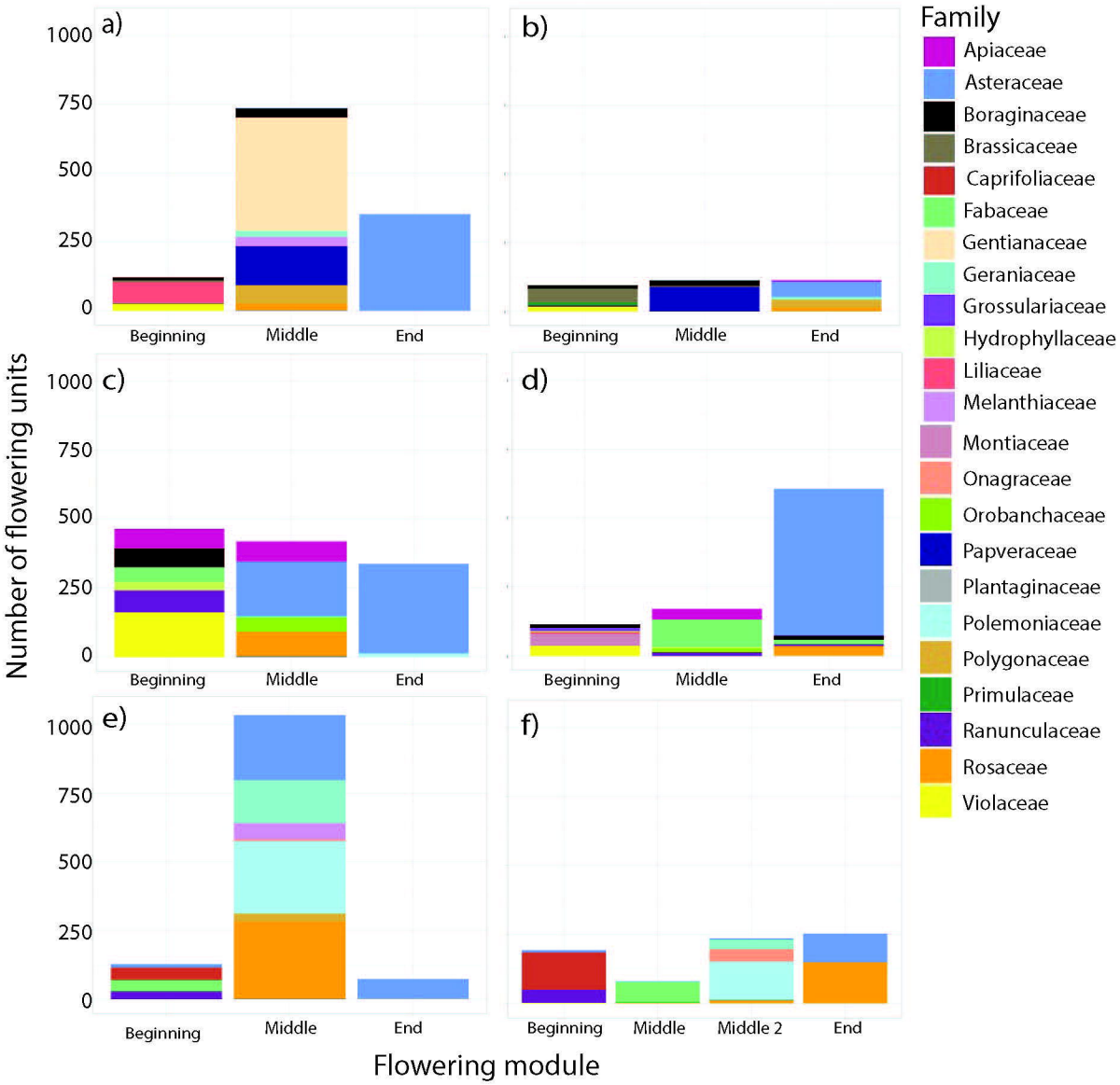
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Fabaceae
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Liliaceae
Melanthiaceae
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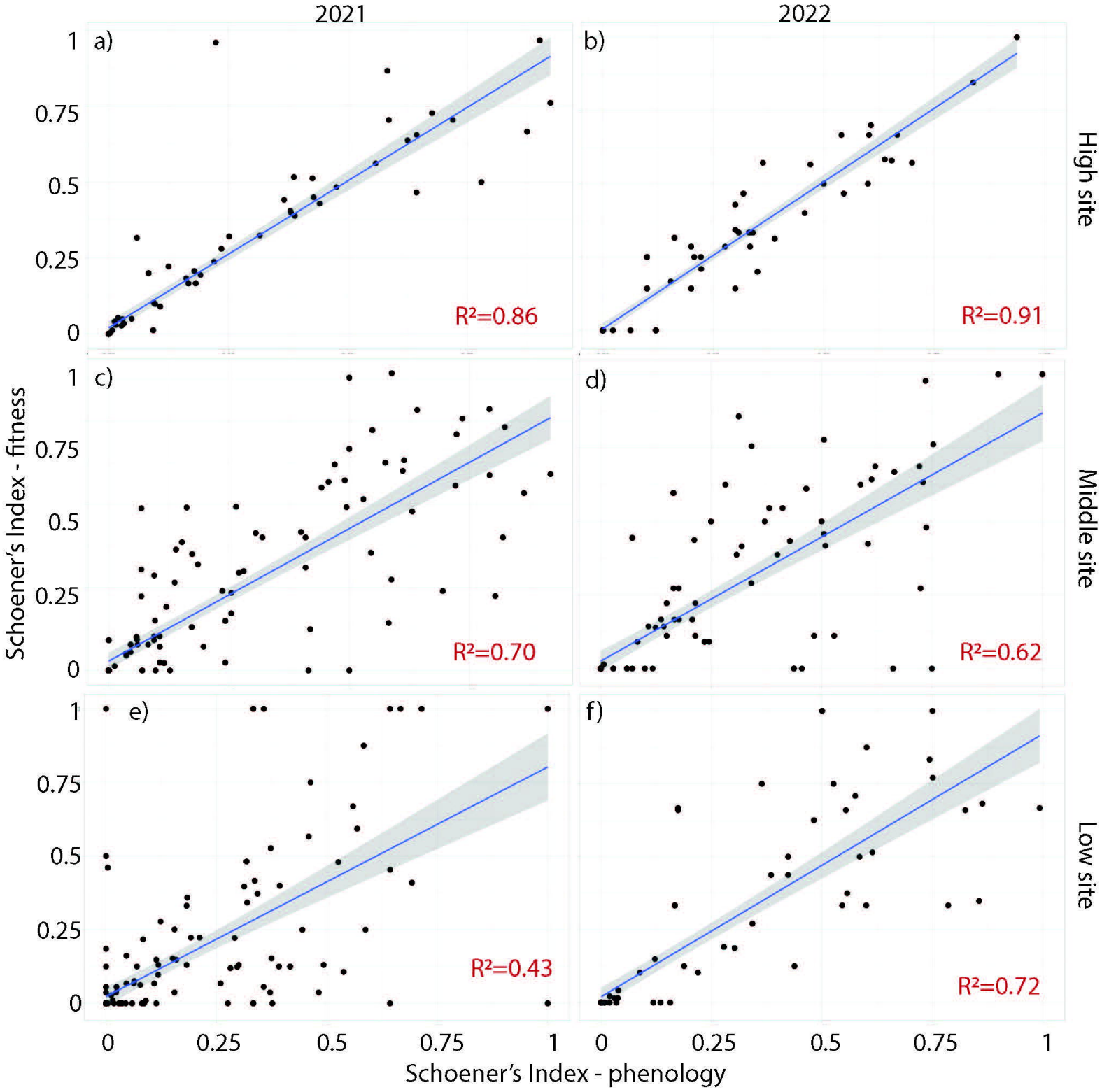
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High site
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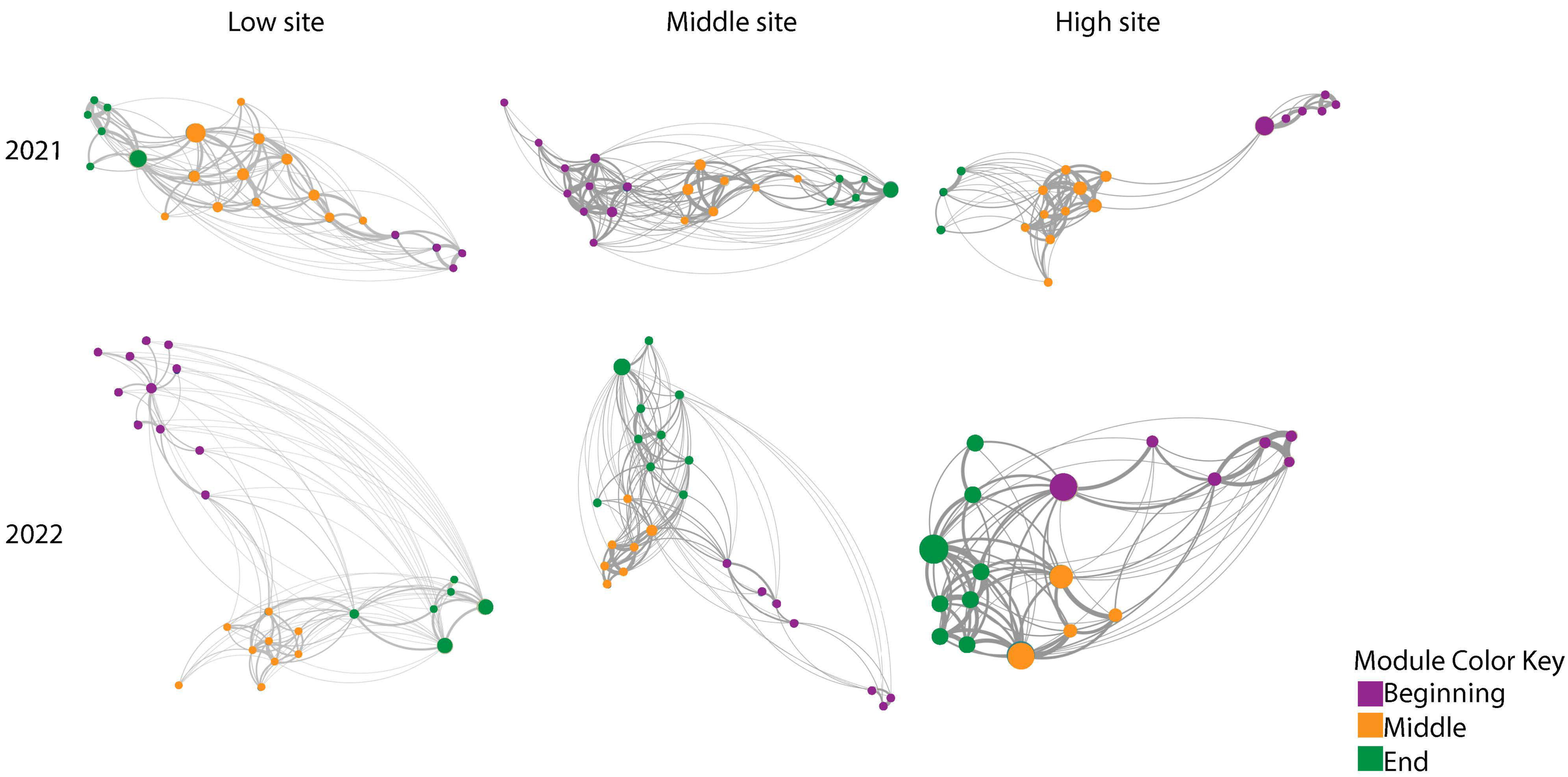
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Module Color Key
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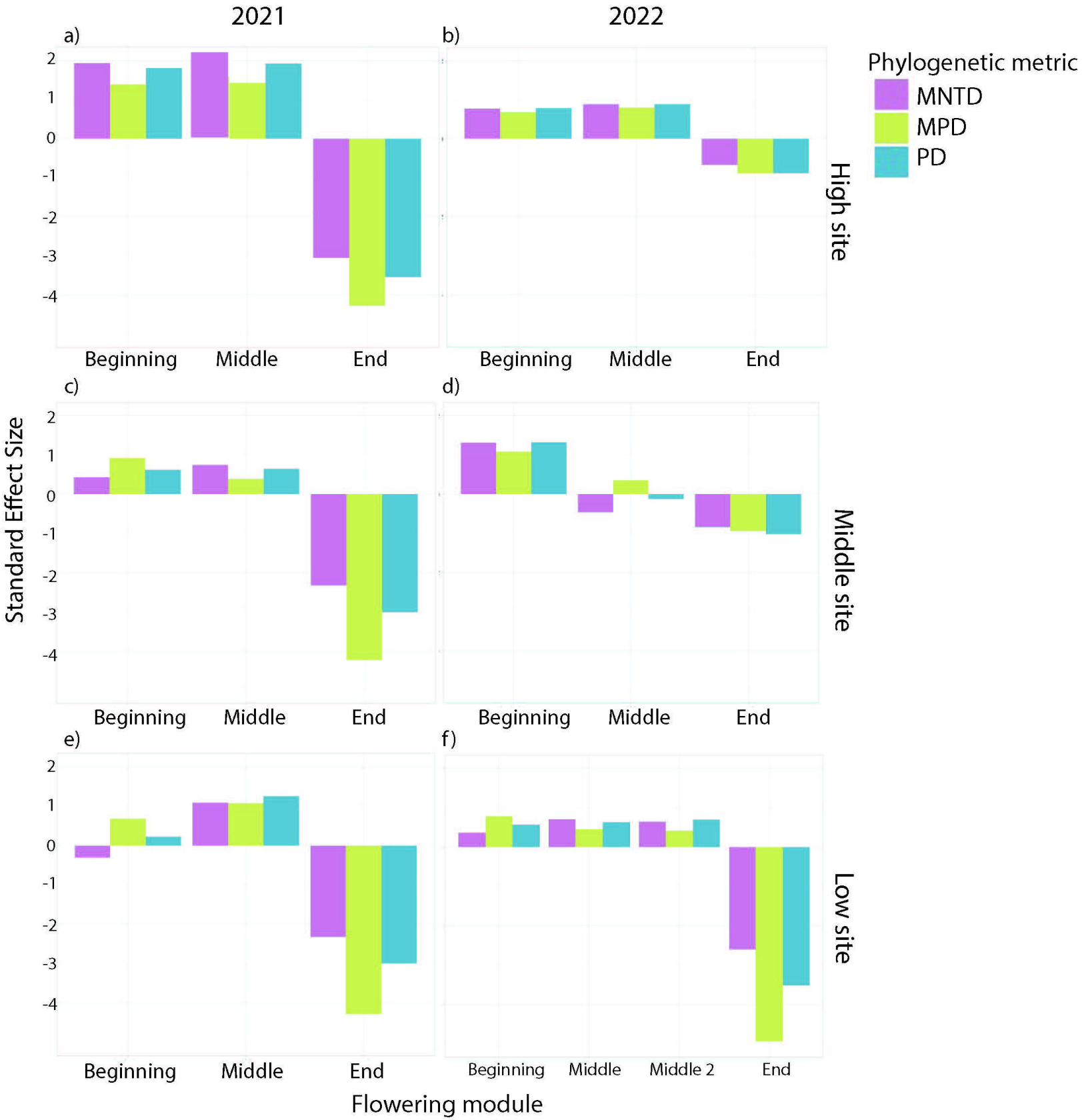
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Phylogenetic metric
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Flowering module