

# Persistence of plant–pollinator interactions in time and space

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## Abstract

Generalist species are important for maintaining network structure and function. Previous studies showed that interactions between generalists persist across sites and years. However, the mechanisms for persistence across spatiotemporal scales are not clear. To address this gap, we collected data on plant–pollinator interactions throughout the flowering period for five years across six plots in a subalpine meadow. We hypothesized that tolerance of environmental variation across time and space plays a key role in species’ generalization by regulating spatiotemporal overlap with partners. We found that interactions between species with broader temporal and spatial distributions tended to be more generalized such that interactions near the network core were more persistent across years and plots and within seasons. These results further understanding of networks by linking the role of environmental variation in time and space in organizing interactions, marrying niche concepts that emphasize species environmental constraints and their role in the community.

**Running title:** *Spatiotemporal persistence of interactions*

## Persistence of plant–pollinator interactions in time and space

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**Abstract** Generalist species are important for maintaining network structure and function. Previous studies showed that interactions between generalists persist across sites and years. However, the mechanisms for persistence across spatiotemporal scales are not clear. To address this gap, we collected data on plant–pollinator interactions throughout the flowering period for five years across six plots in a subalpine meadow. We hypothesized that tolerance of environmental variation across time and space plays a key role in species’ generalization by regulating spatiotemporal overlap with partners. We found that interactions between species with broader temporal and spatial distributions tended to be more generalized such that interactions near the network core were more persistent across years and plots and within seasons. These results further understanding of networks by linking the role of environmental variation in time and space in organizing interactions, marrying niche concepts that emphasize species environmental constraints and their role in the community.

## Introduction

Species interaction networks may be regarded as blueprints of the architecture of biodiversity, depicting complex webs of interactions among species (Bascompte & Jordano 2007). These networks are typically represented and analysed as observations aggregated over time and space; but, explicitly examining the temporal and spatial dimensions of these networks can increase our understanding of the ecological and evolutionary processes that shape their structure and their robustness to human-caused environmental change (Trøjelsgaard & Olesen 2016; CaraDonna *et al.* in press).

In recent years there has been increased interest in the temporal and spatial aspects of species interaction networks (Bascompte & Jordano 2014; Trøjelsgaard & Olesen 2016; Schwarz *et al.* 2020; CaraDonna *et al.* in press). A consistent pattern emerging from such studies is that most interactions are highly dynamic while few are persistently observed over time and space. For example, Aizen *et al.* (2012) observed few plant–pollinator interactions consistently throughout a series of isolated hilltops, while Chacoff *et al.* (2018) observed few interactions consistently across six years. In both studies, the interactions that occurred consistently across time or space tended to involve generalist species, those that interact with many other species, at the network core, the most densely connected part of the network. Understanding how interactions persist across time and space at multiple scales is important for predicting their vulnerability to anthropogenic stressors and for prioritizing the conservation of species that contribute to community robustness (Simmons *et al.* 2019).

Conceivably species’ tolerances to environmental conditions across time and space may affect generalization and thus network position. For example, pollinator species that tolerate a broad range of environmental conditions across time and space could interact with more plant species, as they are more likely to encounter more species compared to pollinators with narrower tolerances and restricted spatiotemporal activity. Similarly, plant species that flower under a broad range of environmental conditions could interact with more pollinator species due to greater spatiotemporal overlap with pollinator partner species.

We collected data on plant–pollinator interactions throughout the flowering season for five years across six plots in a subalpine meadow in the Colorado Rocky Mountains with the goal of identifying the attributes of interactions that determine their persistence across time and space. We hypothesized that species tolerance to environmental conditions over time and space may determine interaction persistence by constraining temporal and spatial overlap with partner species. Thus, we predicted that interactions with higher temporal and

spatial persistence (i.e., those with longer phenophases, higher inter-annual persistence, and broader spatial occurrence) would occur at the network core.

## Material and Methods

We conducted this study in a subalpine meadow at the University of Colorado’s Mountain Research Station (40°01’48”N 105°32’26”W), located at 2900 m of elevation 22 km west of Boulder, CO, USA. The meadow faces east and is surrounded by aspen and spruce-fir forest. We collected interaction data weekly during the entire flowering period from 2015 to 2019. The flowering season at the study site typically starts after snowmelt in late May to early June and extends to late September. Interactions were recorded on 16 – 18 weeks per year. Sampling was done on average 6.95 days apart (SD = 1.17 days).

On each sampling date, we sampled plant–pollinator interactions in six 20–30 m × 2 m plots (five 30 m × 2 m and one 20 m × 2 m) by observing flowers (plant-centred sampling). Sampling was conducted in fair weather during mornings between 8:00 am and 12:00 pm, a time range when pollinator activity is high and before the onset of thunderstorms that often occur at mid-day during the summer in the Rocky Mountains. We sampled plant–pollinator interactions within each plot (in random order) by doing 15-min surveys in which we carefully observed all flowers for visitors while walking the periphery of plots to minimize trampling. When we observed an interaction, defined as a pollinator contacting the reproductive structures of a flower, we recorded the identity of the plant and pollinator species. Insect pollinators were collected with aspirators or aerial nets for later identification in the laboratory. Expert entomologists (see Acknowledgements) assisted with insects that are difficult to identify. To assess the thoroughness of the sampling effort, we compared observed richness of plants, pollinators, and interactions to values from three commonly used richness estimators: Chao2, first-order jackknife (Jack1), and bootstrapped values (Chacoff *et al.* 2011; Gotelli & Colwell 2011).

We recorded temporal and spatial variation in abiotic conditions. Temperature is fundamental in constraining pollinator foraging (Corbet *et al.* 1993; Willmer & Stone 2004) and plant flowering (Schemske *et al.* 1978). To measure temporal variation in temperature at the site, we compiled air temperature data from every morning (8 am–12 pm) during which sampling was conducted from a weather station located ~1 km away at a similar elevation, 3020 m (SNOTEL Site Niwot, 663). Soil moisture affects plant growth and reproduction (Fayet *et al.* 2000). To quantify aspects of spatial variation in abiotic conditions among plots we measured ground temperature and soil moisture every 2 meters along sampling plots on one occasion at 7:55–8:38 am on 6 July 2018. To measure ground temperature, we used a handheld infrared thermometer. To measure soil moisture, we used a time-domain reflectometry (TDR) moisture sensor.

To test the relationship between the network position of interactions and their temporal or spatial persistence we used Spearman’s rank-order correlation tests between the proximity to the core of the nested network and each variable of temporal or spatial persistence: the number of years, the span of days (phenophase), and the number of plots in which interactions were recorded. The position of each interaction was calculated using a maximally nested matrix. To this end, we first compiled all the observations from the study into a plant–pollinator interaction matrix, sorting rows and columns to maximize matrix binary nestedness. This sorting organizes plant species (in rows) and pollinator species (in columns) from most specialist to most generalist such that generalist species are packed into the top left corner of the matrix. We then used this matrix organization to assess the relationship between proximity to the core of the nested network and persistence values for each temporal and spatial variable. The proximity of interactions to the core of the nested network was calculated as one minus the standardized Euclidean distance of each interaction to the upper-left cell in the nested matrix with the distance between each adjacent cell equal to one (as in Chacoff *et al.* 2018). We tested for the number of modules present to determine if the network could have multiple cores.

To assess the ecological significance of our results, we compared the observed Spearman’s correlation coefficients for the relationships between proximity to the core of the nested network and temporal or spatial

persistence values and compared these coefficients to those from null models. Null models generated 1000 randomized matrices by shuffling persistence values within matrices while fixing marginal totals and connectance, which we judged to represent a conservative null model. To determine how temporal and spatial variables are related to one another, e.g., whether interactions that have longer phenophases tend to be more persistent across years, we tested for correlations between each combination of temporal or spatial persistence variables with Spearman’s rank correlation tests.

We used linear regressions with a 2<sup>nd</sup> degree polynomial to assess how plant and pollinator *species*’ proximity to the network core (row or column number in the nested network divided by the total number of rows or columns) relate to inter-annual occurrence, intra-annual occurrence, and inter-plot occurrence. Species proximity to the nested core was correlated with degree, the number of interacting partner species, a common metric of species specialization (for plants: Pearson’s  $r = 0.87$ ; for pollinators: Pearson’s  $r = 0.70$ ). Finally, to link species’ phenophases to their environmental tolerances, we correlated the range of days in which pollinator or plant species were recorded as interacting with the range of temperature recorded in the mornings during those ranges of dates.

All analyses were performed in R version 4.0.2 (R Core Team 2020). We used the vegan package version 2.5-6 for calculating richness estimates (Oksanen *et al.* 2010), the bipartite package version 2.15 for network analyses, visualization, and null models (using the `swap.web` function) (Dormann *et al.* 2008), and the reshape2 package version for data formatting (Wickham 2007).

## Results

Over the 5 years of study, we observed 4,261 total interactions across 836 links between 267 species of animal visitors to 41 species of plants. Flower visitor species consisted of 109 Hymenoptera, 63 Diptera, 36 Coleoptera, 35 Hemiptera, 21 Lepidoptera, 3 Orthoptera, 1 Raphidioptera (*Agulla* sp.), and 1 hummingbird (*Selasphorus platycercus*). Plant species consisted of 14 Asteraceae, 5 Rosaceae, 3 Fabaceae, 3 Orobanchaceae, 2 Ranunculaceae, and 1 of each Apiaceae, Boraginaceae, Campanulaceae, Crassulaceae, Gentianaceae, Geraniaceae, Hydrophyllaceae, Melanthiaceae, Onagraceae, Primulaceae, and Rubiaceae. Removal of flower visitor groups not commonly regarded to be pollinators (Hemiptera, Orthoptera, Raphidioptera; but see (Wardhaugh 2015)) before analysis yielded nearly identical results. The aggregated network showed a nested structure (NODF = 25) and connectance values (0.08) that are typical of plant–pollinator networks (Schwarz *et al.* 2020). The network had one module. Observed sampling completeness of interaction richness was at 52% of the Chao2 estimator, 64% of the Jack1 estimator, and 81% of the bootstrapped estimator. Observed sampling completeness of pollinator richness was at 62% of the Chao2 estimator, 71% of the Jack1 estimator, and 85% of the bootstrapped estimator. Observed sampling completeness of plant richness was at 90% of the Chao2 estimator, 93% of the Jack1 estimator, and 97% of the bootstrapped estimator. Environmental conditions, such as temperature, varied temporally throughout the season and across years (Fig S1), and spatially among plots, as did soil moisture (Fig S2).

Interactions between generalists showed higher temporal and spatial persistence. Interactions in the core of the nested network tended to have higher inter-annual persistence (Spearman’s rank correlation coefficient = 0.35,  $P < 0.001$ ; Fig 1a), intra-annual persistence (Spearman’s rank correlation coefficient = 0.22,  $P < 0.001$ ; Fig 1b), and inter-plot persistence (Spearman’s rank correlation coefficient = 0.35,  $P < 0.001$ ; Fig 1c). Observed Spearman’s rank correlation coefficients for all three persistence variables were higher than those expected under null models (Fig S3).

Temporal and spatial interaction persistence values were interrelated. That is, interactions with higher inter-annual persistence tended to have longer phenophases (Spearman’s rank correlation coefficient: 0.59,  $P < 0.001$ ) and be more widespread among plots (Spearman’s rank correlation coefficient: 0.73,  $P < 0.001$ ). Interactions with longer phenophases tended to be more widespread among plots (Spearman’s rank correlation coefficient: 0.78,  $P < 0.001$ ).

At the species level, inter-annual persistence, longer phenophases, and higher plot occurrence were associa-

ted with generalization (Fig 2, S4). For both plants and pollinators, species that had higher inter-annual persistence were closer to the core of the nested network (Fig 2a, b; for plants:  $R^2 = 0.73$ ,  $P < 0.001$ , for pollinators  $R^2 = 0.61$ ,  $P < 0.001$ ). Both plant and pollinator species with longer phenophases were closer to the core of the nested network (Fig 2a, b; for plants:  $R^2 = 0.72$ ,  $P < 0.001$ , for pollinators  $R^2 = 0.70$ ,  $P < 0.001$ ). Both plant and pollinator species that were more widespread among plots were closer to the core of the nested network (Fig 2c, d; for plants:  $R^2 = 0.58$ ,  $P < 0.001$ , for pollinators  $R^2 = 0.57$ ,  $P < 0.001$ ). Using degree (number of links), as a proxy for generalization showed similar patterns as species proximity to the network core (Fig S4). Finally, phenophase length for plants and pollinators was associated with broader ranges of temperatures on the mornings of sampling days (for plants: Pearson's  $r = 0.67$ ; for pollinators Pearson's  $r = 0.81$ ).

## Discussion

We found that interactions involving generalist plants and pollinators are more persistent in time and space. More specifically, interactions near the network core were more persistent across the five years, more persistent within seasons, and more persistent across plots. Moreover, the same interactions that were persistent within seasons also tended to be persistent across years and among plots, and that interactions persistent across years are persistent across plots. Generalist species tended to be more widespread in time and space. These patterns suggest that tolerance to environmental variation across space and time is associated with interaction generalization through the increased spatiotemporal overlap of interacting partners.

Our study conceptually and empirically links the persistence of interactions in time and space. The patterns of temporal and spatial persistence are consistent with previous studies that have found this relationship in either space or time (Aizen *et al.* 2012; Chacoff *et al.* 2018). Our study links these disparate patterns in temporal and spatial persistence of interactions with the tolerances of environmental conditions as a proposed mechanism linking them. At the species level, the connection between distributions and generalization also relates disparate concepts of niche breadth that emphasize species environmental constraints (Grinnellian niche) and their role in the community via interactions (Eltonian niche) (Chase & Leibold 2003; Devictor *et al.* 2010; Gravel *et al.* 2019). We define generalization focusing on the number of partners of each species across a range of spatial and environmental conditions. We recognize that species' roles themselves are dynamic and context-dependent (Devictor *et al.* 2010; CaraDonna & Waser 2020; Miele *et al.* 2020) and that generalization can be quantified in different ways to describe different aspects of species (Blüthgen *et al.* 2006).

As the specificity of environmental conditions and spatiotemporal distributions can be interrelated with abundance (Rabinowitz 1981; Brown 1984) it is important to consider the role of abundance in the patterns observed. Species that are widespread in time and space are likely to have larger population sizes. Large population sizes could make species of plants and pollinators less susceptible to local extinctions and thus allow greater spatiotemporal persistence allowing for greater generalization. Because spatiotemporal overlap of interacting partners and abundance are primary factors in driving interaction patterns it supports the view that interactions are strongly driven by opportunism (Waser *et al.* 1996; Memmott 1999). Higher abundances could also increase the detectability of species and their interactions (McCarthy *et al.* 2013; Chacoff *et al.* 2018). While the observation methods of this study aimed to minimize biases stemming from detectability by observing all flowers in plots during the survey period, disentangling sampling effects from biological processes in network studies remains an important challenge and priority (Vázquez *et al.* 2009; CaraDonna *et al.* in press).

Despite these promising results, much work remains to be done. With the increasing availability of interaction network datasets, there is an opportunity to synthesize patterns of spatiotemporal interaction persistence across studies with different environmental contexts and temporal and spatial scales. To this end, whenever possible future studies should record interaction data that are temporally and spatially explicit. Also, associated data on environmental conditions in the context of the interactions and the physiology of organisms (e.g., thermal tolerances) would allow further assessing the role of environmental variation on interaction

persistence.

Generalist species are the linchpins of networks, as their presence promotes network robustness to environmental perturbations (Bascompte & Stouffer 2009). Despite their pivotal roles, common and generalist species are taken for granted and lack conservation protections that are conventionally aimed at rare species (Lindenmayer *et al.* 2011). However, we know that abundant, generalized species may be susceptible to decline and extinction in the face of environmental change (Wagner 2020), e.g., *Bombus dahlbomii* in Patagonia, see (Morales *et al.* 2013). The possibility of such declines puts the stability of ecological communities in jeopardy. Therefore, conservation priorities should not overlook the pivotal roles that generalists play in supporting biodiversity across time and space.

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## Figures

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**Figure 1.** Matrices depicting interactions between plants and pollinators across five entire flowering seasons of study among six plots in a subalpine meadow in the Colorado Rocky Mountains, USA. Interactions are organized in a nested organization such that interactions on the top-left corner represent the most generalized interactions in the network. Cells coloured in grey represent unrecorded interactions while those filled with heat ramp colours indicate the occurrence of interactions with higher values represented by “hotter” colours. These values indicate: A) number of years in which an interaction was recorded, B) average interaction phenophase (maximum date – minimum date in which an interaction was recorded) across five years of study depicted in weeks (7-day bins), and C) number of plots in which each interaction was recorded.

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**Figure 2.** Species-level relationships between generalization, measured as proximity to the core of the nested network, and (A, B) number of years in which species were recorded interacting, (C, D) phenophase lengths, and (E, F) number of plots in which species were recorded interacting. Plant phenophases are defined as the last (maximum) minus the first (minimum) day of the year in which each species was recorded interacting with pollinators, while pollinator phenophases are defined as the last minus the first day of the year in which each species was recorded interacting with flowers. Blue shaded areas display 95% CIs around means of model estimates.

## Supporting Information

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**Figure S1.** Morning temperatures (between 8:00 am and 12:00 pm), over the flowering season for 2015 – 2019. X-axis extends from the earliest date to the latest date in which interactions were recorded May 24 – September 30.

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**Figure S2.** Violin plots depicting abiotic variations among plots. A) Surface temperature measured every two meters across plots. B) Soil moisture measured every two meters across plots.

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**Figure S3.** Observed Spearman’s correlation coefficients (blue dots) for relationships between temporal (“Years”, “Days”) and spatial (“Plots”) persistence variables and the proximity to the core of the nested network. Observed Spearman’s correlation coefficients are compared to those from null models shown in gray. Clouds of rings represent 1000 randomizations, gray dots in the center of the clouds represent mean values while segments approximate 95% CIs ( $\text{mean} \pm 2 \times \text{SD}$ ).

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**Fig S4 .** Species-level relationships between generalization, measured as degree (number of links), and A, B: number of years in which species were recorded interacting, C, D: phenophase lengths, and E, F: number of plots in which species were recorded interacting. Plant phenophases are defined as the last (maximum) minus the first (minimum) day of the year in which each species was recorded interacting with pollinators, while pollinator phenophases are defined as the last minus the first day of the year in which each species was recorded interacting with flowers. Inter-annual persistence, longer phenophases, and higher plot occurrence were associated with a higher degree. For both plants and pollinators, species that had higher inter-annual persistence were had a higher degree (A, B; for plants:  $R^2 = 0.73$ ,  $P < 0.001$ , for pollinators  $R^2 = 0.61$ ,  $P < 0.001$ ). Both plant and pollinator species with longer phenophases had a higher degree (C, D;  $R^2 = 0.70$ ,  $P < 0.001$ , for pollinators  $R^2 = 0.56$ ,  $P < 0.001$ ). Both plant and pollinator species that were more widespread among plots were closer to the core of the nested network (E, F;  $R^2 = 0.60$ ,  $P < 0.001$ , for pollinators  $R^2 = 0.57$ ,  $P < 0.001$ ). Blue shaded areas display 95% CIs around means of model estimates.