

# Reports

*Ecology*, 102(6), 2021, e03359  
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## Plant–pollinator interactions between generalists persist over time and space

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*Citation:* Resasco, J., N. P. Chacoff, and D. P. Vázquez. 2021. Plant–pollinator interactions between generalists persist over time and space. *Ecology* 102(6):e03359. 10.1002/ecy.3359

**Abstract.** Generalist species are the linchpins of networks, as they are important for maintaining network structure and function. Previous studies have shown that interactions between generalists tend to occur consistently across years and sites. However, the link between temporal and spatial interaction persistence across scales remains unclear. To address this gap, we collected data on plant–pollinator interactions throughout the flowering period for 5 yr across six plots in a subalpine meadow in the Rocky Mountains. We found that interactions between generalists tended to persist more in time and space such that interactions near the network core were more frequently recorded across years, within seasons, and among plots. We posit that species' tolerance of environmental variation across time and space plays a key role in generalization by regulating spatiotemporal overlap with interaction partners. Our results imply a role of spatiotemporal environmental variation in organizing species interactions, marrying niche concepts that emphasize species environmental constraints and their community role.

**Key words:** ecological network; mutualistic network; nestedness; niche; phenology; pollination; specialization; stability.

### INTRODUCTION

Species interaction networks may be regarded as blueprints of the architecture of biodiversity, depicting complex webs of interactions among species (Bascompte and Jordano 2007). These networks are typically represented and analyzed 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 and Olesen 2016, CaraDonna et al. 2021).

In recent years, there has been increased interest in the temporal and spatial aspects of species interaction networks (Alarcon et al. 2008, Bascompte and Jordano 2014, Trøjelsgaard and Olesen 2016, Schwarz et al. 2020, CaraDonna et al. 2021). A pattern emerging

from such studies is that most interactions are highly inconsistent; few interactions persist (have extended durations of observation) over time and space (Dupont et al. 2009, Aizen et al. 2012, Carstensen et al. 2014, Chacoff et al. 2018). 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 6 yr. 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 qualitative 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. 2020).

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

Manuscript received 21 December 2020; revised 14 March 2021; accepted 22 March 2021. Corresponding Editor: Nicholas J. Gotelli.

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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.

With the goal of understanding attributes of interactions associated with their persistence across time and space, we recorded pollinator visits to flowers throughout the flowering season for five years across six plots in a subalpine meadow in the Colorado Rocky Mountains. 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 between generalists at the network core. Such relationships would allow linking previously observed persistence patterns of plant–pollinator interactions in either time or space and suggest that species tolerance to environmental conditions may influence interaction persistence by constraining temporal and spatial overlap with partner species.

#### 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 2,900 m of elevation 22 km west of Boulder, Colorado, 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. We sampled on average  $6.95 \pm 1.17$  (mean  $\pm$  SD) days apart.

On each sampling date, we sampled plant–pollinator interactions in six 20–30  $\times$  2 m plots (five 30  $\times$  2 m and one 20  $\times$  2 m) by observing flowers (plant-centered sampling). Plots were at a similar elevation, 2,962–2,978 m. Sampling was conducted in fair weather during mornings between 08:00 and 12:00, a time range when pollinator activity is high and before the onset of thunderstorms that often occur at midday during the summer in the Rocky Mountains. We sampled plant–pollinator interactions within each plot (in random order) by doing 15-minute 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 *Acknowledgments*) 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 (Gotelli and Colwell 2011, Chacoff et al. 2012).

We recorded temporal and spatial variation in abiotic conditions. Temperature is fundamental in constraining pollinator foraging (Corbet et al. 1993, Willmer and 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 (08:00–12:00) during which sampling was conducted from a weather station located ~1 km away at a similar elevation, 3,020 m (SNOTEL Site Niwot, 663). Plot locations varied in the shade they received from nearby trees, which affects temperature and snowmelt. Soil moisture affects plant growth and reproduction (Fay et al. 2000). To quantify aspects of spatial variation in abiotic conditions among plots we measured ground temperature and soil moisture every 2 m along sampling plots on one occasion at 07:55–08:38 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.

We compiled all the observations from the study into a species  $\times$  species plant–pollinator interaction matrix, sorting rows and columns to maximize binary nestedness. This sorting organizes plant species (top-to-bottom in rows) and pollinator species (left-to-right in columns) from most to least generalist according to their degree (number of partner species) such that generalist species are packed into the top left corner of the matrix. Nestedness is a commonly observed pattern in mutualistic networks in which specialists interact with species that form perfect subsets of the species with which generalists interact (Bascompte and Jordano 2007). Using this matrix organization, we created three matrices with cell values representing each variable of temporal or spatial persistence: the number of years, the span of days (phenophase, the maximum date minus the minimum date in which an interaction was recorded), and the number of plots in which interactions were recorded. 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 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 1,000 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 second-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 (phenophase), and inter-plot occurrence. Species inter-annual and inter-plot occurrences were defined as the number of years and plots, respectively, in which a given species was recorded interacting. Species phenophases were defined as the maximum date minus the minimum date in which species were recorded interacting. 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 assess the relationship between 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 yr 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, five Rosaceae, 3 Fabaceae, 3 Orobanchaceae, 2 Ranunculaceae, and 1 each of Apiaceae, Boraginaceae, Campanulaceae, Crassulaceae, Gentianaceae, Geraniaceae, Hydrophyllaceae, Melanthiaceae, Onagraceae, Primulaceae, and Rubiaceae. Removal of flower visitor groups not commonly regarded to be pollinators (Hymenoptera, 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 (Appendix S1: Fig. S1), and spatially among plots, as did soil moisture (Appendix S1: 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,  $P \ll 0.001$ ; Fig. 1A), intra-annual persistence (Spearman's rank correlation coefficient = 0.22,  $P \ll 0.001$ ; Fig. 1B), and inter-plot persistence (Spearman's rank correlation coefficient = 0.35,  $P \ll 0.001$ ; Fig. 1C). Observed Spearman's rank correlation coefficients for all three persistence variables were higher than those expected under null models (Appendix S1: 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,  $P \ll 0.001$ ) and be more widespread among plots (Spearman's rank correlation coefficient: 0.73,  $P \ll 0.001$ ). Interactions with longer phenophases tended to be more widespread among plots (Spearman's rank correlation coefficient: 0.78,  $P \ll 0.001$ ).

At the species level, inter-annual persistence, longer phenophases, and higher plot occurrence were associated with generalization (Fig. 2, Appendix S1: S4). For both plants and pollinators, species that had higher inter-annual persistence were closer to the core of the nested network (Fig. 2A and B; for plants  $R^2 = 0.73$ ,  $P \ll 0.001$ ; for pollinators  $R^2 = 0.61$ ,  $P \ll 0.001$ ). Both plant and pollinator species with longer phenophases were closer to the core of the nested network (Fig. 2C and D; for plants  $R^2 = 0.72$ ,  $P \ll 0.001$ ; for pollinators  $R^2 = 0.70$ ,  $P \ll 0.001$ ). Both plant and pollinator species that were more widespread among plots were closer to the core of the nested network (Fig. 2E and F; for plants  $R^2 = 0.58$ ,  $P \ll 0.001$ ; for pollinators  $R^2 = 0.57$ ,  $P \ll 0.001$ ). Using degree (number of links), as a proxy for generalization showed similar patterns as species proximity to the network core (Appendix S1: Fig. S4). Finally, phenophase length for plants and pollinators was associated with broader ranges of temperatures in the mornings of sampling days (for plants Pearson's  $r = 0.67$ ; for pollinators Pearson's  $r = 0.81$ ).

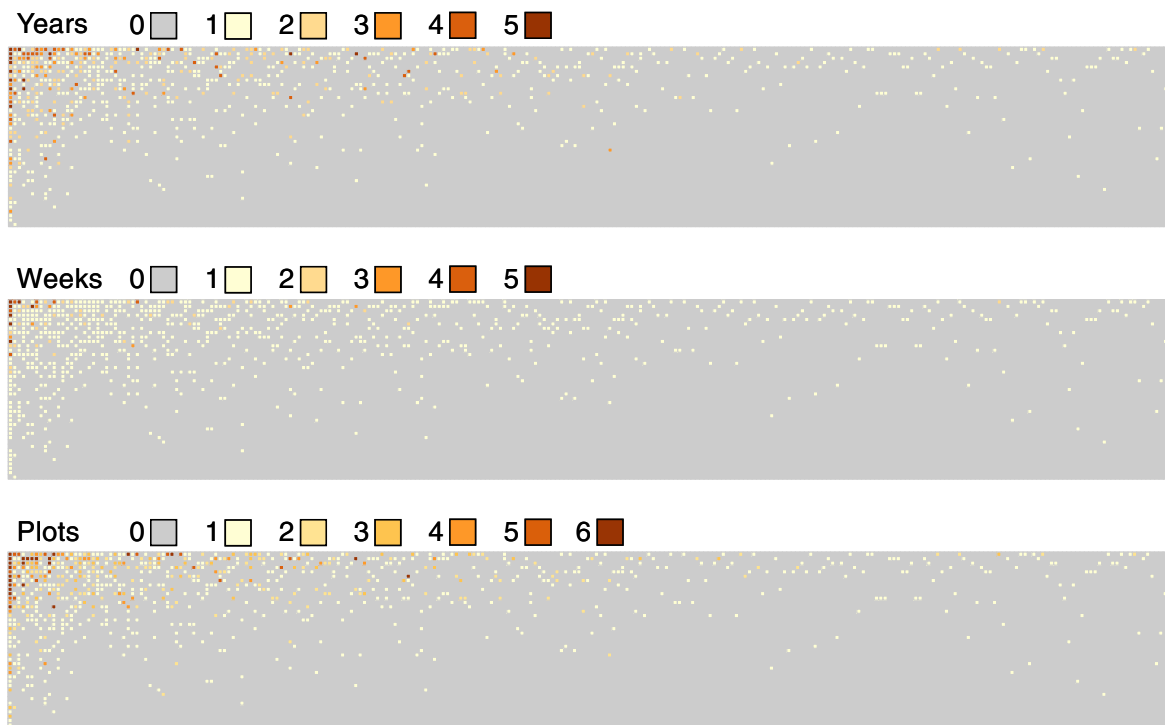


FIG. 1. Matrices depicting interactions between plants (rows) and pollinators (columns) across five entire flowering seasons of study among six plots in a subalpine meadow in the Colorado Rocky Mountains, USA. Interactions are organized in a nested organization such that interactions on the top left corner represent the most generalized interactions in the network. Cells colored in gray represent unrecorded interactions while those filled with heat ramp colors indicate the occurrence of interactions with higher values represented by “hotter” colors. These values indicate number of years in which an interaction was recorded (top), average interaction phenophase (maximum date minus minimum date in which an interaction was recorded) across 5 yr of study depicted in weeks (7-d bins; center), and number of plots in which each interaction was recorded (bottom).

## 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 time and space is associated with interaction generalization through the increased spatiotemporal overlap of interacting partners.

Our study conceptually and empirically associates 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 time or space (e.g., Aizen et al. 2012, Chacoff et al. 2018). Our study relates 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 and 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 and 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

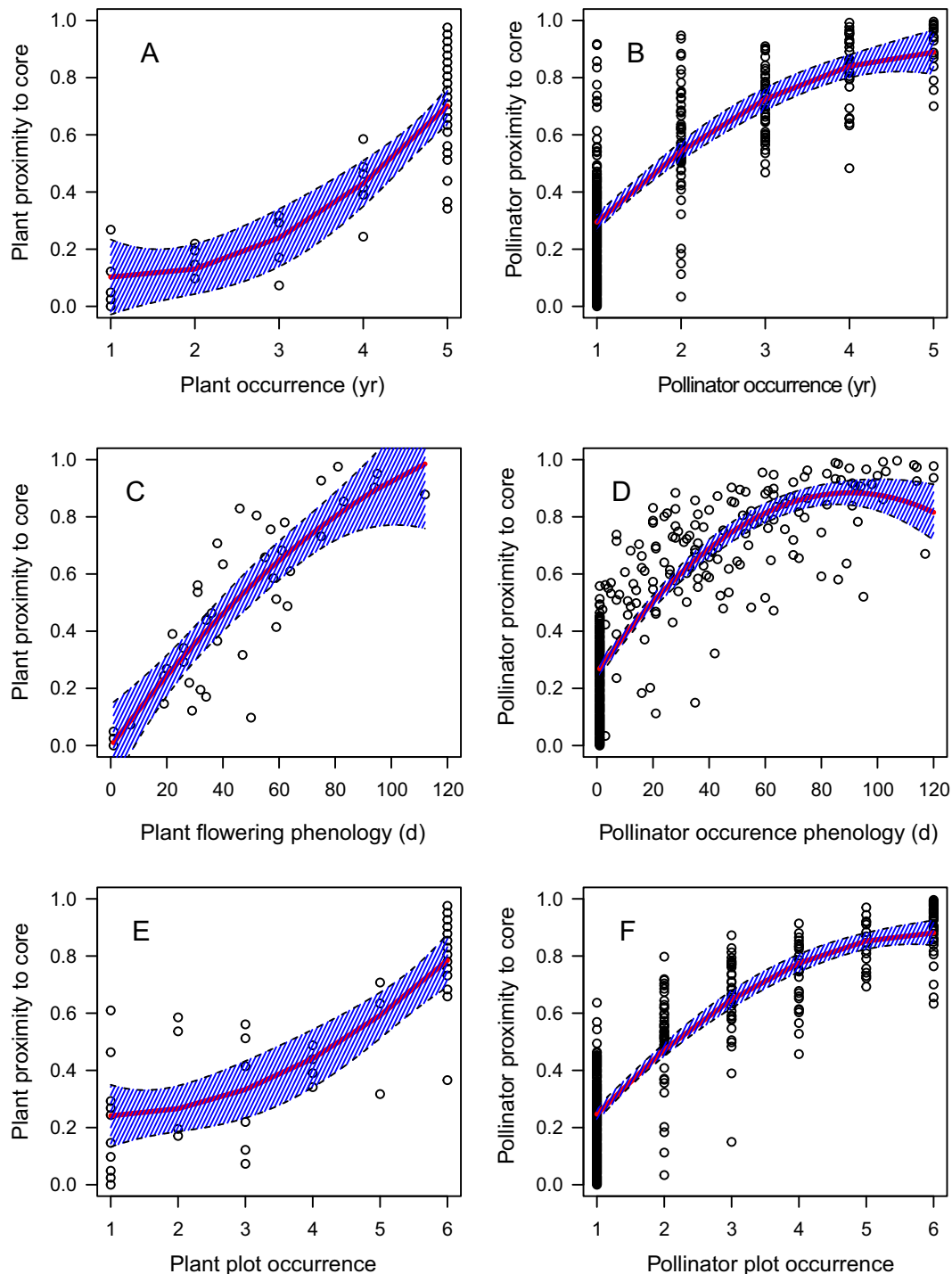


FIG. 2. Species-level relationships between generalization, measured as proximity to the core of the nested network, and (A, B) number of years in which species were recorded interacting, (C, D) phenophase lengths, and (E, F) number of plots in which species were recorded interacting. Plant phenophases 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.



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. 2021).

Despite these promising results, much work remains to be done toward a better understanding of patterns and mechanisms of persistence of core interactions in networks. Other studies have found that, while the structure of plant–pollinator networks is relatively invariant, the composition of core species is highly dynamic (Alarcon et al. 2008, Miele et al. 2020), yet a small subset of species may consistently belong to the network core (Miele et al. 2020). It would be interesting to test the generality of our results for other types of interactions and in other environmental contexts to contrast with the setting of our study, a temperate sub-alpine ecosystem along a steep environmental gradient with punctuated seasonality. 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 temporally and spatially explicit interaction data. 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 and Stouffer 2009). Despite their pivotal roles, common and generalist species are often 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 (Memmott et al. 2004). Therefore, conservation priorities should not overlook the pivotal roles that generalists play in supporting biodiversity across time and space.

#### ACKNOWLEDGMENTS

We thank Bill Bowman, Kris Hess, and César Nufio for facilitating research at the University of Colorado's Mountain Research Station. For help with species identifications of insects, we thank Virginia Scott, Boris Kondratieff, Adrian

Carper, Andy Hicks, Jade Savage, Joel Gardner, and Tim Szewczyk. We thank students who helped with data collection in the field, especially Tyrah Delger, Hector Castillo-Rosado, Samantha Skerlec, Emily Joy, and Claire Stufflebeam. During this study, Julian Resasco was supported by an NSF Postdoctoral Research Fellowship in Biology (award 1309192) and Chancellor's Postdoctoral Fellowship from the University of Colorado.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.3359/supinfo>

## OPEN RESEARCH

Data (Resasco, et al. 2021) are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.rfj6q579h>