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LETTER

# Interaction rewiring and the rapid turnover of plant–pollinator networks

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**Abstract**

Whether species interactions are static or change over time has wide-reaching ecological and evolutionary consequences. However, species interaction networks are typically constructed from temporally aggregated interaction data, thereby implicitly assuming that interactions are fixed. This approach has advanced our understanding of communities, but it obscures the timescale at which interactions form (or dissolve) and the drivers and consequences of such dynamics. We address this knowledge gap by quantifying the within-season turnover of plant–pollinator interactions from weekly censuses across 3 years in a subalpine ecosystem. Week-to-week turnover of interactions (1) was high, (2) followed a consistent seasonal progression in all years of study and (3) was dominated by interaction rewiring (the reassembly of interactions among species). Simulation models revealed that species' phenologies and relative abundances constrained both total interaction turnover and rewiring. Our findings reveal the diversity of species interactions that may be missed when the temporal dynamics of networks are ignored.

**Keywords**

Adaptive foraging, beta-diversity, community composition, food webs, interaction turnover, mutualism, networks, null models, optimal foraging theory, phenology.

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## INTRODUCTION

Interspecific interactions link species within communities and ultimately generate community structure: which species co-occur, their relative abundances, and their phenotypes (e.g. Elton 1927; Hutchinson 1959). A fundamental challenge of community ecology has been to understand the consequences of interactions for the generation and maintenance of biodiversity, and for the functioning of communities and ecosystems in space and time (Paine 1966; Odum 1969; Thompson 2005; Bascompte *et al*. 2006; Thébault & Fontaine 2010).

Despite a clear appreciation of the temporally-dynamic nature of populations and communities (e.g. Cowles 1899; Clements 1936; Chesson & Huntly 1989), interaction networks are typically treated as temporally static entities (Poisot *et al*. 2015). Whereas this static view has profoundly advanced our understanding of communities and their function, it has also overlooked the scale at which interactions form and the ecological and evolutionary consequences of their dynamic nature. Although empirical examples are scarce, there is compelling evidence that interactions vary within a year or season (Winemiller 1990; Medan *et al*. 2006; Olesen *et al*. 2008; Carnicer *et al*. 2009), among years (Alarcón *et al*. 2008; Petanidou *et al*. 2008; MacLeod *et al*. 2016), and over longer time spans such as decades or centuries (Burkle *et al*. 2013; Yeakel *et al*. 2014). Nevertheless, beyond simply documenting that temporal variation exists, we have a poor understanding of the extent to which interactions are dynamic over the short term, and of the consistency and causes of any such dynamic patterns. In light of this mismatch between biology and methodology, several authors have stressed the need to fill this critical knowledge gap (Bascompte & Stouffer 2009; Burkle & Alarcón 2011; Bascompte & Jordano 2014; McMeans *et al*. 2015; Poisot *et al*. 2015).

A promising approach to address species interactions at the appropriate scale is to more precisely quantify temporal interaction turnover (i.e. interaction β-diversity: changes in the composition of interactions; Poisot *et al*. 2012). Interaction turnover consists of two additive components (Fig. 1). The first component is *species turnover*: interactions in a community are lost or gained as individuals of a species become active or inactive, through time. The second component is *interaction rewiring*: interactions are reassembled over time because of changes in who is interacting with whom among the same pool of co-occurring species. Currently we lack a basic understanding of the temporal scale of interaction turnover and have virtually no knowledge of the relative importance of rewiring vs. species turnover (Burkle *et al*. 2015;

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**Figure 1** Conceptual diagram illustrating the two components of interaction turnover ($\beta_{int}$). The first is species turnover: interactions are lost or gained because of the loss or gain of species ($\beta_{st}$). The second is interaction rewiring: interactions are reassembled because of changes in who is interacting with whom; that is the same species interact in different combinations across time ($\beta_{rw}$). Both components of interaction turnover can simultaneously occur from one transition to the next, but are shown separately for clarity.

Poisot *et al*. 2015). Furthermore, although previous studies show that phenology, abundance and morphology of species can contribute to structural patterns of static networks, (e.g. Petchey *et al*. 2008; Vázquez *et al*. 2009a), we do not know how these ecological factors may constrain patterns of interaction once temporal dynamics of networks are more fully characterised. Quantifying how and why interaction networks change over time has important implications for our understanding of the assembly and disassembly of ecological networks and their resilience to anthropogenic pressures.

In this study, we quantify the within-season temporal turnover of plant–pollinator interaction networks within a subalpine ecosystem. Using weekly censuses of plant–pollinator interactions over 3 years, collectively representing 41 weekly networks and nearly 30 000 individual interactions, we ask: (1) What are the relative contributions of species turnover and rewiring for the temporal turnover of interactions? (2) What is the magnitude of interaction turnover and its two components from week to week within a season? and (3) Are patterns of interaction turnover and its components consistent among years? We then employ probability-based simulation models to ask: (4) Are within-season interaction turnover and rewiring constrained by phenology, morphology, species relative abundances or combinations of these ecological factors? Our approach reveals that much of the basic ecology of species interactions is overlooked when networks are temporally aggregated and interactions among species are assumed to be static. These findings help to fill in a key gap in our understanding of the assembly and disassembly of species interaction networks, with implications for all types of ecological networks.

## METHODS

### Study system

We worked at The Rocky Mountain Biological Laboratory (RMBL) in Gothic, CO, USA (38°57.5′ N, 106°59.3′ W, 2900 m a.s.l.). RMBL is surrounded by a mosaic of wet and dry meadows and aspen and conifer forest. The area is snow-covered for much of the year, with a short summer growing season of 3–5 months (CaraDonna *et al*. 2014). The plant and pollinator communities of the subalpine in this area are relatively generalised (e.g. Burkle and Irwin 2009; Table S3), and those we studied consist almost exclusively of native taxa (except the plant *Taraxacum officinale*). The honey bee (*Apis mellifera*), a non-native generalist, does not occur in the area.

### Plant–pollinator observations

We observed plant–pollinator interactions at weekly intervals across the flowering season for 11 weeks in 2013, 15 weeks in 2014 and 16 weeks in 2015. Snowfall in the second week of the 2015 season prevented sampling during that period. All observations took place in two adjacent dry meadows that cover *c*. 2800 and 3015 $m^2$, respectively, and are separated by *c*. 100 m of forest. Observations began about 1 week after snowmelt each year (Table S1), coinciding with the first emergence of flowers and pollinators. Within each week, we conducted 32 15-min observation periods for a total of 8 h per week. Each complete weekly interaction census (i.e. all 32 observation periods) took place over 2–3 consecutive days and was separated from the start of the next weekly census by 3–5 days. We randomly selected one of four quadrants within each meadow during each 15-min observation period, we then sampled the remaining quadrants in random order, and then repeated this in the other meadow; we alternated the starting meadow on successive days. During each 15-min observation period, we walked around the focal quadrant and recorded all observed plant–pollinator interactions. We defined an interaction as taking place when a floral visitor of any species unambiguously contacted the reproductive structures of flowers; we refer to floral visitors as pollinators while recognising that their quality as mutualists may vary widely. To prevent observer bias, observations in each season were made by the same two researchers (PJC and JLC in 2013, PJC and RMB in 2014 and 2015). All observations took place between 0900 and 1700 h during weather conditions favourable for pollinator activity (ambient temperature > 8°C, not snowing or raining). We constructed a single plant–pollinator interaction matrix from each complete set of 32 weekly observation periods.

All flowering plants were identified to species, and all pollinators were identified to species or to the finest taxonomic level possible (Table S3). A total of 85% of pollinators (63 out of 74) were identified to species; of the 11 remaining pollinators, six were identified to genus, and five were identified to family (all of the latter were Diptera). During field

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observations, pollinators were identified to either species or morphospecies on the wing. A reference specimen was collected for each morphospecies and later identified using the RMBL Entomology Reference Collection. Otherwise, pollinators were not collected during observations to avoid artefacts of destructive sampling.

#### Plant and pollinator abundance

Within each meadow quadrant we established a permanent 25 × 1 m transect to monitor floral abundance and flowering phenology. Once per week, all open flowers or flowering heads (for species with small clustered flowers, such as Asteraceae) were counted for all species present within each transect (*following* CaraDonna *et al*. 2014). The number of observation periods during which a given pollinator species was observed was used as an estimate of its relative abundance. For example if a given species was observed in 10 of 32 observation periods in a given week – regardless of the number of visits made by this species during this week – its abundance value was 10. We used this estimation method instead of interaction frequency (number of visits) because it is influenced less strongly by floral abundance.

#### Plant and pollinator morphology

We measured plant and pollinator morphology for all species present during the 3-year study (Table S3). For plants, we measured the functional depth at which nectar could be reached on 10–20 individual flowers for each species (*following* Stang *et al*. 2009; *details in* Table S3). Because pollen was presented at or near the opening of all the flowers in our meadows we assumed it was accessible to all pollinators. Proboscis length was measured on 2–15 individuals of each insect pollinator species using the RMBL Entomology Reference Collection. For the one observed hummingbird pollinator, the Broad-tailed Hummingbird (*Selasphorus platycercus*), bill length was measured by one of us (NMW) on live birds captured at the RMBL and on specimens in the University of Arizona, University of Utah, and RMBL vertebrate collections.

#### Components of interaction turnover

Following Poisot *et al*. (2012), we quantified the absolute turnover of plant–pollinator interactions across each growing season using Whittaker's (1960) dissimilarity index:

$$\beta_{int} = \frac{a + b + c}{(2a + b + c)/2} - 1$$

where $\beta_{int}$ is interaction turnover (i.e. interaction β-diversity or interaction dissimilarity) between two successive weekly networks, $a$ is the number of pairwise interactions shared between the networks, and $b$ and $c$ are the number of pairwise interactions unique to each of the networks respectively. Values for this index range from 0 to 1; higher values indicate higher turnover, or greater change between weeks in who is interacting with whom. This index treats interactions as present or absent, directly addressing our goal of exploring the absolute gain or loss of interactions through time. The overall patterns of $\beta_{int}$ were qualitatively similar when we used a frequency-based metric of interaction dissimilarity (Bray–Curtis dissimilarity; Table S4). Because we were interested in the processes that govern the formation of interactions, we do not address frequency-based β-diversity metrics further.

An appealing property of presence-based interaction turnover metrics is that they can be partitioned as $\beta_{int} = \beta_{st} + \beta_{rw}$, where the two additive components are the contribution of species turnover ($\beta_{st}$) and interaction rewiring ($\beta_{rw}$) (Poisot *et al*. 2012; Fig. 1). (Our notation for rewiring, $\beta_{rw}$, is equivalent to $\beta_{os}$ in Poisot *et al*. [2012].) This partitioning of interaction turnover reveals whether the dynamics of interaction networks arise (1) because of changes in species composition ($\beta_{st}$), (2) because of the reassembly of interactions among species ($\beta_{rw}$) or (3) by some combination of both (Fig. 1). While this approach (including our definition of rewiring) identifies how and why interaction networks are changing, it does not provide any information on whether those changes arise because of deterministic (niche-based) or stochastic (neutral) processes (or both; *sensu* MacLeod *et al*. 2016).

Notice that the contribution of species turnover to interaction turnover, $\beta_{st}$, is constrained by, but not synonymous with, the turnover of the species themselves, $\beta_s$, (see Poisot *et al*. 2012). For example high species turnover necessitates a relatively higher contribution of species turnover to interaction turnover; however, the loss of a single species can bring about either the loss of a single interaction or the loss of many interactions. For brevity, we do not discuss $\beta_s$ further, although we report all species turnover values in Figure S2 and Tables S6–S8.

This interaction turnover partitioning approach is highly robust to sampling effects (Poisot *et al*. 2012); nevertheless, we conducted several additional analyses to ensure that our results do not stem from sampling artefacts. First, interaction rarefaction curves and abundance-based richness estimators indicated that our sampling effort sufficed to detect most (on average 85–93%) of the pairwise interactions that occurred in each week (Fig. S1; Table S2). Second, two different sensitivity analyses showed that observed patterns of interaction turnover were qualitatively the same when we (1) removed singletons (rare or ephemeral interactions occurring only once within a week) and when we (2) aggregated sampling periods over a broader, 2-week sampling window (Tables S6–S7). These analyses provide strong and consistent evidence that sampling effects were unlikely to bias our results.

#### Simulation models

We constructed four probability-based simulation models to explore ecological factors that may constrain within-season interaction turnover (Box 1). Each model expresses a set of constraints that adjusts the likelihood that a given plant–pollinator interaction will occur at a given time point. By including these alternate sets of constraints in the simulations, we can determine the patterns of interaction turnover that result from each scenario and reject the scenarios whose patterns deviate from our observations.

(1) *Phenology* – Plants must bloom and pollinators must forage at the same time for them to interact. In each run of the

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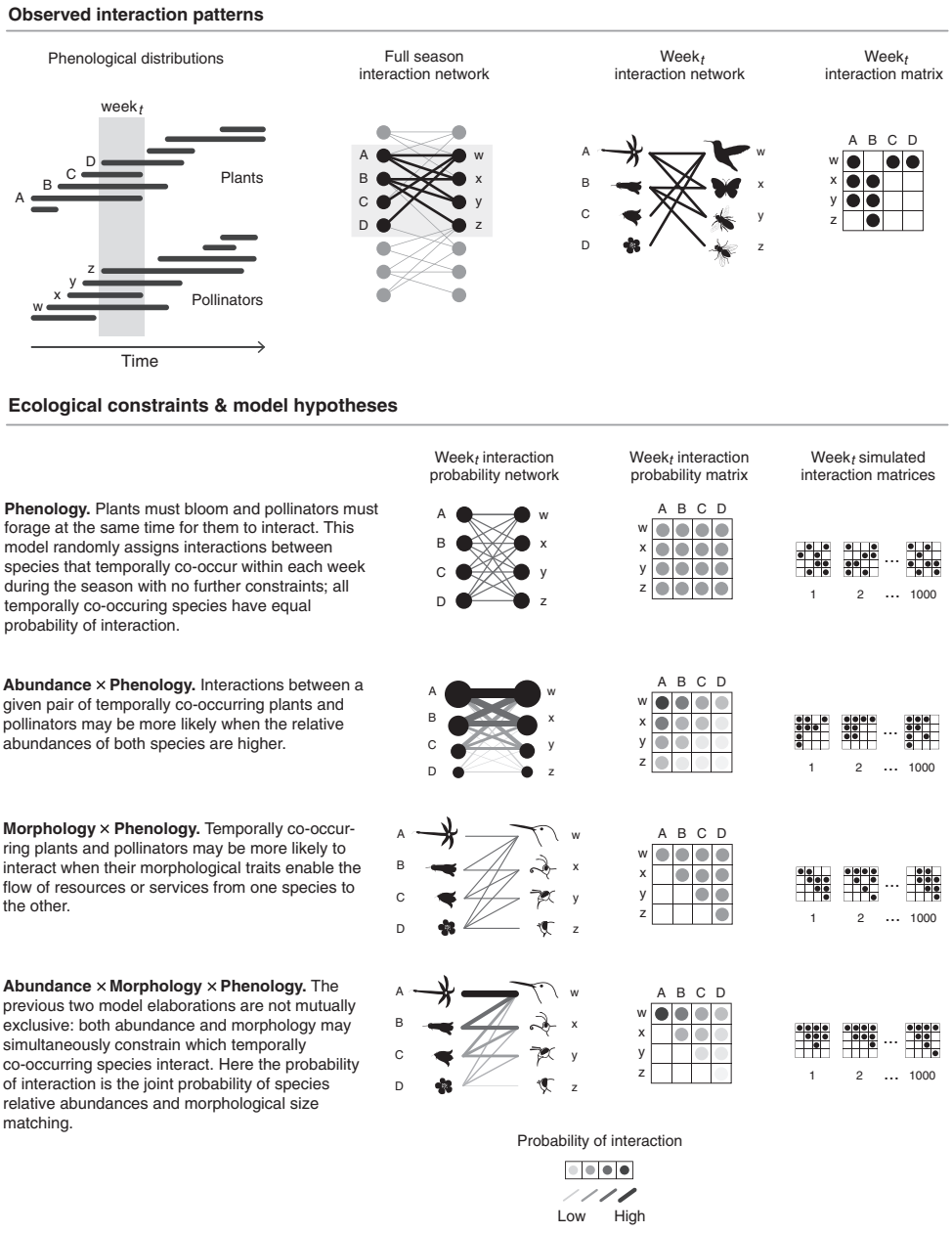
**Box 1 Hypothesised ecological constraints to explain the temporal turnover of who interacts with whom in species interaction networks**

Several basic hypotheses have been proposed to explain how and why species interactions form within ecological networks (Váquez *et al*. 2009a,b; Poisot *et al*. 2015). Here we extend these hypotheses to explore the potential constraints on the within-season temporal dynamics of plant–pollinator interactions. First, we provide a hypothetical diagram of an observed plant–pollinator community, illustrating that the interactions that occur at one specific time point (e.g. within a week) are a subset of all the interactions that have occurred during the entire season, and that local temporal co-occurrence (phenological overlap) is necessary for interactions to occur. Second, we provide a description of each hypothesised ecological constraint and associated model. We illustrate how the model assumes the interaction network is constrained and how we translate this information into an interaction probability matrix. These probability matrices are used to simulate interactions within each week (holding the number of links within each week equal to the number actually observed). These simulated interactions are then used to explore evidence for different ecological constraints that may give rise to the observed patterns of interaction turnover. Further information regarding our measurements of plant and pollinator phenology, morphology and abundance, as well as additional model details, are included in the main text.

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simulation and for each week of the season, this model randomly assigns interactions to pairs of plants and pollinators that were active during that week. Therefore, all active species pairs were equally likely to be assigned an interaction (i.e. interaction formation in each instantiation was purely stochastic). This is a null model in the sense that it provides a baseline expectation of interaction turnover and rewiring based only on the most fundamental constraint, phenological overlap. (Spatial co-occurrence is also a fundamental constraint, but it is implicit here because all our networks involve species that share the same adjacent small meadows.)

(2) *Abundance* × *phenology* – Interactions between a given pair of temporally co-occurring plants and pollinators may be more likely when the local relative abundances of species are greater. This model builds on the phenology null model described above by weighting the probability that a given pair of plants and pollinators will interact by their abundances during that week.

(3) *Morphology* × *phenology* – Temporally co-occurring plants and pollinators may be more likely to interact when their morphological traits enable the flow of resources or services from one species to the other. This model builds on the phenology null model by accounting for the length of pollinator feeding apparatus and the functional nectar depth of flowers. A morphological match was assumed to occur whenever the feeding apparatus of a pollinator was at least as long as the functional nectar depth of the flower. In other words, flowers with greater nectar depths are more restrictive, whereas pollinators with longer tongues are relatively unconstrained. Nectar depth and tongue length are only one set of many potential phenotypic constraints (e.g. colour, scent), but it remains unclear how to incorporate such complex traits into models of interaction (Vázquez *et al*. 2009a).

(4) *Abundance* × *morphology* × *phenology* – The previous two models are not mutually exclusive: both species relative abundances and morphology may simultaneously constrain which temporally co-occurring species interact (Box 1). Here, the probability of interaction is the joint probability of relative abundances and morphological size matching for temporally co-occurring plants and pollinators.

For each of the four classes of models we constructed a matrix describing the probability of interaction between plants and pollinators observed in each week of each year (*following* Vázquez *et al*. 2009b). We then used a Monte Carlo process to generate 1000 predicted interaction matrices based on the underlying probability matrix for each set of ecological constraints for each week (Box 1). For example if the probability of interaction between plant *i* and pollinator *j* is 0.1 in a given week under a model, then these two species will interact in *c*. 100 of the 1000 simulated matrices for that week. For each weekly simulation, we held the number of links between species equal to the number of links actually observed (i.e. network connectance in the simulated interaction matrices always equalled that of the observed interaction matrix; Box 1). Our simulations do not deviate from the observed species composition within each week, but allowed for changes in the occurrence of interactions among temporally co-occurring species. We then calculated expected interaction turnover using these simulated matrices and compared the values expected under each model to the values actually observed. The greatest amount of information comes from comparing $\beta_{int}$ and $\beta_{rw}$ between models and observed data; because we fixed simulated species compositions to observed values we expect simulated and observed values of $\beta_{st}$ to be similar across all candidate models.

### Data analysis and model comparisons

Each of the 3 years of study yielded multiple values for the contribution of interaction rewiring ($\beta_{rw}$) and species turnover ($\beta_{st}$) to interaction turnover (one value for each week-to-week transition in each year). We compared the means of each of the two components in each year using a two-tailed t-test. The values of interaction turnover and its components ($\beta_{int}$, $\beta_{rw}$, $\beta_{st}$) were fit as a function of time across the season using linear or second-order polynomial regression, with Akaike information criterion (AIC) to determine best-fit models. We tested for temporal autocorrelation among the residuals of all turnover variables within each season to ensure these time-series data met the assumption of independence; temporal autocorrelation was never detected (Ljung-Box Test, $P > 0.05$). All data met the assumptions of each statistical test.

We compared simulated interaction turnover patterns from each model to the observed patterns using a standardised effect size (SES) approach:

$$\mathrm{SES} = \frac{\beta_{obs} - \mu(\beta_{sim})}{\sigma(\beta_{sim})}$$

SES indicates the number of standard deviations an observed value of interaction turnover or one of its components ($\beta_{obs}$) deviates from the mean of the simulated model [$\mu(\beta_{sim})$], given the standard deviation [$\sigma(\beta_{sim})$] of the model output across 1000 iterations. Assuming a normal distribution of deviations, *c*. 95% of SES values should fall between −1.96 and +1.96. Therefore, for each week-to-week transition, observed values that fall within this range are consistent with the prediction under the model, whereas points that fall outside suggest that the ecological constraint(s) included in the model do not contribute to the observation.

## RESULTS

Over the 3 years of study we observed 566 unique pairwise interactions between 45 flowering plants and 74 pollinators, representing 28 959 individual pollinator visits to flowers (Table S6). In total, we sampled 41 weekly plant–pollinator interaction networks. Compared to other full growing-season surveys of subalpine plant–pollinator interactions (e.g. Olito & Fox 2014; Simanonok & Burkle 2014) our sampling yielded on average *ca*. 10-fold more visitation events per year; at the same time the topological properties of our weekly networks when they are aggregated across entire growing seasons lie well within the range typically observed in other mutualistic networks (e.g. Jordano 1987; Olesen & Jordano 2002; Table S5). Overall, this plant–pollinator community is relatively generalised (Tables S3 and S4). Among all possible plant–pollinator pairs 83% meet the criterion of a

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morphological size match based on functional nectar depth and pollinator tongue length.

*Within-season turnover*

Within-season interaction turnover was consistently high and primarily driven by rewiring (Fig. 2; Table S4). The contribution of rewiring to total interaction turnover exceeded the contribution of species turnover in all three seasons (2013: $t_{18} = 2.77$, $P = 0.012$; 2014: $t_{26} = 3.91$, $P < 0.001$; 2015: $t_{26} = 5.65$, $P < 0.001$). On average, rewiring accounted for almost two-thirds of interaction turnover (mean = 64%; 2013 = 60%; 2014 = 64%; 2015 = 67%) (Table S4).

The magnitude of week-to-week interaction turnover and its two components varied predictably within each growing season, and these patterns were largely consistent across all 3 years of study (Fig. 3). Total interaction turnover ($\beta_{int}$) declined across each season; in 2013 this pattern was weak and non-significant, probably because observations ended earlier in the season (2013: $R^2 = 0.10$, $P = 0.376$; 2014: $R^2 = 0.65$, $P < 0.001$; 2015: $R^2 = 0.77$, $P < 0.001$; Fig. 3). The magnitude of the contribution of rewiring ($\beta_{rw}$) to interaction turnover exhibited a consistent, humped pattern with a peak during mid-season in all 3 years (2013: $R^2 = 0.52$, $P = 0.07$; 2014: $R^2 = 0.50$, $P = 0.02$; 2015: $R^2 = 0.62$, $P = 0.005$; Fig. 3). The magnitude of the contribution of species turnover ($\beta_{st}$) to interaction turnover declined across the season (2013: $R^2 = 0.62$, $P = 0.006$; 2014: $R^2 = 0.31$, $P = 0.039$; 2015: $R^2 = 0.89$, $P < 0.001$); in 2015 there was a slight increase at the end of the season (Fig. 3). Table S8 lists all regression model coefficients.

Our simulation models suggest that phenologies and relative abundances of species were important ecological constraints underlying patterns of interaction turnover and rewiring (Fig. 4, Fig. S3). The phenology null model alone produced values that were a poor match to the observed values, generally overestimating interaction turnover and rewiring in each year; this indicates that the observed patterns of interaction formation from week to week across each season were non-random. The morphology × phenology model was also a poor predictor of observed patterns. In contrast, the abundance × phenology model yielded interaction turnover and rewiring values that matched observed patterns well in all 3 years. The abundance × morphology × phenology model also matched observed patterns; however, this model provided only a modest improvement over the more parsimonious abundance × phenology models alone, and only in some years.

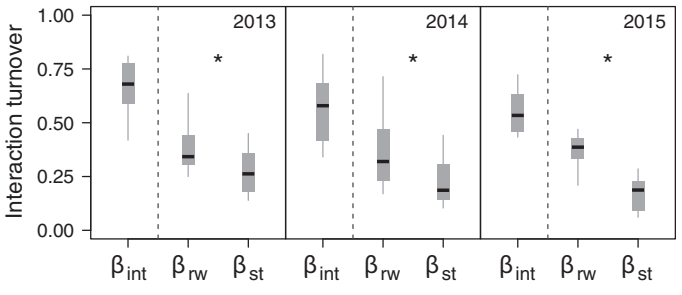


**Figure 2** Comparison of the two components of plant–pollinator interaction turnover ($\beta_{int}$)–species turnover ($\beta_{st}$) and rewiring ($\beta_{rw}$)–across all 3 years of the study. Values represent the raw magnitude of interaction turnover and its partitioned values. Asterisks indicate statistical significance ($P < 0.05$) between $\beta_{st}$ and $\beta_{rw}$ via a two-tailed t-test.

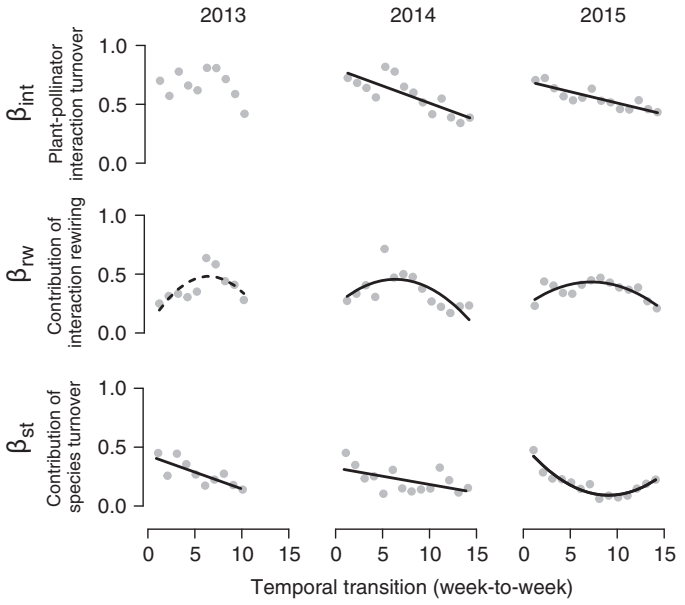


**Figure 3** Within-season temporal dynamics of plant–pollinator interaction turnover ($\beta_{int}$), the contribution of species turnover to interaction turnover ($\beta_{st}$), and the contribution of rewiring to interaction turnover ($\beta_{rw}$) across all 3 years of the study. Values represent the raw magnitude of interaction turnover and its partitioned values. Each panel illustrates the relationship between each successive week-to-week temporal transition. Grey points indicate a single week-to-week turnover value. Solid black lines indicate significant relationships ($P < 0.05$), and dashed black lines indicate marginally significant relationships ($P < 0.10$), using linear or non-linear regression.

As expected, all models provided a reasonable fit to observed patterns of the contribution of species turnover ($\beta_{st}$) to interaction turnover (Fig. 4, Fig. S3). This result is inherent in the way we specified the simulations, because species composition in all models was set to match observed species composition.

*Year-to-year turnover*

Species composition of the meadow flora and pollinator fauna was similar across years. On average, 76% of all plant and pollinator species were present in all 3 years (Table S9). The composition of interactions varied more strongly: on average only about 42% of interactions were observed in all years. As a result, only about 20% of interaction turnover from year-to-year was due to differences in species composition ($\beta_{st}$), whereas, the remaining 80% reflected year-to-year rewiring of interactions ($\beta_{rw}$).

## DISCUSSION

Ecological networks are largely characterised as temporally static entities, and therefore interactions among species are generally assumed to be invariant (Poisot *et al.* 2015). In

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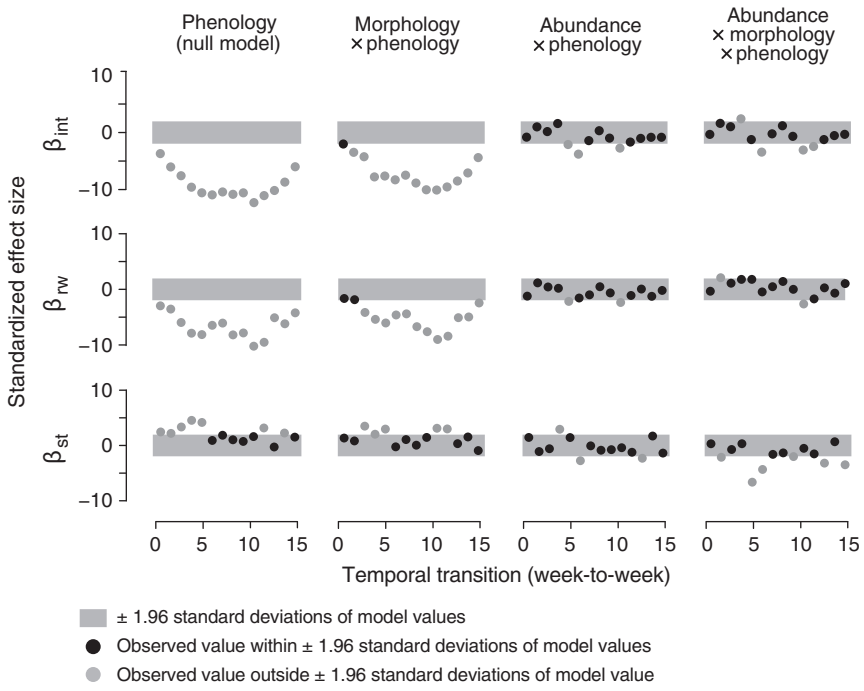


**Figure 4** Standardised effect sizes (SES) comparing observed interaction turnover values to values expected under each probability-based simulation model for the 2015 growing season. The grey-shaded region represents ± 1.96 standard deviations; points that fall within this region indicate that model values and observed values are statistically indistinguishable. Results for 2013 and 2014 are qualitatively similar (Fig. S3).

contrast, we find strong evidence that species interactions form and dissolve rapidly across the season. Furthermore, we show that interaction rewiring, rather than species turnover, was the dominant driver of interaction turnover (Fig. 2). This pattern was repeated in all 3 years of the study, providing concrete evidence that rewiring can play a consistently dominant role in influencing the structure and dynamics of ecological networks.

It is important to note, however, that both species turnover *and* rewiring contribute to these temporal dynamics. Species turnover will always influence interaction turnover to some degree: when species turnover is high its contribution to interaction turnover will also be high (Poisot *et al*. 2012). The elevated interaction turnover early in the season coincides with the rapid seasonal transition of the timing of snowmelt – a time when species turnover is greatest. As the season progresses and moves away from this seasonal transition, the influence of species turnover quickly declines, and the influence of rewiring increases, peaking during the middle of the season in all 3 years of the study. Finally, towards the end of the season, the community becomes less dynamic as species turnover, interaction turnover and rewiring attenuate. The consistent and rapid seasonal progression of interactions we observed illustrates the importance of viewing interaction networks as dynamic entities.

To date, neither theory nor empirical investigations have provided a clear expectation for the relative influences of rewiring and species turnover on interaction turnover, whether for plants and pollinators or for any other species interaction. Any such expectation would help to reveal mechanisms that constrain or facilitate the switching of species' use of available resources. Our phenology null model, which assumes random interactions among plants and pollinators that overlap in time, consistently over-predicted both total interaction turnover and rewiring (Fig. 4). In other words, phenological-coupling alone is an insufficient predictor of who interacts with whom within the network (Box 1). This suggests that there are additional constraints on interaction formation that reduced the values of interaction turnover and rewiring that we observed.

Indeed, our simulation models strongly suggest that temporal patterns of interaction turnover and rewiring are consistently constrained by variation in species phenology *and* relative abundances. Our evidence contributes to the emerging synthesis that abundance and phenology are key predictors of a wide range of interaction network properties by showing that these known predictors of aggregated patterns extend to the scale of interaction assembly and disassembly.

There is considerable opportunity for the abundances of temporally co-occurring flowers and pollinators, and changes in these abundances, to directly influence who interacts with whom and how this changes on short ecological time scales. In early models of optimal foraging (Emlen 1966; MacArthur & Pianka 1966), for example the relative abundance of a resource item of high quality determines entirely whether an item of lower quality is used; this by itself implicates changes in abundance as a critical aspect of resource use and the overall frequency of rewiring. Later models of optimal and adaptive foraging predict flexibility in resource use, in part based on the abundance of available resources, the presence of competitors, and their changes through time (and space) (e.g. Emlen 1968; Stephens & Krebs 1986; Mitchell 1989, 1990).

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Each of these processes has the potential to increase interaction rewiring.

On a longer, evolutionary time scale, a different (and not mutually exclusive) scenario is that the abundance of temporally co-occurring species is correlated with other attributes that contribute to interaction turnover and rewiring. For example in animals, abundance is often correlated with body size (negatively) and longevity (positively) among other ecologically-important traits (Webb *et al.* 2002; White *et al.* 2007). Our simulation models did not include these possible factors, nor do we know the correlations among all of them in this system. One possibility is that learning, memory and other aspects of insect cognitive ability vary with body size, longevity or both, and that this influences resource choice and rewiring. Bees, flies and butterflies, for example may contribute very differently to the rate of turnover and rewiring we observed here, in part based on variation in their cognitive abilities. Although research on insect cognition is advancing rapidly, too little is known at this point to evaluate this possibility further (e.g. Dukas 2008). Still, this example of insect cognitive ability serves to illustrate a mechanistic pathway by which correlates of abundance may translate into interaction turnover and rewiring.

The importance of different ecological constraints underlying interaction turnover and rewiring should partly depend on the degree of specialisation and the amount of variation in relevant traits within a given community, ultimately representing ecological dynamics that are played out on an evolutionary stage. The species we examined in our subalpine community are relatively generalised, each interacting with at least a few other species across the season (Tables S3 and S4), and most plant–pollinator pairs meet the criterion of a morphological size match. Therefore, beyond overlapping phenologies, temporally co-occurring plants and pollinators appear to have few barriers in the way of their interactions. Thus, it is not surprising that morphology does not enter as an important constraint in our simulation models. In contrast, however, morphology may play a much more dominant role in interaction turnover in more specialised communities, such as the Brazilian plant-hummingbird networks studied by Maruyama *et al.* (2014) and Vizentin-Bugoni *et al.* (2014). These communities exhibit much higher diversity in plant and pollinator morphology, but lower absolute abundances and variance in those abundances. Interaction rewiring can potentially be extensive within such specialised communities, but it will occur largely within the constraints of morphological and phenological matching. Furthermore, we caution that high interaction turnover and rewiring are not inevitable properties of systems with few morphological barriers.

The temporal dynamics we report here have implications for reaching a general understanding of interaction flexibility and community stability in the face of ongoing global change. If strong temporal dynamics are a regular component of the seasonal progression of interactions, then dynamic systems may be inherently resilient to perturbations of gain and loss of species and changes in their relative abundances. Several recent studies have explored how phenological mismatch between plants and pollinators might lead to local extinctions or other negative effects (Memmott *et al.* 2007; Hegland *et al.* 2009; McKinney *et al.* 2012; Rafferty *et al.* 2014). In most cases, interactions between species are assumed to be fixed (e.g. Memmott *et al.* 2007; Poisot *et al.* 2015). But, as long as plants and pollinators are at least somewhat flexible in resource use and rapid rewiring is possible, pollination systems may be more resilient to phenological changes than previously expected. Indeed, incorporating rewiring and adaptive foraging into a pollination network, Kaiser-Bunbury *et al.* (2010) found an overall increase in network robustness and stability to species loss. Similarly, Burkle *et al.* (2013) found that many novel interactions between plants and pollinators formed as a result of climate-induced phenological shifts, and that interaction flexibility in generalist plants and pollinators appeared to buffer them from extinction. Of course many specialised species are likely to remain vulnerable, as are all species if complete phenological decoupling of plants and pollinators were to occur. We are only beginning to understand the complexity of fitness consequences resulting from interaction flexibility for individuals and populations; the high levels of interaction turnover and rewiring we observed do not preclude organisms from experiencing adverse fitness effects.

In conclusion, we present consistent evidence that species interaction networks are highly dynamic and labile entities. These findings have implications for all types of ecological interactions. For example our understanding of the ecological and evolutionary consequences of pollination, herbivory, and predation are contingent upon the scale and rate at which interactions form and dissolve. Future studies of fine-scale temporal dynamics of interactions and their drivers in other ecosystems and with other types of interactions will greatly improve our ability to predict the reshuffling of communities in the face of ongoing change.

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## AUTHOR CONTRIBUTIONS

PJC conceived the project; PJC and JLC designed the project; PJC, JLC and NJS obtained funding for the project; PJC, JLC, RMB and NMW collected the data; PJC and WKP conducted analyses; PJC and NMW wrote the manuscript; all authors provided feedback on analyses, interpretation of results and edited the manuscript.

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## DATA ACCESSIBILITY STATEMENT

The primary data used in this study are archived at the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.s91p4 (CaraDonna et al. 2017).

## REFERENCES


Alarcón, R., Waser, N.M. & Ollerton, J. (2008). Year-to-year variation in the topology of a plant–pollinator interaction network. *Oikos*, 117, 1796–1807.

Bascompte, J. & Jordano, P. (2014). *Mutualistic Networks*. Princeton University Press, Princeton, NJ.

Bascompte, J. & Stouffer, D.B. (2009). The assembly and disassembly of ecological networks. *Philos. Trans. R. Soc. B Biol. Sci.*, 364, 1781–1787.

Bascompte, J., Jordano, P. & Olesen, J.M. (2006). Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science*, 312, 431–433.

Burkle, L. & Irwin, R. (2009). The importance of interannual variation and bottom-up nitrogen enrichment for plant–pollinator networks. *Oikos*, 118, 1816–1829.

Burkle, L.A. & Alarcón, R. (2011). The future of plant-pollinator diversity: understanding interaction networks across time, space, and global change. *Am. J. Bot.*, 98, 528–538.

Burkle, L.A., Marlin, J.C. & Knight, T.M. (2013). Plant-pollinator interactions over 120 years: loss of species, co-occurrence, and function. *Science*, 339, 1611–1615.

Burkle, L.A., Myers, J.A. & Belote, R.T. (2015). The beta-diversity of species interactions: untangling the drivers of geographic variation in plant-pollinator diversity and function across scales. *Am. J. Bot.*, 103, 118–128.

CaraDonna, P.J., Iler, A.M. & Inouye, D.W. (2014). Shifts in flowering phenology reshape a subalpine plant community. *Proc. Natl Acad. Sci. USA*, 111, 4916–4921.

CaraDonna, P.J., Petry, W.K., Brennan, R.M., Cunningham, J.L., Bronstein, J.L., Waser, N.M. & Sanders, N.J. (2017). Data from: Interaction rewiring and the rapid turnover of plant-pollinator networks. *Dryad Digital Repository*, doi:10.5061/dryad.s91p4.

Carnicer, J., Jordano, P. & Melián, C.J. (2009). The temporal dynamics of resource use by frugivorous birds: a network approach. *Ecology*, 90, 1958–1970.

Chesson, P. & Huntly, N. (1989). Short-term instabilities and long-term community dynamics. *Trends Ecol. Evol.*, 4, 293–298.

Clements, F.E. (1936). Nature and structure of the climax. *J. Ecol.*, 24, 252–284.

Cowles, H.C. (1899). The ecological relations of the vegetation on the sand dunes of Lake Michigan. Part I. -Geographical relations of the dune floras. *Bot. Gaz.*, 27, 95–117.

Dukas, R. (2008). Evolutionary biology of insect learning. *Annu. Rev. Entomol.*, 53, 145–160.

Elton, C.S. (1927). *Animal Ecology*. Macmillan Co., New York, NY.

Emlen, J.M. (1966). The role of time and energy in food preference. *Am. Nat.*, 100, 611–617.

Emlen, J.M. (1968). Optimal choice in animals. *Am. Nat.*, 102, 385–389.

Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.-L. & Totland, Ø. (2009). How does climate warming affect plant-pollinator interactions? *Ecol. Letters*, 12, 184–195.

Hutchinson, G. (1959). Homage to Santa Rosalia or why are there so many kinds of animals? *Am. Nat.*, 93, 145–159.

Jordano, P. (1987). Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. *Am. Nat.*, 129, 657–677.

Kaiser-Bunbury, C.N., Muff, S., Memmott, J., Müller, C.B. & Caflisch, A. (2010). The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour. *Ecol. Letters*, 13, 442–452.

MacArthur, R.H. & Pianka, E.R. (1966). On optimal use of a patchy environment. *Am. Nat.*, 100, 603–609.

MacLeod, M., Genung, M.A., Ascher, J.S. & Winfree, R. (2016). Measuring partner choice in plant-pollinator networks: using null models to separate rewiring and fidelity from chance. *Ecology*, 97, 2925–2931. DOI:10.1002/ecy.1574.

Maruyama, P.K., Vizentin-Bugoni, J., Oliveira, G.M., Oliveira, P.E. & Dalsgaard, B. (2014). Morphological and spatio-temporal mismatches shape a neotropical savanna plant-hummingbird network. *Biotropica*, 46, 740–747.

McKinney, A., CaraDonna, P.J., Inouye, D.W., Barr, W.A., Bertelsen, C.D. & Waser, N.M. (2012). Asynchronous changes in phenology of migrating Broad-tailed Hummingbirds and their early-season nectar resources. *Ecology*, 93, 1987–1993.

McMeans, B.C., McCann, K.S., Humphries, M., Rooney, N. & Fisk, A.T. (2015). Food web structure in temporally-forced ecosystems. *Trends Ecol. Evol.*, 30, 662–672.

Medan, D., Basilio, A.M. & Devoto, M. (2006). Measuring generalization and connectance in temperate, year-long active systems. In: *Plant-Pollinator Interactions: From Specialization to Generalization* (eds Waser, N.M. & Ollerton, J.). University of Chicago Press, Chicago, IL, pp. 245–259.

Memmott, J., Craze, P.G., Waser, N.M. & Price, M.V. (2007). Global warming and the disruption of plant-pollinator interactions. *Ecol. Letters*, 10, 710–717.

Mitchell, W.A. (1989). Informational constraints on the optimal foraging of hummingbirds. *Oikos*, 58, 16–24.

Mitchell, W.A. (1990). An optimal control theory of diet selection: the effects of resource depletion and exploitative competition. *Oikos*, 55, 145–154.

Odum, E. (1969). The strategy of ecosystem development. *Science*, 164, 262–270.

Olesen, J.M. & Jordano, P. (2002). Geographic patterns in plant-pollinator mutualistic networks. *Ecology*, 83, 2416–2424.

Olesen, J.M., Bascompte, J., Elberling, H. & Jordano, P. (2008). Temporal dynamics in a pollination network. *Ecology*, 89, 1573–1582.

Olito, C. & Fox, J.W. (2014). Species traits and abundances predict metrics of plant-pollinator network structure, but not pairwise interactions. *Oikos*, 124, 428–436.

Paine, R. (1966). Food web complexity and species diversity. *Am. Nat.*, 100, 65–75.

Petanidou, T., Kallimanis, A.S., Tzanopoulos, J., Sgardelis, S.P. & Pantis, J.D. (2008). Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization. *Ecol. Letters*, 11, 564–575.

Petchey, O.L., Beckerman, A.P., Riede, J.O. & Warren, P.H. (2008). Size, foraging, and food web structure. *Proc. Natl Acad. Sci. USA*, 105, 4191–4196.

Poisot, T., Canard, E., Mouillot, D., Mouquet, N. & Gravel, D. (2012). The dissimilarity of species interaction networks. *Ecol. Letters*, 15, 1353–1361.

Poisot, T., Stouffer, D.B. & Gravel, D. (2015). Beyond species: why ecological interaction networks vary through space and time. *Oikos*, 124, 243–251.

Rafferty, N.E., CaraDonna, P.J. & Bronstein, J.L. (2014). Phenological shifts and the fate of mutualisms. *Oikos*, 124, 14–21.

Simanonok, M.P. & Burkle, L.A. (2014). Partitioning interaction turnover among alpine pollination networks: spatial, temporal, and environmental patterns. *Ecosphere*, 5, 1–16.

Stang, M., Klinkhamer, P.G.L., Waser, N.M., Stang, I. & Van Der Meijden, E. (2009). Size-specific interaction patterns and size matching in a plant-pollinator interaction web. *Ann. Bot.*, 103, 1459–1469.

Stephens, D.W. & Krebs, J.R. (1986). *Foraging Theory*. Princeton University Press, Princeton, NJ.

Thébault, E. & Fontaine, C. (2010). Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science*, 329, 853–856.


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Thompson, J.N. (2005). *The Geographic Mosaic of Coevolution*. University of Chicago Press, Chicago, IL.

Vázquez, D.P., Bluthgen, N., Cagnolo, L. & Chacoff, N.P. (2009a). Uniting pattern and process in plant-animal mutualistic networks: a review. *Ann. Bot.*, 103, 1445–1457.

Vázquez, D.P., Chacoff, N. & Cagnolo, L. (2009b). Evaluating multiple determinants of the structure of plant–animal mutualistic networks. *Ecology*, 90, 2039–2046.

Vizentin-Bugoni, J., Maruyama, P.K. & Sazima, M. (2014). Processes entangling interactions in communities: forbidden links are more important than abundance in a hummingbird-plant network. *Proc. R. Soc. B Biol. Sci.*, 281, 20132397.

Webb, C.O., Ackerly, D.D., McPeek, M.A. & Donoghue, M.J. (2002). Phylogenies and community ecology. *Annu. Rev. Ecol. Syst.*, 33, 475–505.

White, E.P., Ernest, S.K.M., Kerkhoff, A.J. & Enquist, B.J. (2007). Relationships between body size and abundance in ecology. *Trends Ecol. Evol.*, 22, 323–330.

Whittaker, R. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.*, 30, 279–338.

Winemiller, K.O. (1990). Spatial and temporal variation in tropical fish networks. *Ecol. Monogr.*, 60, 331–367.

Yeakel, J.D., Pires, M.M., Rudolf, L., Dominy, N.J., Koch, P.L., Guimarães, P.R. Jr *et al.* (2014). Collapse of an ecological network in ancient Egypt. *Proc. Natl Acad. Sci. USA*, 111, 14472–14477.

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