1 **Interaction rewiring and the rapid turnover of plant-pollinator networks**

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46   **ABSTRACT**

47   Whether species interactions are static or change over time has wide-reaching ecological

48   and evolutionary consequences. However, species interaction networks are typically constructed

49   from temporally-aggregated interaction data, thereby implicitly assuming that interactions are

50   fixed. This approach has advanced our understanding of communities, but it obscures the

51   timescale at which interactions form (or dissolve) and the drivers and consequences of such

52   dynamics. We address this knowledge gap by quantifying the within-season turnover of plant-

53   pollinator interactions from weekly censuses across three years in a subalpine ecosystem. Week-

54   to-week turnover of interactions (i) was high, (ii) followed a consistent seasonal progression in

55   all years of study, and (iii) was dominated by interaction rewiring (the reassembly of interactions

56   among species). Simulation models revealed that species' phenologies and relative abundances

57   constrained both total interaction turnover and rewiring. Our findings reveal the diversity of

58   species interactions that may be missed when the temporal dynamics of networks are ignored.

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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; Carnicer *et al.* 2009), among years (Alarcón & Waser 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

92   knowledge gap (Bascompte & Stouffer 2009; Burkle & Alarcón 2011; Bascompte &

93   Jordano 2014; McMeans *et al.* 2015; Poisot *et al.* 2015).

94   A promising approach to address species interactions at the appropriate scale is to

95   more precisely quantify temporal interaction turnover (i.e., interaction *β*-diversity:

96   changes in the composition of interactions; Poisot *et al.* 2012). Interaction turnover

97   consists of two additive components (Fig. 1). The first component is *species*

98   *turnover*: interactions in a community are lost or gained as individuals of a species

99   become active or inactive, through time. The second component is *interaction rewiring*:

100   interactions are reassembled over time because of changes in who is interacting with

101   whom among the same pool of co-occurring species. Currently we lack a basic

102   understanding of the temporal scale of interaction turnover and have virtually no

103   knowledge of the relative importance of rewiring versus species turnover (Burkle *et al.*

104   2015; Poisot *et al.* 2015). Furthermore, although previous studies show that phenology,

105   abundance, and morphology of species can contribute to structural patterns of static

106   networks, (e.g., Petchey *et al.* 2008; Vázquez *et al.* 2009a), we do not know how these

107   ecological factors may constrain patterns of interaction once temporal dynamics of

108   networks are more fully characterized. Quantifying how and why interaction networks

109   change over time has important implications for our understanding of the assembly and

110   disassembly of ecological networks and their resilience to anthropogenic pressures.

111   In this study, we quantify the within-season temporal turnover of plant-pollinator

112   interaction networks within a subalpine ecosystem. Using weekly censuses of plant-

113   pollinator interactions over three years, collectively representing 41 weekly networks and

114   nearly 30,000 individual interactions, we ask: (1) What are the relative contributions of

115   species turnover and rewiring for the temporal turnover of interactions? (2) What is the

116   magnitude of interaction turnover and its two components from week to week within a

117   season? and (3) Are patterns of interaction turnover and its components consistent among

118   years? We then employ probability-based simulation models to ask: (4) Are within-

119   season interaction turnover and rewiring constrained by phenology, morphology, species

120   relative abundances, or combinations of these ecological factors? Our approach reveals

121   that much of the basic ecology of species interactions is overlooked when networks are

122   temporally-aggregated and interactions among species are assumed to be static. These

123   findings help to fill in a key gap in our understanding of the assembly and disassembly of

124   species interaction networks, with implications for all types of ecological networks.

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126   **METHODS**

127   **Study system.** We worked at The Rocky Mountain Biological Laboratory (RMBL) in

128   Gothic, Colorado, USA (38°57.5′N, 106°59.3′W, 2900 m a.s.l.). RMBL is surrounded by

129   a mosaic of wet and dry meadows and aspen and conifer forest. The area is snow-covered

130   for much of the year, with a short summer growing season of 3–5 months (CaraDonna *et*

131   *al.* 2014). The plant and pollinator communities of the subalpine in this area are relatively

132   generalized (e.g., Burkle and Irwin 2009; Table S3), and those we studied consist almost

133   exclusively of native taxa (except the plant *Taraxacum officinale*). The honey bee (*Apis*

134   *mellifera*), a non-native generalist, does not occur in the area.

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136   **Plant-pollinator observations.** We observed plant-pollinator interactions at weekly

137   intervals across the flowering season for 11 weeks in 2013, 15 weeks in 2014, and 16

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138   weeks in 2015. Snowfall in the second week of the 2015 season prevented sampling

139   during that period. All observations took place in two adjacent dry meadows that cover

140   approximately 2800 m^2 and 3015 m^2, respectively, and are separated by ca. 100 m of

141   forest. Observations began about one week after snowmelt each year (Table S1),

142   coinciding with the first emergence of flowers and pollinators. Within each week, we

143   conducted 32 15-min observation periods for a total of 8 hours per week. Each complete

144   weekly interaction census (i.e., all 32 observation periods) took place over 2–3

145   consecutive days and was separated from the start of the next weekly census by 3–5 days.

146   We randomly selected one of four quadrants within each meadow during each 15-min

147   observation period, we then sampled the remaining quadrants in random order, and then

148   repeated this in the other meadow; we alternated the starting meadow on successive days.

149   During each 15-min observation period, we walked around the focal quadrant and

150   recorded all observed plant-pollinator interactions. We defined an interaction as taking

151   place when a floral visitor of any species unambiguously contacted the reproductive

152   structures of flowers; we refer to floral visitors as pollinators while recognizing that their

153   quality as mutualists may vary widely. To prevent observer bias, observations in each

154   season were made by the same two researchers (PJC and JLC in 2013, PJC and RMB in

155   2014 and 2015). All observations took place between 0900–1700 hours during weather

156   conditions favorable for pollinator activity (ambient temperature > 8˚C, not snowing or

157   raining). We constructed a single plant-pollinator interaction matrix from each complete

158   set of 32 weekly observation periods.

159   All flowering plants were identified to species, and all pollinators were identified

160   to species or to the finest taxonomic level possible (Table S3). A total of 85% of

161   pollinators (63 out of 74) were identified to species; of the 11 remaining pollinators, 6

162   were identified to genus, and 5 were identified to family (all of the latter were Diptera).

163   During field observations, pollinators were identified to either species or morphospecies

164   on the wing. A reference specimen was collected for each morphospecies and later

165   identified using the RMBL Entomology Reference Collection. Otherwise, pollinators

166   were not collected during observations to avoid artefacts of destructive sampling.

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168   **Plant and pollinator abundance.** Within each meadow quadrant we established a

169   permanent 25 × 1m transect to monitor floral abundance and flowering phenology. Once

170   per week, all open flowers or flowering heads (for species with small clustered flowers,

171   such as Asteraceae) were counted for all species present within each transect (*following*

172   CaraDonna *et al.* 2014). The number of observation periods during which a given

173   pollinator species was observed was used as an estimate of its relative abundance. For

174   example, if a given species was observed in 10 of 32 observation periods in a given

175   week—regardless of the number of visits made by this species during this week—its

176   abundance value was 10. We used this estimation method instead of interaction

177   frequency (number of visits) because it is influenced less strongly by floral abundance.

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179   **Plant and pollinator morphology.** We measured plant and pollinator morphology for all

180   species present during the three-year study (Table S3). For plants, we measured the

181   functional depth at which nectar could be reached on 10–20 individual flowers for each

182   species (*following* Stang *et al.* 2009; *details in* Table S3). Because pollen was presented

183   at or near the opening of all the flowers in our meadows we assumed it was accessible to

184   all pollinators. Proboscis length was measured on 2–15 individuals of each insect

185   pollinator species using the RMBL Entomology Reference Collection. For the one

186   observed hummingbird pollinator, the Broad-tailed Hummingbird (*Selasphorus*

187   *platycercus*), bill length was measured by one of us (NMW) on live birds captured at the

188   RMBL and on specimens in the University of Arizona, University of Utah, and RMBL

189   vertebrate collections.

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191   **Components of interaction turnover.** Following Poisot *et al*. (2012), we quantified the

192   absolute turnover of plant-pollinator interactions across each growing season using

193   Whittaker's (1960) dissimilarity index:

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

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195   where β_{int} is interaction turnover (i.e., interaction β-diversity or interaction dissimilarity)

196   between two successive weekly networks, a is the number of pairwise interactions shared

197   between the networks, and b and c are the number of pairwise interactions unique to each

198   of the networks, respectively. Values for this index range from 0 to 1; higher values

199   indicate higher turnover, or greater change between weeks in who is interacting with

200   whom. This index treats interactions as present or absent, directly addressing our goal of

201   exploring the absolute gain or loss of interactions through time. The overall patterns of

202   β_{int} were qualitatively similar when we used a frequency-based metric of interaction

203   dissimilarity (Bray-Curtis dissimilarity; Table S4). Because we were interested in the

204   processes that govern the formation of interactions, we do not address frequency-based β-

205   diversity metrics further.

206   An appealing property of presence-based interaction turnover metrics is that they

207   can be partitioned as $\beta_{int} = \beta_{st} + \beta_{rw}$, where the two additive components are the

208   contribution of species turnover (β_{st}) and interaction rewiring (β_{rw}) (Poisot *et al.* 2012;

209   Fig. 1). (Our notation for rewiring, β_{rw}, is equivalent to β_{os} in Poisot *et al.* [2012].) This

210   partitioning of interaction turnover reveals whether the dynamics of interaction networks

211   arise (i) because of changes in species composition (β_{st}), (ii) because of the reassembly of

212   interactions among species (β_{rw}), or (iii) by some combination of both (Fig. 1). While this

213   approach (including our definition of rewiring) identifies how and why interaction

214   networks are changing, it does not provide any information on whether those changes

215   arise because of deterministic (niche-based) or stochastic (neutral) processes (or both;

216   *sensu* MacLeod et al. 2016).

217   Notice that the contribution of species turnover to interaction turnover, β_{st}, is

218   constrained by, but not synonymous with, the turnover of the species themselves, β_s, (*see*

219   Poisot *et al.* 2012). For example, high species turnover necessitates a relatively higher

220   contribution of species turnover to interaction turnover; however, the loss of a single

221   species can bring about either the loss of a single interaction or the loss of many

222   interactions. For brevity, we do not discuss β_s further, although we report all species

223   turnover values in Figure S2 and Tables S6–S8.

224   This interaction turnover partitioning approach is highly robust to sampling

225   effects (Poisot *et al.* 2012); nevertheless, we conducted several additional analyses to

226   ensure that our results do not stem from sampling artefacts. First, interaction rarefaction

227 curves and abundance-based richness estimators indicated that our sampling effort

228 suffced to detect most (on average 85–93%) of the pairwise interactions that occurred in

229 each week (Fig. S1; Table S2). Second, two different sensitivity analyses showed that

230 observed patterns of interaction turnover were qualitatively the same when we (i)

231 removed singletons (rare or ephemeral interactions occurring only once within a week)

232 and when we (ii) aggregated sampling periods over a broader, two-week sampling

233 window (Tables S6–S7). These analyses provide strong and consistent evidence that

234 sampling effects were unlikely to bias our results.

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236 **Simulation models**. We constructed four probability-based simulation models to explore

237 ecological factors that may constrain within-season interaction turnover (Box 1). Each

238 model expresses a set of constraints that adjusts the likelihood that a given plant-

239 pollinator interaction will occur at a given time point. By including these alternate sets of

240 constraints in the simulations, we can determine the patterns of interaction turnover that

241 result from each scenario and reject the scenarios whose patterns deviate from our

242 observations.

243 *(i) Phenology* – Plants must bloom and pollinators must forage at the same time for them

244 to interact. In each run of the simulation and for each week of the season, this model

245 randomly assigns interactions to pairs of plants and pollinators that were active during

246 that week. Therefore, all active species pairs were equally likely to be assigned an

247 interaction (i.e., interaction formation in each instantiation was purely stochastic). This is

248 a null model in the sense that it provides a baseline expectation of interaction turnover

249 and rewiring based only on the most fundamental constraint, phenological overlap.

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250   (Spatial co-occurrence is also a fundamental constraint, but it is implicit here because all

251   our networks involve species that share the same adjacent small meadows.)

252   *(ii) Abundance × phenology* – Interactions between a given pair of temporally co-

253   occurring plants and pollinators may be more likely when the local relative abundances

254   of species are greater. This model builds on the phenology null model described above by

255   weighting the probability that a given pair of plants and pollinators will interact by their

256   abundances during that week.

257   *(iii) Morphology × phenology* – Temporally co-occurring plants and pollinators may be

258   more likely to interact when their morphological traits enable the flow of resources or

259   services from one species to the other. This model builds on the phenology null model by

260   accounting for the length of pollinator feeding apparatus and the functional nectar depth

261   of flowers. A morphological match was assumed to occur whenever the feeding

262   apparatus of a pollinator was at least as long as the functional nectar depth of the flower.

263   In other words, flowers with greater nectar depths are more restrictive, whereas

264   pollinators with longer tongues are relatively unconstrained. Nectar depth and tongue

265   length are only one set of many potential phenotypic constraints (e.g., color, scent), but it

266   remains unclear how to incorporate such complex traits into models of interaction

267   (Vázquez *et al.* 2009a).

268   *(iv) Abundance × morphology × phenology* – The previous two models are not mutually

269   exclusive: both species relative abundances and morphology may simultaneously

270   constrain which temporally co-occurring species interact (Box 1). Here, the probability of

271   interaction is the joint probability of relative abundances and morphological size-

272   matching for temporally co-occurring plants and pollinators.

273   For each of the four classes of models we constructed a matrix describing the

274   probability of interaction between plants and pollinators observed in each week of each

275   year (*following* Vázquez *et al.* 2009b). We then used a Monte Carlo process to generate

276   1000 predicted interaction matrices based on the underlying probability matrix for each

277   set of ecological constraints for each week (Box 1). For example, if the probability of

278   interaction between plant i and pollinator j is 0.1 in a given week under a model, then

279   these two species will interact in approximately 100 of the 1000 simulated matrices for

280   that week. For each weekly simulation, we held the number of links between species

281   equal to the number of links actually observed (i.e., network connectance in the simulated

282   interaction matrices always equaled that of the observed interaction matrix; Box 1). Our

283   simulations do not deviate from the observed species composition within each week, but

284   allowed for changes in the occurrence of interactions among temporally co-occurring

285   species. We then calculated expected interaction turnover using these simulated matrices

286   and compared the values expected under each model to the values actually observed. The

287   greatest amount of information comes from comparing β_{int} and β_{rw} between models and

288   observed data; because we fixed simulated species compositions to observed values we

289   expect simulated and observed values of β_{st} to be similar across all candidate models.

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291   **Data analysis & model comparisons.** Each of the three years of study yielded multiple

292   values for the contribution of interaction rewiring (β_{rw}) and species turnover (β_{st}) to

293   interaction turnover (one value for each week-to-week transition in each year). We

294   compared the means of each of the two components in each year using a two-tailed t-test.

295   The values of interaction turnover and its components (β_{int}, β_{rw}, β_{st}) were fit as a function

296   of time across the season using linear or second-order polynomial regression, with AIC to

297   determine best-fit models. We tested for temporal autocorrelation among the residuals of

298   all turnover variables within each season to ensure these time-series data met the

299   assumption of independence; temporal autocorrelation was never detected (Ljung-Box

300   Test, $P > 0.05$). All data met the assumptions of each statistical test.

301   We compared simulated interaction turnover patterns from each model to the

302   observed patterns using a standardized effect size (SES) approach:

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

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304   SES indicates the number of standard deviations an observed value of interaction

305   turnover or one of its components (β_{obs}) deviates from the mean of the simulated model

306   [$\mu(\beta_{sim})$], given the standard deviation [$\sigma(\beta_{sim})$] of the model output across 1000

307   iterations. Assuming a normal distribution of deviations, approximately 95% of SES

308   values should fall between -1.96 and $+1.96$. Therefore, for each week-to-week transition,

309   observed values that fall within this range are consistent with the prediction under the

310   model, whereas points that fall outside suggest that the ecological constraint(s) included

311   in the model do not contribute to the observation.

312

313   **RESULTS**

314   Over the three years of study we observed 566 unique pairwise interactions

315   between 45 flowering plants and 74 pollinators, representing 28,959 individual pollinator

316   visits to flowers (Table S6). In total, we sampled 41 weekly plant-pollinator interaction

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317 networks. Compared to other full growing-season surveys of subalpine plant-pollinator

318 interactions (e.g., Olito & Fox 2014; Simanonok & Burkle 2014) our sampling yielded on

319 average *ca.* 10-fold more visitation events per year; at the same time the topological

320 properties of our weekly networks when they are aggregated across entire growing

321 seasons lie well within the range typically observed in other mutualistic networks (e.g.,

322 Jordano 1987; Olesen and Jordano 2002; Table S5). Overall, this plant-pollinator

323 community is relatively generalized (Tables S3 and S4). Among all possible plant-

324 pollinator pairs 83% meet the criterion of a morphological size match based on functional

325 nectar depth and pollinator tongue length.

326

327 *Within-season turnover.* Within-season interaction turnover was consistently high and

328 primarily driven by rewiring (Fig. 2; Table S4). The contribution of rewiring to total

329 interaction turnover exceeded the contribution of species turnover in all three seasons

330 (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

331 average, rewiring accounted for almost two-thirds of interaction turnover (mean = 64%;

332 2013 = 60%; 2014 = 64%; 2015 = 67%) (Table S4).

333   The magnitude of week-to-week interaction turnover and its two components

334 varied predictably within each growing season, and these patterns were largely consistent

335 across all three years of study (Fig. 3). Total interaction turnover (β_{int}) declined across

336 each season; in 2013 this pattern was weak and non-significant, probably because

337 observations ended earlier in the season (2013: $R^2 = 0.10$, $P = 0.376$; 2014: $R^2 = 0.65$, $P <$

338 0.001; 2015: $R^2 = 0.77$, $P < 0.001$; Fig. 3). The magnitude of the contribution of rewiring

339 (β_{rw}) to interaction turnover exhibited a consistent, humped pattern with a peak during

340 mid-season in all three years (2013: $R^2 = 0.52$, $P = 0.07$; 2014: $R^2 = 0.50$, $P = 0.02$; 2015:

341 $R^2 = 0.62$, $P = 0.005$; Fig. 3). The magnitude of the contribution of species turnover (β_{st})

342 to interaction turnover declined across the season (2013: $R^2 = 0.62$, $P = 0.006$; 2014: $R^2 = $

343 0.31, $P = 0.039$; 2015: $R^2 = 0.89$, $P < 0.001$); in 2015 there was a slight increase at the

344 end of the season (Fig. 3). Table S8 lists all regression model coefficients.

345   Our simulation models suggest that phenologies and relative abundances of

346 species were important ecological constraints underlying patterns of interaction turnover

347 and rewiring (Fig 4, Fig. S3). The phenology null model alone produced values that were

348 a poor match to those observed values, generally overestimating turnover and rewiring in

349 each year; this indicates that our observed patterns of interaction turnover and rewiring

350 are not solely the result of random processes. The morphology × phenology model was

351 also a poor predictor of observed patterns. In contrast, the abundance × phenology model

352 yielded interaction turnover and rewiring values that matched observed patterns well in

353 all three years. The abundance × morphology × phenology model also matched observed

354 patterns; however, this model provided only a modest improvement over the more

355 parsimonious abundance × phenology models alone, and only in some years.

356   As expected, all models provided a reasonable fit to observed patterns of the

357 contribution of species turnover (β_{st}) to interaction turnover (Fig. 4, Fig. S3). This result

358 is inherent in the way we specified the simulations, because species composition in all

359 models was set to match observed species composition.

360

361 *Year-to-year turnover* – Species composition of the meadow flora and pollinator fauna

362 was similar across years. On average, 76% of all plant and pollinator species were present

363   in all three years (Table S9). The composition of interactions varied more strongly: on

364   average only about 42% of interactions were observed in all years. As a result, only about

365   20% of interaction turnover from year-to-year was due to differences in species

366   composition (β_{st}), whereas, the remaining 80% reflected year-to-year rewiring of

367   interactions (β_{rw}).

368

369   **DISCUSSION**

370   Ecological networks are largely characterized as temporally-static entities, and

371   therefore interactions among species are generally assumed to be invariant (Poisot *et al.*

372   2015). In contrast, we find strong evidence that species interactions form and dissolve

373   rapidly across the season. Furthermore, we show that interaction rewiring, rather than

374   species turnover, was the dominant driver of interaction turnover (Fig. 2). This pattern

375   was repeated in all three years of the study, providing concrete evidence that rewiring can

376   play a consistently dominant role in influencing the structure and dynamics of ecological

377   networks.

378   It is important to note, however, that both species turnover *and* rewiring

379   contribute to these temporal dynamics. Species turnover will always influence interaction

380   turnover to some degree: when species turnover is high its contribution to interaction

381   turnover will also be high (Poisot *et al.* 2012). The elevated interaction turnover early in

382   the season coincides with the rapid seasonal transition of the timing of snowmelt—a time

383   when species turnover is greatest. As the season progresses and moves away from this

384   seasonal transition, the influence of species turnover quickly declines, and the influence

385   of rewiring increases, peaking during the middle of the season in all three years of the

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386   study. Finally, toward the end of the season, the community becomes less dynamic as

387   species turnover, interaction turnover, and rewiring attenuate. The consistent and rapid

388   seasonal progression of interactions we observed illustrates the importance of viewing

389   interaction networks as dynamic entities.

390   To date, neither theory nor empirical investigations have provided a clear

391   expectation for the relative influences of rewiring and species turnover on interaction

392   turnover, whether for plants and pollinators or for any other species interaction. Any such

393   expectation would help to reveal mechanisms that constrain or facilitate the switching of

394   species' use of available resources. Our phenology null model, which assumes random

395   interactions among plants and pollinators that overlap in time, consistently over-predicted

396   both total interaction and rewiring turnover (Fig. 4). In other words, phenological-

397   coupling alone is an insufficient predictor of who interacts with whom within the network

398   (Box 1). This suggests that there are additional constraints on interaction formation that

399   reduced the values of interaction turnover and rewiring that we observed.

400   Indeed, our simulation models strongly suggest that temporal patterns of

401   interaction turnover and rewiring are consistently constrained by variation in species

402   phenology *and* relative abundances. Our evidence contributes to the emerging synthesis

403   that abundance and phenology are key predictors of a wide range of interaction network

404   properties by showing that these known predictors of aggregated patterns extend to the

405   scale of interaction assembly and disassembly.

406   There is considerable opportunity for the abundances of temporally co-occurring

407   flowers and pollinators, and changes in these abundances, to directly influence who

408   interacts with whom and how this changes on short ecological time scales. In early

409   models of optimal foraging (Emlen 1966; MacArthur & Pianka 1966), for example, the

410   relative abundance of a resource item of high quality determines entirely whether an item

411   of lower quality is used; this by itself implicates changes in abundance as a critical aspect

412   of resource use and the overall frequency of rewiring. Later models of optimal and

413   adaptive foraging predict flexibility in resource use, in part based on the abundance of

414   available resources, the presence of competitors, and their changes through time (and

415   space) (e.g., Emlen 1968; Stephens and Krebs 1986; Mitchell 1989, 1990). Each of these

416   processes has the potential to increase interaction rewiring.

417   On a longer, evolutionary time scale, a different (and not mutually exclusive)

418   scenario is that the abundance of temporally co-occurring species is correlated with other

419   attributes that contribute to interaction turnover and rewiring. For example, in animals,

420   abundance is often correlated with body size (negatively) and longevity (positively)

421   among other ecologically-important traits (Webb *et al.* 2002; White *et al.* 2007). Our

422   simulation models did not include these possible factors, nor do we know the correlations

423   among all of them in this system. One possibility is that learning, memory, and other

424   aspects of insect cognitive ability vary with body size, longevity, or both, and that this

425   influences resource choice and rewiring. Bees, flies, and butterflies, for example, may

426   contribute very differently to the rate of turnover and rewiring we observed here, in part

427   based on variation in their cognitive abilities. Although research on insect cognition is

428   advancing rapidly, too little is known at this point to evaluate this possibility further (e.g.,

429   Dukas 2008). Still, this example of insect cognitive ability serves to illustrate a

430   mechanistic pathway by which correlates of abundance may translate into interaction

431   turnover and rewiring.

432   The importance of different ecological constraints underlying interaction turnover

433   and rewiring should partly depend on the degree of specialization and the amount of

434   variation in relevant traits within a given community, ultimately representing ecological

435   dynamics that are played out on an evolutionary stage. The species we examined in our

436   subalpine community are relatively generalized, each interacting with at least a few other

437   species across the season (Tables S3 & S4), and most plant-pollinator pairs meet the

438   criterion of a morphological size match. Therefore, beyond overlapping phenologies,

439   temporally co-occurring plants and pollinators appear to have few barriers in the way of

440   their interactions. Thus, it is not surprising that morphology does not enter as an

441   important constraint in our simulation models. In contrast, however, morphology may

442   play a much more dominant role in interaction turnover in more specialized communities,

443   such as the Brazilian plant-hummingbird networks studied by Maruyama *et al.* (2014)

444   and Vizentin-Bugoni *et al.* (2014). These communities exhibit much higher diversity in

445   plant and pollinator morphology, but lower absolute abundances and variance in those

446   abundances. Interaction rewiring can potentially be extensive within such specialized

447   communities, but it will occur largely within the constraints of morphological and

448   phenological matching. Furthermore, we caution that high interaction turnover and

449   rewiring are not inevitable properties of systems with few morphological barriers.

450   The temporal dynamics we report here have implications for reaching a general

451   understanding of interaction flexibility and community stability in the face of ongoing

452   global change. If strong temporal dynamics are a regular component of the seasonal

453   progression of interactions, then dynamic systems may be inherently resilient to

454   perturbations of gain and loss of species and changes in their relative abundances. Several

455 recent studies have explored how phenological mismatch between plants and pollinators

456 might lead to local extinctions or other negative effects (Memmott *et al.* 2007; Hegland *et*

457 *al.* 2009; McKinney *et al.* 2012; Rafferty *et al.* 2014). In most cases, interactions between

458 species are assumed to be fixed (e.g., Memmott *et al.* 2007; Poisot *et al.* 2015). But, as

459 long as plants and pollinators are at least somewhat flexible in resource use and rapid

460 rewiring is possible, pollination systems may be more resilient to phenological changes

461 than previously expected. Indeed, incorporating rewiring and adaptive foraging into a

462 pollination network, Kaiser-Bunbury *et al.* (2010) found an overall increase in network

463 robustness and stability to species loss. Similarly, Burkle *et al.* (2013) found that many

464 novel interactions between plants and pollinators formed as a result of climate-induced

465 phenological shifts, and that interaction flexibility in generalist plants and pollinators

466 appeared to buffer them from extinction. Of course many specialized species are likely to

467 remain vulnerable, as are all species if complete phenological decoupling of plants and

468 pollinators were to occur. We are only beginning to understand the complexity of fitness

469 consequences resulting from interaction flexibility for individuals and populations; the

470 high levels of interaction turnover and rewiring we observed do not preclude organisms

471 from experiencing adverse fitness effects.

472   In conclusion, we present consistent evidence that species interaction networks

473 are highly dynamic and labile entities. These findings have implications for all types of

474 ecological interactions. For example, our understanding of the ecological and

475 evolutionary consequences of pollination, herbivory, and predation are contingent upon

476 the scale and rate at which interactions form and dissolve. Future studies of fine-scale

477 temporal dynamics of interactions and their drivers in other ecosystems and with other

478 types of interactions will greatly improve our ability to predict the reshuffling of

479 communities in the face of ongoing change.

480

490

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602

603

604   **Figure Captions**

605

606   **Figure 1.** Conceptual diagram illustrating the two components of interaction turnover (β_{int}). The

607   first is species turnover: interactions are lost or gained because of the loss or gain of species (β_{st}).

608   The second is interaction rewiring: interactions are reassembled because of changes in who is

609   interacting with whom; i.e., the same species interact in different combinations across time (β_{rw}).

610   Both components of interaction turnover can simultaneously occur from one transition to the

611   next, but are shown separately for clarity.

612

613   **Figure 2**. Comparison of the two components of plant-pollinator interaction turnover

614   (β_{int})–species turnover (β_{st}) and rewiring (β_{rw})–across all three years of the study. Values

615   represent the raw magnitude of interaction turnover and its partitioned values. Asterisks

616   indicate statistical significance ($P < 0.05$) between β_{st} and β_{rw} via a two-tailed t-test.

617

618   **Figure 3.** Within-season temporal dynamics of plant-pollinator interaction turnover (β_{int}),

619   the contribution of species turnover to interaction turnover (β_{st}), and the contribution of

620   rewiring to interaction turnover (β_{rw}) across all three years of the study. Values represent

621   the raw magnitude of interaction turnover and its partitioned values. Each panel

622   illustrates the relationship between each successive week-to-week temporal transition.

623   Grey points indicate a single week-to-week turnover value. Solid black lines indicate

624   significant relationships ($P < 0.05$), and dashed black lines indicate marginally significant

625   relationships ($P < 0.10$), using linear or non-linear regression.

626

627   **Figure 4.** Standardized effect sizes (SES) comparing observed interaction turnover values to

628   values expected under each probability-based simulation model for the 2015 growing season.

629   The grey shaded region represents ± 1.96 standard deviations; points that fall within this region

630   indicate that model values and observed values are statistically indistinguishable. Results for

631   2013 and 2014 are qualitatively similar (Fig. S3).

632

633   **Box 1. Hypothesized ecological constraints to explain the temporal turnover of who**

634   **interacts with whom in species interaction networks.** Several basic hypotheses have been

635   proposed to explain how and why species interactions form within ecological networks (Váquez

636   *et al.* 2009a, b; Poisot *et al.* 2015). Here we extend these hypotheses to explore the potential

637   constraints on the within-season temporal dynamics of plant-pollinator interactions. First, we

638   provide a hypothetical diagram of an observed plant-pollinator community, illustrating that the

639   interactions that occur at one specific time point (e.g., within a week) are a subset of all the

640   interactions that have occurred during the entire season, and that local temporal co-occurrence

641   (phenological overlap) is necessary for interactions to occur. Second, we provide a description of

642   each hypothesized ecological constraint and associated model. We illustrate how the model

643   assumes the interaction network is constrained and how we translate this information into an

644   interaction probability matrix. These probability matrices are used to simulate interactions within

645   each week (holding the number of links within each week equal to the number actually observed).

646   These simulated interactions are then used to explore evidence for different ecological

647   constraints that may give rise to the observed patterns of interaction turnover. Further

648   information regarding our measurements of plant and pollinator phenology, morphology, and

649   abundance, as well as additional model details, are included in the main text.

Figure 1
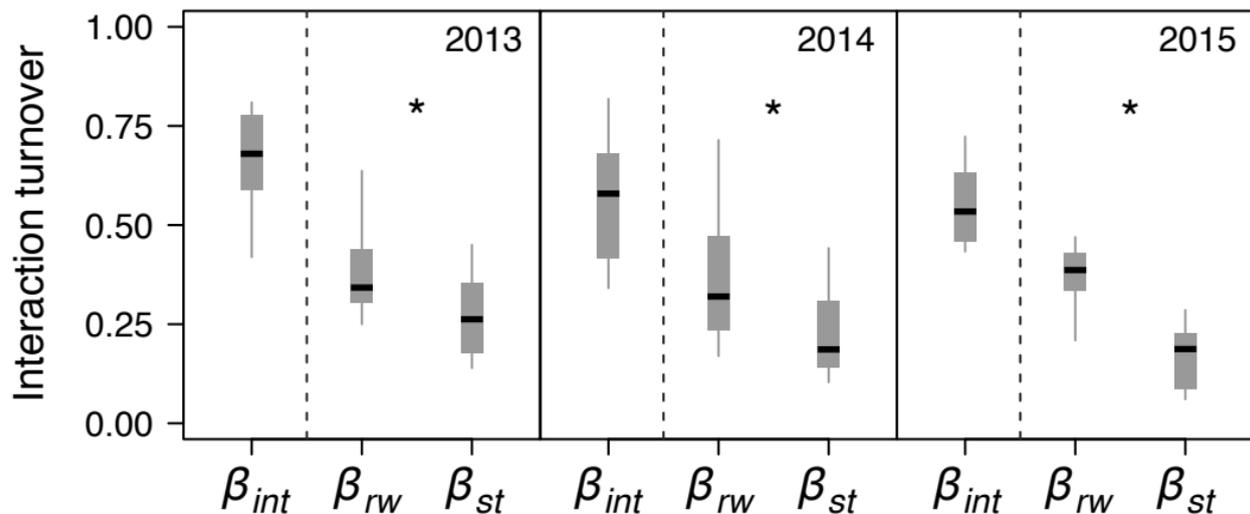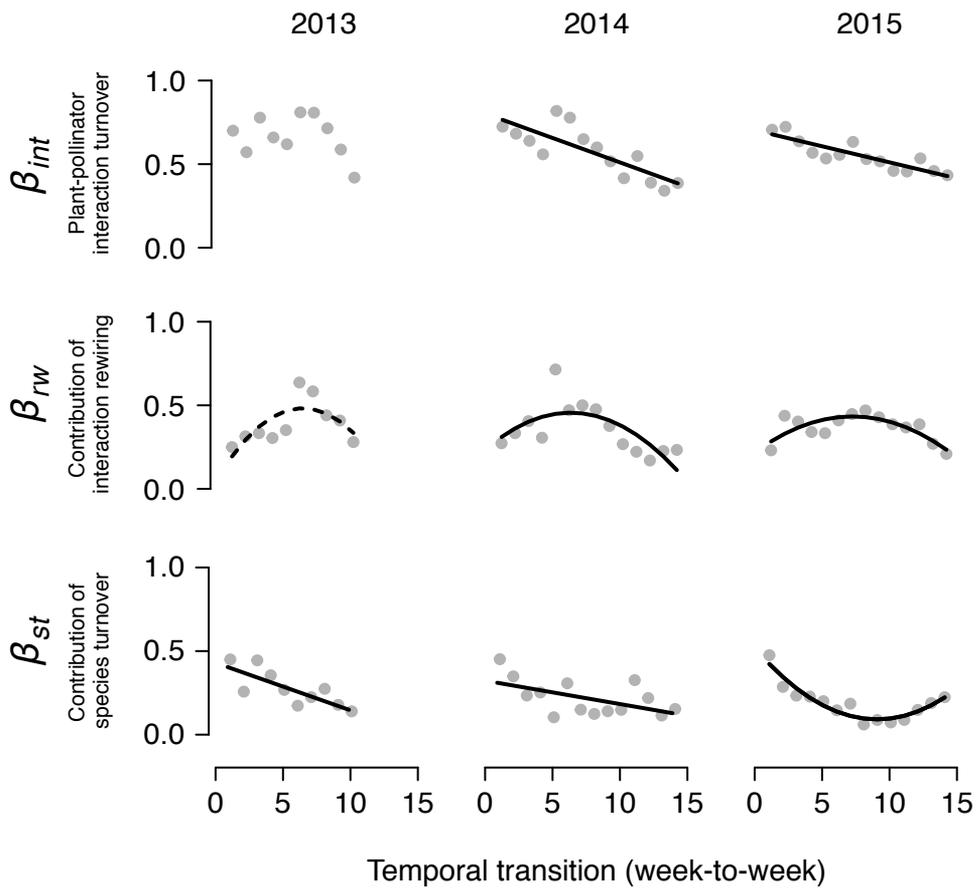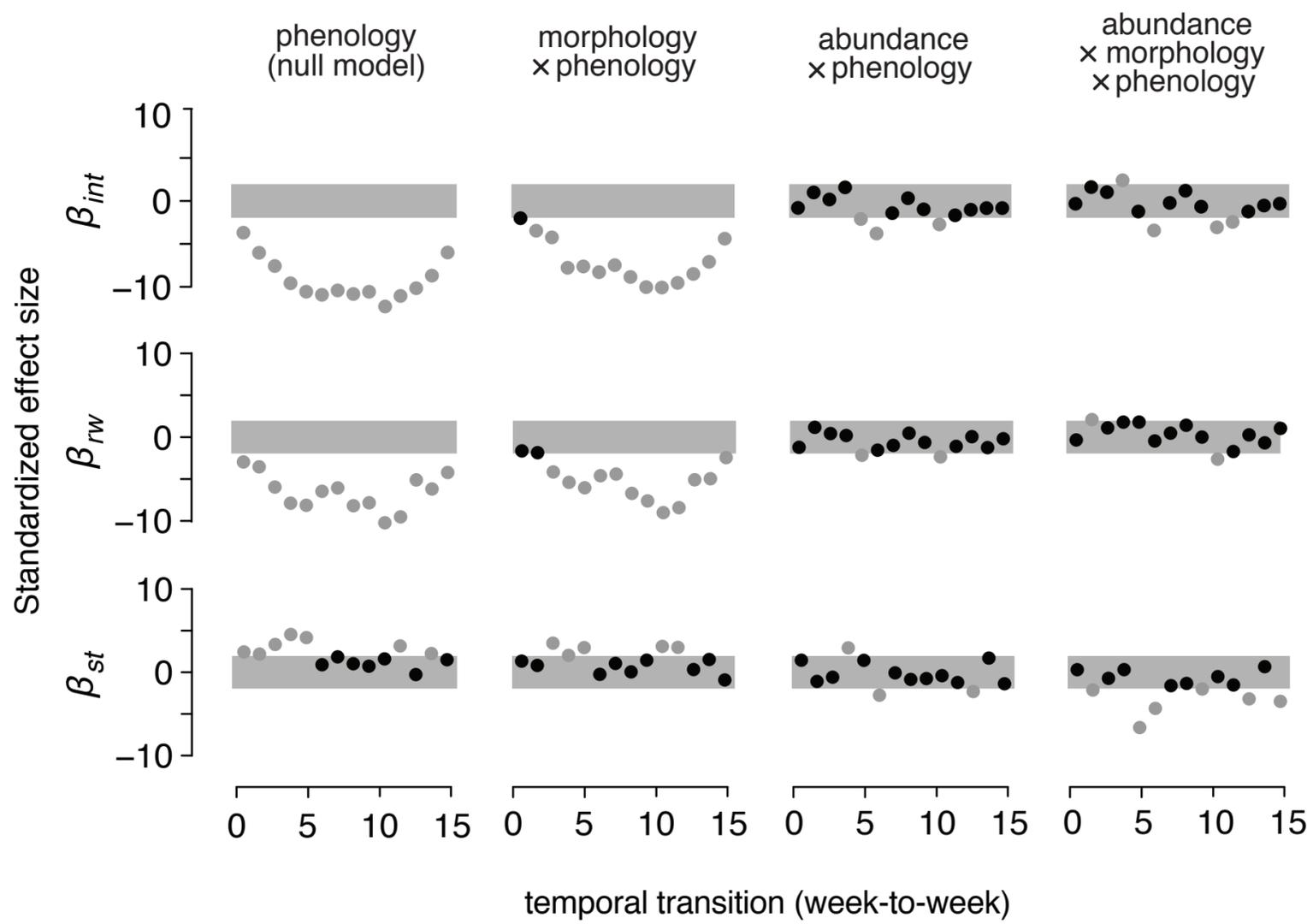

interaction rewiring (β_{rw})

effect of
species turnover (β_{st})

Figure 2
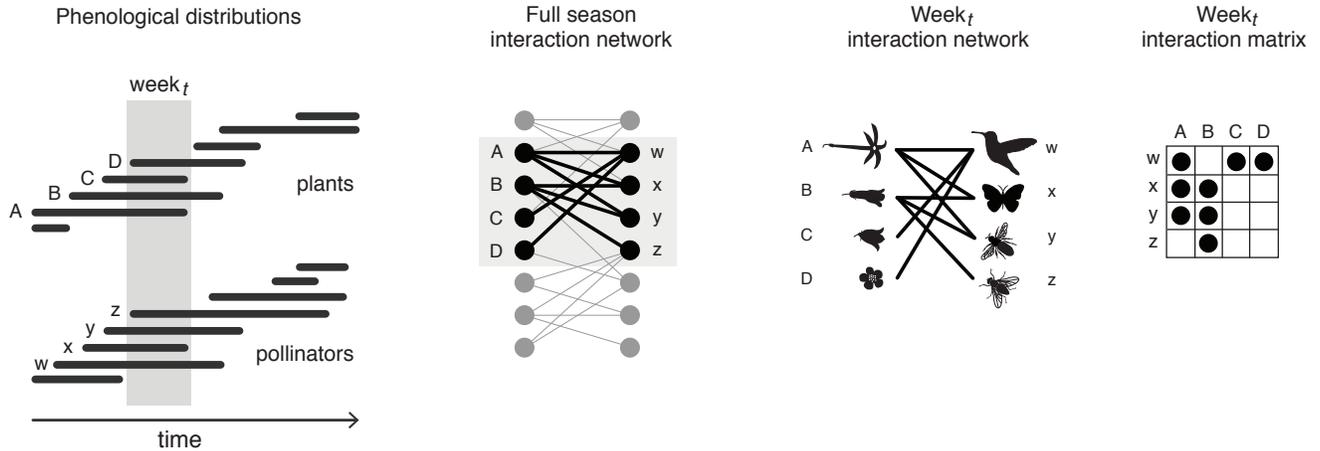
Figure 3



Temporal transition (week-to-week)

Figure 4

Legend:
- ±1.96 standard deviations of model values
- observed value within ±1.96 standard deviations of model values
- observed value outside ±1.96 standard deviations of model values

Box 1

Observed interaction patterns

| Phenological distributions | Full season interaction network | Week$_t$ interaction network | Week$_t$ interaction matrix |

Ecological constraints & model hypotheses

| | Week$_t$ interaction probability network | Week$_t$ interaction probability matrix | Week$_t$ simulated interaction matrices |

Phenology. Plants must bloom and pollinators must forage at the same time for them to interact. This model randomly assigns interactions between species that temporally co-occur within each week during the season with no further constraints; all temporally co-occuring species have equal probability of interaction.
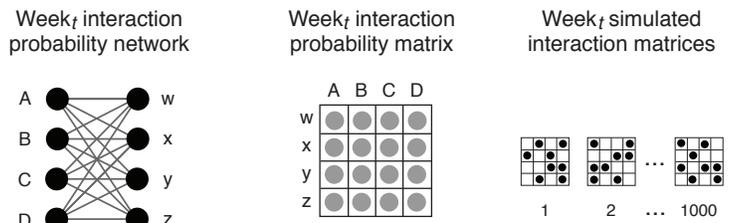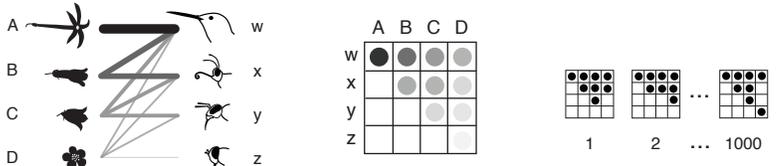
Abundance × Phenology. Interactions between a given pair of temporally co-occurring plants and pollinators may be more likely when the relative abundances of both species are higher.
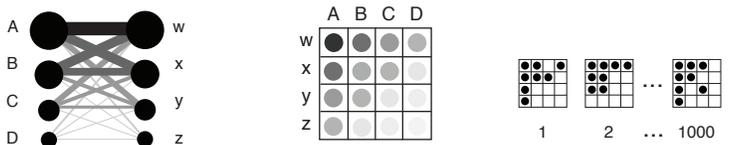
Morphology × Phenology. Temporally co-occur-ring plants and pollinators may be more likely to interact when their morphological traits enable the flow of resources or services from one species to the other.
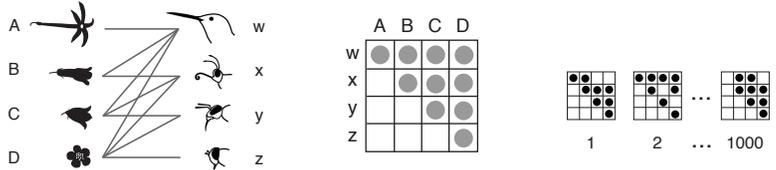
Abundance × Morphology × Phenology. The previous two model elaborations are not mutually exclusive: both abundance and morphology may simultaneously constrain which temporally co-occurring species interact. Here the probability of interaction is the joint probability of species relative abundances and morphological size matching.

Probability of interaction

low   high