1 **Density dependent interactions during growth mask the effect of interactions during**

2 **flowering in pollinator-sharing annual plants**

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4 Running head: Density dependence in growth and flowering

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Abstract

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12 Density dependent interactions are fundamental to community ecology, but studies often reduce

13 the complex nature of species interactions. In plant ecology, interactions during vegetative

14 growth and flowering are often considered separately, though both can affect reproductive

15 output. Here we use communities of annual flowering plants in the genus *Clarkia* to ask how

16 interactions during growth and flowering contribute to density dependence in plant seed

17 production, and if pollinator behaviors explain apparent patterns in plant interactions during

18 flowering. We measure seed set (seed number per ovule) and total fecundity (whole-plant seed

19 production) of *Clarkia* focal plants in experimental interaction plots with the effect of pollinators

20 experimentally removed through supplemental pollination or retained. We also observe

21 pollinator behaviors in the plots and experimental arrays to document pollinator preference,

22 constancy and joint attraction. During flowering, pollinators significantly changed the density

23 dependent effects of *Clarkia* interactions on seed set in 31% of species interactions, and these

24 changes corresponded to pollinator behaviors. Total fecundity, however, did not depend on

25 interactions between *Clarkia*; instead, earlier-flowering, non-*Clarkia* forbs limited total fecundity.

26 Our study shows that interactions during vegetative growth can preclude the effect of pollinator-

27 mediated interactions on fecundity by limiting potential reproductive output. Simultaneously

28 studying different types of species interactions allows for understanding the contingency of

29 ecological outcomes.

Introduction

Density dependent interactions shape population dynamics and community structure. In communities, co-occurring species are typically engaged in multiple types of interactions within and between trophic levels that can affect density dependence (e.g., plant-plant resource competition and pollinator-mediated plant interactions). Typically, studies aimed at quantifying the strength and magnitude of density dependent interactions either estimate the combined effects of multiple interaction types on performance or focus on a single interaction type (Losapio et al. 2019). For example, studies in plant community ecology estimate the effects of species interactions on coexistence (e.g. Angert et al. 2009, Godoy et al. 2014, Kraft et al. 2015, Bimler et al. 2018, Wainwright et al. 2019), but do not parse the contribution of plant-plant interactions during vegetative growth from the effects of pollinator-mediated interactions during flowering (but see Lanuza et al. 2018 for an example of how variation in pollination affects pairwise coexistence dynamics). Conversely, recent work in pollination ecology demonstrates that pollinator-mediated plant interactions are key to understanding seed production and density dependence (Lázaro et al. 2014, Benadi & Pauw 2018, Bergamo et al. 2020, Opedal & Hegland 2020, Phillips et al. 2020), but rarely do these studies investigate how interactions during vegetative growth also contribute to seed production. On one hand, the 'combined effects' approach cannot identify how interaction types combine to determine overall patterns in density dependence, which lowers its predictive value. The 'single interaction' approach, on the other hand, assumes that only one interaction type is relevant for reproductive output and therefore may overestimate its importance, which lowers the explanatory value. One way to unite these two approaches in plant ecology is to quantify density dependence arising from interactions during growth and flowering and determine their relative contributions to seed production. This should illuminate the ways in which interactions during these two life stages might combine to affect plant species' performance, population persistence, and coexistence (Bartomeus et al. 2021).

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57   For plant species that grow together and share pollinators, density dependent interactions

58   during vegetative growth determine plant survivorship, size, and potential fecundity (e.g., flower

59   and ovule production). Interactions during the reproductive stage determine whether flowers are

60   pollinated and produce seed. Whereas the mechanisms driving interactions during vegetative

61   growth have been widely explored (e.g. Dybzinski & Tilman 2007), pollinator-mediated

62   interactions during flowering are less understood. Two aspects of pollinator foraging behavior,

63   pollinator preference and constancy, have the potential to explain the effect of pollinator

64   mediated interactions on seed set. Preference reflects a pollinator's choice in visiting one plant

65   species over others when all are available and can introduce or intensify competition between

66   plant species by affecting the quantity of conspecific pollen that plants receive. Conspecific

67   pollen receipt and seed set for a particular plant should decline with declining pollinator

68   preference (Pauw 2012, Song & Feldman 2014, Benadi 2015). Constancy is the tendency of

69   pollinators to visit one species of plant in a foraging bout. If pollinators are inconstant, they can

70   introduce incompatible, heterospecific pollen to co-flowering plants. Heterospecific pollen

71   transfer is widespread in plant communities and is a form of reproductive interference between

72   plant species that decreases seed set (Morales & Traveset 2008, Arceo-Gómez et al. 2016,

73   Arceo-Gómez et al. 2019, Moreira-Hernández & Muchhala 2019). Plant interactions via shared

74   pollinators can also be facilitative. Patches of many co-flowering plants may attract more

75   pollinators than when growing alone, which can increase pollinator visitation rates and thus

76   pollination service; this phenomenon is known as joint attraction (Kunin & Iwasa 1996, Moeller

77   2004, Feldman et al. 2004, Bizecki Robson 2013). The potential for facilitation via joint attraction

78   is contingent on low interspecific pollen transfer, and thus high pollinator constancy. Lastly,

79   because different pollinator taxa exhibit different degrees of preference and constancy (Waser

80   et al. 1996; e.g. Eckhart et al. 2006, Barrios et al. 2016), the composition of the pollinator

81   community will also modulate the extent to which pollinator-mediated interactions affect plant

82   reproduction.

83

84   Studies of in natural plant-pollinator communities (Lanuza et al. 2018) and small mesocosms of

85   plant and pollinator species (Bartomeus et al. 2021) confirm the importance of examining plant-

86   plant interactions during both vegetative growth and flowering. However, no experimental study

87   has quantified the relationship between density dependence arising from interactions during

88   vegetative growth versus flowering, nor demonstrated the link between pollinator-mediated

89   interactions during flowering and pollinator foraging behavior. In this study, we do both in a

90   group of four sympatric and co-flowering winter annuals in the genus *Clarkia* (Onagraceae).

91   The four *Clarkia* species commonly co-occur throughout their range of geographic overlap

92   (Eisen & Geber 2018) and share bee pollinators specialized on the genus (MacSwain et al.

93   1973, Moeller 2005, Singh 2014), suggesting that they interact during both vegetative growth

94   and flowering. Furthermore, because *Clarkia* species flower late in the season after almost all

95   other annual plants in the area have senesced, the main interaction during flowering is through

96   pollinators that they share with each other (MacSwain et al. 1973).

97

98   To investigate the separate and combined effects of density dependent interactions during

99   growth and flowering on plant reproductive success, we use experimental pairwise interaction

100   plots of sown *Clarkia* and pollen supplementation via hand pollination (Figure 1). In the pairwise

101   interaction plots, interactions during growth affect plant size, and hence reproductive potential,

102   while interactions via shared pollinators during flowering affect pollination and seed set. The

103   pollen supplementation alleviates any effect of pollen limitation to seed set, allowing the effect of

104   interactions during growth to be separated from the effect of pollinator-mediated interactions

105   during flowering. We also investigate the link between pollinator behavior and *Clarkia*

106   interactions during flowering using pollinator observations in our experimental interaction plots,

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107   and in experimental floral arrays, to measure pollinator preference, constancy, and visitation

108   rate in response to floral density.

109

110   **Methods**

111   ***Natural history***

112   *Clarkia* is a genus of winter annual plants which germinate in late winter and grow over the

113   course of the spring. All *Clarkia* species are self-compatible, but 2/3 of the species are

114   predominantly outcrossing due to pronounced spatial separation (herkogamy) of anthers and

115   stigmas within flowers and temporal separation (protandry) between anther dehiscence and

116   stigma maturation (Lewis & Lewis 1955). All four *Clarkia* taxa in this study (*C. cylindrica* ssp.

117   *clavicarpa* (Jeps.) Lewis & Lewis*, C. speciosa* ssp. *polyantha* Lewis & Lewis*, C. unguiculata*

118   Lindl.*, C. xantiana* ssp. *xantiana* A. Gray, family Onagraceae) exhibit pronounced herkogamy

119   and protandry, and in the two taxa where outcrossing rates have been measured, outcrossing

120   rates range from 0.53-0.95 in *C. xantiana* ssp. *xantiana* (Moeller et al. 2012; Hove et al. 2016)

121   and 0.80-0.94 in *C. unguiculata* (Hove et al. 2016). In the remainder of the paper, we drop

122   subspecies designations and refer to the four taxa as species.

123

124   The four *Clarkia* species are sympatric in the southernmost portion of the Sierra Nevada

125   Mountain range. This region and our study are on Tübatulabal land known commonly as the

126   Kern River Canyon (KRC; Kern County, California, USA). We pay our respects to the

127   Tübatulabal people and recognize their past and ongoing connection to the land and its ecology.

128   The *Clarkia* in the KRC co-occur in communities of varying congeneric composition (from one to

129   four *Clarkia* species) embedded in low-elevation grassland, chaparral, and oak woodlands. In

130   their range of sympatry, *Clarkia* begin to flower in early May, and flowering lasts until mid- to late

131   June. All four species overlap in flowering time for about two weeks in late May and share a

132   group of bee pollinators specialized on the genus rather than any one species (MacSwain et al.

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133   1973, Singh 2014). Pollen limitation to reproduction has been found in *C. xantiana* (Moeller et

134   al. 2012, Hove et al. 2016) and *C. cylindrica* (Eisen et al. 2020), but not *C. unguiculata* (Hove et

135   al. 2016). Where present, pollen limitation is variable across sites and years (Moeller et al.

136   2012, Hove et al. 2016, Eisen et al. 2020). Research has shown that at least one species, *C.*

137   *xantiana*, has higher seed set when it grows in multi-species *Clarkia* communities than at sites

138   where it occurs alone, and that this effect is explained by increased visitation from shared

139   pollinators at multi-species sites (Moeller 2004).

140

141   We use two different experiments to understand how pollinator-mediated interactions factor into

142   interactions between *Clarkia*. First, we use an *in-situ* common garden experiment to determine

143   (1) how focal *Clarkia* seed production and total fecundity respond to variation in neighborhood

144   density; (2) how pollinator-mediated interactions contributed to patterns in observed density-

145   dependence; and (3) pollinator preference and joint attraction. Because pollinator constancy

146   was impossible to estimate in pairwise interaction plots due to low species richness, we

147   additionally recorded pollinator visitation in multi-species experimental arrays of *Clarkia* plants to

148   estimate pollinator constancy.

149

150   ***Experimental Design***

151   *Pairwise Interaction Plots*

152   Interactions during growth and flowering

153

154   To determine the combined effects of *Clarkia* growing and flowering together on reproductive

155   success, we used an experimental design closely modeled after work done to estimate

156   competitive interactions in annual plant communities (Godoy & Levine 2014, Godoy et al. 2014,

157   Kraft et al. 2015, Wainwright et al. 2019). In short, seeds of one *Clarkia* species were sown into

158   a plot as a competitive background, and then seeds of the same and different *Clarkia* species

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159   were sown as focal plants (Figure 1A, B). The identity of the background *Clarkia* species, and

160   the density of background *Clarkia* varied across plots. This allowed us to estimate the effect of

161   increasing density of background *Clarkia* on focal plant fecundity for each pair of focal species

162   and background species.

163

164   In the pairwise interaction plots, we measured two metrics of reproductive success on focal

165   *Clarkia* plants in response to neighborhood density. First, we measured seed set as the success

166   of converting ovules in a fruit into seeds (number of seeds per ovule or the proportion of ovules

167   that result in filled seed) (Figure 1C). This metric is determined by interactions that occur during

168   pollination. Second, we measured total fecundity, or the total number of filled seeds produced

169   by a plant (Figure 1C), determined by interactions over the entire lifespan of the plant. Total

170   fecundity is the product of the total number of ovules a plant produces, which is determined

171   during growth and represents a plant's maximum potential fecundity, and seed set, as described

172   above. In our experiment, both seed set and total fecundity are potentially determined by the

173   density and identity of background sown *Clarkia*.

174

175   To remove the effects of pollinator-mediated pollen limitation to seed set, we added conspecific

176   pollen to one flower on each focal plant (Figure 1B). Comparison of seed set in the pollen

177   supplemented fruit, whose flower received additional pollen, to seed set in a control fruit, whose

178   flower did not receive additional pollen quantifies the effect of pollinator-mediated pollen

179   limitation to seed set (Figure 1C). We refer to these two fruits as "pollen-supplemented" and

180   "control" fruits in the rest of the paper. Total fecundity calculated from the seed set of control

181   fruits reflects the combined effects of plant-plant interactions during growth and, via pollinators,

182   during flowering on plant reproductive success, while total fecundity calculated from the seed

183   set of pollen-supplemented fruits reflects only the effects of plant-plant interactions during

184   growth on reproductive success (Figure 1C).

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185

186   In late June through early July 2016, we set up 160, 1X1 meter experimental plots in a

187   community where all four species naturally occur in the Kern River Canyon (35°31'45N,

188   118°39'36W; Area = 0.57ha). We arranged plots in blocks of four, where plots were separated

189   by ~1/4 meters, and blocks were separated by ~1/2 meter. We cleared plots of all naturally

190   occurring *Clarkia* to prevent natural seed rain into the plots but did not disturb the soil. We also

191   left non-*Clarkia* forbs and grasses in place for two reasons: because it was infeasible to weed

192   them, and because grasses and forbs make up a substantial component of the vegetation;

193   removing them could disrupt interactions among *Clarkia*, and our intention was to study

194   interactions among *Clarkia* species in as natural a setting as possible (Table of common grass

195   and forb species in Table S1).

196

197   *Clarkia* seeds for the experimental sowing were collected at the study site as well as nearby

198   sites in the Kern River Canyon at the end of the 2016 growing season (late June). We used a

199   hand deawner (Hoffman Manufacturing, Inc, Fogelsville PA, USA) to break open the fruits and

200   extract seed, and a seed blower to separate seed from fruit walls. We sowed the seed into

201   experimental plots in October 2016 before the onset of winter rains that trigger germination.

202   Each block was haphazardly assigned a background *Clarkia* species, and each plot within the

203   block was haphazardly assigned one of five seeding densities (0, 0.04, 0.16, 0.64, and 2.56

204   g/m^2). For a given background seeding density, we chose to plant the same mass of seed

205   because the four species differ in seed size, and seed size correlates with adult plant size. Had

206   we planted equal seed numbers for a given seeding density, the background biomass, and

207   hence competitive effect, of large seeded species (*C. unguiculata* and *C. xantiana*) would have

208   been greater than that of the smaller seeded species (*C. cylindrica* and *C. speciosa*).

209   Background seeding densities were chosen based on previous estimates of naturally occurring

210   seed production at the field site (James, unpublished data). For *C. xantiana*, with an average

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211   seed mass of 0.025 mg (Gould et al. 2014), the five seeding densities corresponded to 0, 1600,

212   6400, 25600, and 102400 seeds per m^2. In total, our design yielded 20 background species X

213   density treatments, with eight plot replicates per treatment.

214

215   To establish focal plants of each species on which to measure reproductive output, we planted

216   twenty focal seeds into one of four designated locations (one for each species) in each plot. The

217   locations were delimited using 2.5cm radius cabone craft rings (CSS Industries, Inc., PA, USA)

218   secured in the ground with two 3.8cm fence staples. In the spring of 2017, we thinned the focal

219   seedlings in the cabone rings to one focal *Clarkia* plant. To prevent bias in selecting a focal

220   seedling, we left the seedling that was closest to the center of the ring and removed the rest. In

221   this same period, we counted the number of seedlings of background *Clarkia* species that had

222   germinated and the number of non-target grasses and forbs growing within a 5cm radius from

223   the focal seedling. We also weeded any seedlings of non-target *Clarkia* species in the

224   background of all plots.

225

226   During the two-week flowering stage in late May 2017 we haphazardly assigned one flower as

227   the control to receive no additional pollen, and another flower to receive additional conspecific

228   pollen on all focal plants with $\geq$ 2 flowers. We selected pairs of flowers that were at a similar

229   reproductive stage so that they were exposed to similar environments during pollination. To add

230   conspecific pollen to the pollen addition flowers, we harvested mature, dehiscing anthers from

231   3-4 flowers from naturally occurring conspecific *Clarkia* growing nearby by 8 am before

232   pollinators began foraging for the day. The pollen was applied to the freshly opened and

233   receptive stigmas on the selected flower of a focal plant immediately after harvesting the

234   anthers. Applying pollen to freshly opened stigmas ensured that they had not received any con-

235   or heterospecific pollen prior to applying our treatment. Application of pollen in this manner

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236   coats the stigma with >300 pollen grains, well in excess of the number of ovules (20-100) in

237   each ovary (M.A. Geber, pers. obs.).

238

239   We counted the number of fruits on each focal plant and collected the treatment fruits at the end

240   of the growing season. We also counted the number of filled seeds, aborted seeds, and

241   unfertilized ovules in each treatment fruit. We harvested all background *Clarkia* in each plot and

242   weighed the above ground biomass after drying plants at 65 C for 48 hours.

243

244   Pollinator visitation in the interaction plots

245   During the co-flowering period in 2017, we observed bee visitation in the pairwise interaction

246   plots to quantify pollinator preferences and joint attraction (Figure S1). Due to time limitation and

247   the fact that some plots did not have surviving focal plants, not all $1m^2$ plots were observed;

248   however, at least one plot from each block was observed during the co-flowering period.

249   Observations were made in ten-minute periods. Bees entering plots were identified to genus or

250   species and tracked as they made visits to *Clarkia* flowers. After the 10-minute observation

251   period, we counted and recorded the number and identity of open *Clarkia* flowers in the plot.

252

253   *Pollinator Arrays to assess constancy*

254   We assembled cut-stem arrays of the four *Clarkia* species to observe pollinator behavior during

255   the 2015 and 2016 *Clarkia* growing seasons. We cleared a 5 x 5m patch of all naturally

256   occurring *Clarkia* in the middle of the experimental site in late April before *Clarkia* plants had

257   started flowering. We constructed a grid with nodes at every 0.5m increment for a total of 100

258   nodes and buried a floral water pick at each node to fill with water and hold *Clarkia* stems.

259

260   Each array contained equal numbers of cut stems of all four *Clarkia* species planted at one of

261   four densities (in 2015: 10, 20, 40, or 100 stems; in 2016: 12, 24, 64, or 100 *Clarkia* stems)

262   (Table S1). This design allowed us to observe pollinator constancy across a range of plant

263   densities, holding diversity relatively constant. Because different bee species forage at different

264   times of day (Hart & Eckhart 2010), we ran most treatments in the morning and afternoon on

265   different days. For each array run, we gathered *Clarkia* stems before 8am to assemble in the

266   grid. We arranged *Clarkia* stems in the grid according to a randomly generated map of a

267   particular treatment, where locations in the grid were either left 'blank' or received one *Clarkia*

268   stem of a prescribed *Clarkia* species depending on the treatment density.

269

270   During the array runs, we identified and monitored bees as they entered and foraged in arrays.

271   When a bee entered the array and landed on a flower, one person called out the grid location of

272   the flower/bee, identified the bee to species or genus, and tracked the bee's movements until it

273   left the array, while another person recorded. At the end of each array run, we counted the

274   number of open flowers of each species and then disposed of wilted *Clarkia* stems. Rarely, we

275   re-used stems if they still had visibly turgid petals and leaves, though we never retained stems

276   for more than two runs. Array treatments lasted 40 or 60 minutes; many treatments in 2016

277   were stopped at 40 minutes due to wilting. We did not run the experiment on days when the

278   predicted peak temperature was below 21°C or wind was stronger than a light breeze.

279

280   ***Statistical Analysis***

281   All calculations and statistical analyses were performed in R (R version 3.5.2, R Core Team,

282   2018). We used two different analyses to understand the effects of density dependent

283   interactions on *Clarkia* seed production. We first investigated density dependent interactions in

284   the flowering stage by determining how *Clarkia* densities affected seed set (the number of

285   seeds per ovule in a fruit), and then investigated the density dependent effects of the

286   neighborhood on *Clarkia* total fecundity using glmms. We then analyzed the three pollinator

287   foraging behaviors that contribute to density dependence during the flowering stage.

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288

289   *Seed set*

290   For each fruit, we defined 'successes' as filled seeds, and 'failures' as the sum of unfertilized

291   ovules and aborted seeds. We built a set of candidate models to determine which combination

292   of four fixed effects factors best explained variation in seed set – the pollination treatment

293   (pollen supplemented vs. control), the focal *Clarkia* species identity, the background *Clarkia*

294   species identity, and the biomass of background *Clarkia* in the plot. We did not include non-

295   *Clarkia* grasses or forbs in this analysis because they flower before *Clarkia* during the

296   experiment, and therefore would not affect the pollination interactions of *Clarkia*. We also used

297   one random effect, the identity of the focal plant, in all models. We did not include random

298   effects for plot nested within block or for block because models with these effects were

299   unidentifiable. To avoid model dredging, we built a set of models relevant to our questions and

300   hypotheses with which to perform model selection (Table S3). We fit the data to all candidate

301   models using the lme4 package (Bates et al. 2015) and selected the model with the lowest AICc

302   (the best-fit model) for ecological inference. The most complex model included an interaction of

303   all four fixed effects and represents our prediction that successful seed set depends on the

304   density dependent effect of the background *Clarkia* on the focal *Clarkia* and varies according to

305   pollination treatment.

306

307   After identifying the best-fit model, we used estimated marginal means to determine the

308   predicted density dependent effect of background *Clarkia* on focal *Clarkia* seed set, with and

309   without pollen addition (package emmeans, Lenth 2019). Here, the effect of pollinators on the

310   interaction is the change in the density dependent effect of background *Clarkia* on focal *Clarkia*

311   seed set between the two pollination treatments (pollen addition and no pollen addition). If

312   pollinators change the strength or direction of the interaction, then the effect of increasing

313   background *Clarkia* biomass will be significantly different between the two pollination

13

314   treatments. We also tested if the estimated density dependent effect of background *Clarkia* on

315   focal *Clarkia* was significantly different from zero for both pollination treatments to examine if

316   and when pairwise *Clarkia* interactions were significantly different from zero (no effect of

317   increasing density). Finally, we estimated pollen limitation to successful seed set of each *Clarkia*

318   species as the difference in the probability of successful seed set between pollen addition vs. no

319   addition treatments.

320

321   *Total fecundity*

322   The second analysis focused on the total fecundity (total seed number) of focal plants in the

323   interaction plot. We calculated total fecundity as the product of fruit number on a plant, the

324   average number of ovules, seeds, and aborted seeds across the two sampled fruits (control and

325   pollen-supplemented), and the proportion of successful seeds in fruits under each pollination

326   treatment. This allowed us to calculate total estimated reproductive output of the whole plant

327   under the two treatment scenarios. We used generalized linear mixed effects models with a

328   Poisson error distribution to model total reproductive output with six potential fixed effects:

329   pollination treatment, focal *Clarkia* species identity, background *Clarkia* species identity,

330   background *Clarkia* biomass, and the number of forbs and number of grasses within 5cm of the

331   focal seedling. Forb and grass counts were centered and standardized to improve model

332   performance. We included two random effects: an observation-level random effect to account

333   for over-dispersion in the data, and plant identity. We again did not include random effects for

334   plot and block because such a model was unidentifiable.

335

336   As before, we built a set of candidate models relevant to the study with which to perform model

337   selection. The most complex candidate model included an interaction between the pollination

338   treatment, background *Clarkia* identity, focal *Clarkia* identity, and background *Clarkia* biomass,

339   as well as the additive effects of forb and grasses (Table S3). This candidate model represented

14

340   our prediction that whole-plant seed production depends on the density dependent effect of the

341   background *Clarkia* on the focal *Clarkia*, which is modified by the activity of pollinators. We

342   again selected the model with the lowest AICc score for ecological inference. With the best-fit

343   model, we used the Wald test to determine the significance of the predictors on total

344   reproductive output.

345

346   *Pollinator preference in the pairwise interaction plots*

347   We built an interaction network using the R package bipartite to understand pollinator

348   preference (Dormann et al. 2008). In the network, we only included the first visit of each

349   pollinator to a plot because each plot was dominated by a single background species such that

350   subsequent movements within a plot were likely to be to the same species (visits to focal plants

351   in plots against a common background species were rare). We first estimated d', or network

352   specialization, of the three most common pollinator taxa (Blüthgen et al. 2006). Higher values of

353   d' indicate higher values of pollinator specialization within the network, which we interpret as

354   taxon-level pollinator preferences for different *Clarkia*. We only included the three most common

355   pollinator taxa because all other pollinators accounted less than 2% of the sample (Table S2).

356   Next, we used a chi-squared test to compare the proportion of first-choice visits to each *Clarkia*

357   species with the proportion of each background plot type we observed. If bees have no

358   preference among *Clarkia*, then the proportion of first-choice visits to each plant species should

359   be equal to the proportion of plots we observed where that species was sown into the

360   background.

361

362   *Pollinator constancy in the experimental arrays*

363   To understand the potential for pollinator (in)constancy to affect pairwise interactions between

364   species, we built a 4x4 matrix for each array run, where rows represent the *Clarkia* species first

365   visited by a pollinator, and columns represent the species visited next in a sequence of two

15

366   sequential flower visits. On-diagonal entries in the matrix represent pollinator movements to the

367   same species of *Clarkia* (constancy), and off-diagonal movements between different species

368   (inconstancy). We divided the sum of all inconstant movements by the total number of moves in

369   arrays to quantify the proportion inconstant movements that might lead to incompatible pollen

370   transfer in *Clarkia*. We also tabulated the number of inconstant movements between each pair

371   of *Clarkia* species and conducted a chi-squared test to determine which pairs of species are at

372   higher risk for incompatible pollen transfer.

373

374   *Joint attraction in the pairwise interaction plots*

375   We used a generalized linear mixed effects model of visitation rate (visits per 10-minute

376   observation interval) with a Poisson error distribution to determine the potential for joint

377   attraction in the pairwise interaction plots. Log-transformed floral abundance was used as a

378   fixed effect in the model, and we included random effects for plot and observation period. Joint

379   attraction in this analysis would be an increase in visitation rate as a function of floral

380   abundance.

381

382   **Results**

383   ***The effect of interactions during growth and flowering on seed production***

384   We collected 371 fruits from 232 focal *Clarkia* plants in the pairwise interaction plots. The

385   uneven number of fruits collected was due to fruit loss from herbivory. We found that the best-fit

386   model of the probability of successful seed set included the four-way interaction between focal

387   *Clarkia* species identity, background *Clarkia* species identity, background *Clarkia* biomass, and

388   pollination treatment (Table S3). In other words, the best fit model of the probability of seed set

389   depended on the species-specific, density dependent effect of background *Clarkia* on focal

390   *Clarkia*, and this effect was modified by pollination treatments.

391

16

392   Pollination significantly changed the density dependent effect of background *Clarkia* on focal

393   *Clarkia* seed set in 31% of the interactions (five of 16 interactions: Figure 2, Table 1). In three of

394   these interactions, the density dependent effect was more competitive when the effect of

395   pollinators was included (no pollen addition treatment) than when the effect of pollinators was

396   removed (pollen addition treatment). In other words, pollinator-mediated interactions introduced

397   a competitive effect of the background *Clarkia* on focal *Clarkia* for the following three

398   background/focal species combinations: *C. unguiculata/C. xantiana; C. xantiana/C. unguiculata;*

399   and *C. cylindrica/C. xantiana*. Conversely, in the other two cases, the density dependent effect

400   of the background was more positive with the effect of pollinators than without; that is, pollinator-

401   mediated interactions introduced a facilitative effect of the background on focal *Clarkia* in *C.*

402   *speciosa/C. cylindrica* and *C. speciosa/C. speciosa* background/focal combinations. Of these

403   interactions, only two of the 32 density dependent effects of background *Clarkia* density on

404   *Clarkia* seed set were significantly different from zero. One was the competitive effect of *C.*

405   *unguiculata* on *C. xantiana* in the pollen addition treatment ($z = -2.49$, $p = 0.01$), and the other was

406   the competitive effect of *C. cylindrica* on *C. xantiana* in the no pollen addition treatment ($z = -$

407   4.89, $p < 0.001$) (Figure 2).

408

409   Finally, the average pollen limitation to successful seed set varied by focal species. Additional

410   pollen increased seed set in three of the four species: *C. unguiculata, C. cylindrica,* and *C.*

411   *xantiana*. The treatment effect was highest for *C. unguiculata*, indicating that pollination service

412   limited its successful seed set the most of the four species (Figure 3, Table S4). The treatment

413   effect was lowest in *C. speciosa*, which experienced slightly lower seed success under pollen

414   supplementation (Figure 3, Table S4).

415

416   The best-fit model for total fecundity included the additive fixed effects of (1) pollination

417   treatment and (2) the number of forbs surrounding the focal plant when it was a seedling (Table

418   S2). In other words, total fecundity of focal *Clarkia* plants was best predicted by the effect that

419   non-*Clarkia* forbs had on focal plants during growth, and wholesale pollen limitation in *Clarkia*

420   during flowering (Figure 4). Total fecundity strongly declined with increasing forbs (-0.77 ± 0.15

421   SE; Wald p-value < 0.001, Table S5) and was significantly higher in the pollen addition

422   treatment relative to the no pollen addition treatment (1.17 ± 0.20 SE; Wald p-value < 0.001,

423   Table S5).

424

425   ***Pollinator foraging behaviors***

426   *Preference and joint attraction in the interaction plots*

427   We performed 193, 10-minute observation periods and observed 446 pollinators in the *Clarkia*

428   interaction plots in 2017. The three most abundant pollinator visitors, in order of abundance,

429   were *Diadasia angusticeps* (Apidae), *Hesperapis regularis* (Mellitidae), and *Lasioglossum spp.*

430   (Halictidae) bees, which made up more than 99% of all observed pollinators (Table S2). The

431   preference of these three pollinators varied: *D. anguisticeps* exhibited the most specialized

432   behavior, visiting *Clarkia speciosa* to the near exclusion of the other *Clarkia* (d' = 0.79), followed

433   by *H. regularis* (d'=0.33), and *Lasioglossum sp.* (d'=17), both of which visited all four *Clarkia*, but

434   most commonly *C. xantiana* and *C. cylindrica* (Figure 5, Panel A).

435

436   Overall visitation to the different *Clarkia* was significantly different from the null expectation that

437   visitation to each species is proportional to the frequency with which we observed plots with

438   each background-sown *Clarkia* (χ^2(3)=104.47; p<0.001). The residuals of the chi-squared

439   analysis indicate pollinator preference for *C. speciosa* and *C. xantiana* (Pearson residuals = 7.6

440   and 2.4, respectively), and avoidance of *C. cylindrica* and *C. unguiculata* (Pearson residuals = -

441   3.7, -5.2, respectively).

442

443   *Pollinator constancy in the experimental arrays*

18

444   We performed 17 array runs with all four *Clarkia* species, observing 664 pollinator movements

445   from 418 bees across 2015 and 2016. Only 100 of the 664 movements (15%) were between

446   different plant species (and thus inconstant); therefore, *Clarkia* pollinators are by and large

447   constant foragers, even when equally exposed to all four *Clarkia* species. Interspecific

448   movements were significantly different from the null expectation of being evenly divided among

449   species pairs ($\chi^2(5)=65.56$; $p<0.001$). The species pairs where switching occurred most

450   frequently were *C. xantiana* and *C. unguiculata* and *C. xantiana* and *C. cylindrica*. These were

451   the only species pairs with Pearson residuals > 1 (Pearson residuals=6.45 and 1.55

452   respectively). Movements between individuals in these pairs of accounted for more than 60% of

453   inconstant movements in the dataset (Figure 5, Panel B).

454

455   *Pollinator Joint Attraction*

456   Pollinator visitation rate (in visits per 10-minute observation periods) increased with log floral

457   abundance in the interaction plots, indicating joint attraction (0.86±0.11, p<0.001; Figure 5,

458   Panel C).

459

460   **Discussion**

461   In community ecology, density dependent species interactions are the building blocks of

462   theories of community function and species persistence. In focusing on either the combined

463   effects of interaction types on species interactions or a single interaction type, studies often

464   overlook the multiplex nature of species interactions which can result in overly simplistic

465   predictions about plant community dynamics (Losapio et al. 2019, Bartomeus et al. 2021). In

466   this study we do our best to reconcile that plant interactions during both growth and flowering

467   can affect density dependent interactions between co-flowering plant species in a group of four

468   sympatric pollinator-sharing *Clarkia* species.

469

470 ***The importance of studying multiple life history stages to understand plant interactions***

471 We found that the contribution of pollinator-mediated interactions during flowering to total plant

472 fecundity is, above all, contingent on what transpires during growth. Whereas successful seed

473 set depended on pollinator-mediated *Clarkia* interactions (discussed below), the only density

474 dependent interaction explaining the total fecundity of focal plants was that of the non-*Clarkia*

475 forbs surrounding seedlings during growth. We anticipated that the effect of interactions during

476 flowering might change the direction and/or magnitude of density dependence independently of

477 the effects of growing together, which is how previous studies have typically framed the

478 question of how pollinators could affect plant coexistence dynamics (e.g. Benadi & Pauw 2018,

479 Bergamo et al. 2020, Lanuza et al. 2018, Lázaro et al. 2014, Rathcke 1983). In contrast, our

480 findings were surprising in two ways: first, the competitive effect exerted by plants during growth

481 limited total fecundity so strongly, by limiting total ovule production, that it masked the effect of

482 pollinator-mediated interactions on seed production per ovule during flowering. This

483 demonstrates that the significance of pollinator-mediated plant interactions for plant fecundity is

484 constrained by, rather than independent of, plant interactions during growth.

485

486 Second, density dependent competition during growth was exerted by non-*Clarkia* forbs on

487 *Clarkia* seedlings, whereas the density dependent effects of pollinator-mediated interactions

488 during flowering were exerted by *Clarkia* on *Clarkia*. This result demonstrates that the density

489 dependent effects of particular species (in this case, congeneric *Clarkia*) are potentially only

490 relevant during one, rather than all, life stages (Leslie 2005). Stage-dependent interactions

491 have been explored in animal communities in terms of ontogenetic niche shifts (Werner &

492 Gillam 1984, Bassar et al. 2017), and our results suggest that accounting for ontogeny may be

493 appropriate for understanding plant community coexistence as well. This result also highlighted

494 that studying *Clarkia* interactions without removing background grasses and forbs was revealing

495 of the ecology of the plant community. Had we taken a more traditional approach of studying

20

496   pairwise interactions without the rest of the annual plant community (by weeding, for example),

497   we may have concluded that interactions during flowering are strong drivers of *Clarkia*

498   interaction dynamics, because it would have been impossible to detect the density dependent

499   effects introduced by non-*Clarkia* forbs. Our results support the idea that studying species

500   interactions in a pairwise fashion can limit our understanding of community structure and

501   function (Abrams 1983, Chesson 2018, Levine et al. 2017, Mayfield & Stouffer 2017). One way

502   to incorporate such complexity into predictive models may be to leverage the growing body of

503   network theory (Godoy et al. 2018, Opedal & Heglend 2020, Valdovinos 2019, Losapio et al.

504   2019) to build models that capture how the stage-specificity and contingency of density

505   dependent species interactions affect population persistence and community structure.

506   Alternatively, the implications of our findings could be explored by using population models to

507   compare plant species persistence in communities where interactions during growth take

508   precedence in determining fecundity, versus communities where pollinator-mediated

509   interactions determine fecundity.

510

511   ***Pollinator-mediated interactions correspond to foraging behavior and affect seed set***

512   We have shown that pollinator-mediated interactions during flowering affect seed set at the

513   scale of the fruit and can be linked to the foraging behaviors of pollinators. This links two types

514   of pollination ecology: studies that show that pollinator foraging varies according to community

515   context (Eckhart et al. 2006, Lázaro et al. 2009, Valdovinos et al. 2013), and that pollinator

516   sharing among species affects focal plant performance (Bergamo et al. 2019, Moeller 2004,

517   Lanuza et al. 2018). Here we found that pollinators changed the positive, negative, or neutral

518   effect of background *Clarkia* density on seed set in five of 16 species interactions. A few

519   patterns stand out from this analysis. First, the *Clarkia* pairs that exhibited density dependent

520   interactions significantly different than zero (*C. cylindrica* background*/C. xantiana* focal*,* and *C.*

521   *unguiculata* background*/C. xantiana* focal) shared pollinators and represented the two species

21

522   pairs where pollinators were most likely to make interspecific (inconstant) visits (Figure 5, Panel

523   B). In one of these interactions, the significantly competitive effect of *C. unguiculata* density on

524   *C. xantiana* was neutralized when including the effect of pollinator sharing. To wit, pollinators

525   acted as a facilitative force and 'rescued' *C. xantiana* from the otherwise competitive effect of

526   increasing *C. unguiculata* density. This result may be explained by joint attraction, where

527   increasing *Clarkia* density in the plot attracted more pollinators overall, and that pollinators

528   preferred *C. xantiana* much more than they did *C. unguiculata*, resulting in *C. xantiana* receiving

529   a disproportionate amount of pollinator visits. In the other species interaction significantly

530   different from zero, pollinators introduced a competitive effect of *C. cylindrica* on *C. xantiana*.

531   We suspect this can be explained simply by incompatible pollen transfer between plants from

532   inconstant shared pollinators. Alternatively, the fact that pollinators alleviated competition in one

533   case but exacerbated competition in another could be explained by potential differences in how

534   different species tolerate incompatible pollen. For example, previous work has shown that

535   flowering plants, including *Clarkia*, exhibit species-specific sensitivity or tolerance to

536   heterospecific pollens (Arceo-Gómez et al. 2016, Arceo-Gómez et al. 2019); it is possible that

537   *C. xantiana* tolerates *C. unguiculata* pollen better than it does *C. cylindrica* pollen, resulting in

538   the differences in pollinator-mediated interactions.

539

540   In addition, the only species that exhibited a significant intraspecific pollinator-mediated

541   interaction was *C. speciosa,* which does not share pollinators to a great extent with the other

542   three species and experienced lower rates of inconstant visitation. In this instance, increasing

543   conspecific density trended toward competition when the effect of pollinators was removed but

544   trended toward facilitation when the effect of pollinators was retained. This suggests that joint

545   attraction can introduce a positive density dependent Allee effect in conspecific stands of

546   flowering plants, as suggested by a previous model exploring the relationship between pollinator

547   foraging, plant density, and plant performance (Kunin & Iwasa 1996). However, we would likely

548   not have found positive density dependence if not for *Diadasia angusticeps*, which has a

549   decided preference for *C. speciosa*, and was quite abundant in 2017. Without *D. anguisticeps*,

550   or in years of low abundance, pollination service to *C. speciosa* would likely have been lower in

551   both quantity and quality both because generalists can exacerbate negative reproductive

552   outcomes (Kunin 1993) and because competition for pollinator services generally increases in

553   plant communities when pollinators are scarcer (Lázaro et al. 2014, Ye et al. 2014).

554

555   Finally, the effect of *C. speciosa* backgrounds on *C. cylindrica* seed set trended towards

556   facilitative without the effect of pollinators but became less so with effect of pollinators; in this

557   case, pollinators introduced a competitive effect that dampened *C. speciosa* facilitation of *C.*

558   *cylindrica*. Because these two species do not share pollinators (Figure 4 Panel A), and there is

559   rarely switching between the two (Figure 4 Panel C), the competitive effect from pollinators is

560   likely due to low pollinator service to *C. cylindrica* when surrounded by *C. speciosa* (Table 1).

561

562   ***Plant-pollinator networks are predictive of plant average pollen limitation***

563   In our study, network information corresponded to patterns in plant species' average pollen

564   limitation. Whereas additional compatible pollen did not increase seed set in focal *C. speciosa*, it

565   did increase the average seed set in the three other species: *C. xantiana* experienced a small

566   boost in seed set with additional pollen, *C. cylindrica* a slightly higher boost, and *C. unguiculata*

567   saw the greatest effect of additional pollen on seed set. Thus, high pollinator preference and low

568   rates of pollinator sharing translated to high rates of compatible pollen transfer for *C. speciosa*.

569   In contrast, higher rates of pollinator sharing likely resulted in interspecific pollen transfer in the

570   three other *Clarkia* species resulting in pollen limitation, and the magnitude of pollen limitation

571   corresponded to pollinator preference. The promising implication of this result is that

572   comparatively easy-to-collect information from plant-pollinator interaction networks maps closely

573   to average pollen limitation in plant populations, which is more difficult to measure. Testing this

23

574   idea in high diversity plant-pollinator systems would help illuminate the potential relationship

575   between plant population level pollen limitation and plant-pollinator networks.

576

577   ***Conclusion***

578   In this work, we have endeavored to understand how density dependence during growth and

579   flowering, separately and in combination, determine plant seed production. We found that the

580   effects of species interactions in the flowering phase of life were explained by pollinator foraging

581   behaviors, but that these effects on total fecundity were overridden by interactions in the growth

582   phase. In total, this study shows how natural history work describing the complexity of biological

583   interactions can be linked to performance variables relevant to population and community

584   dynamics in ways that are revealing of community function. It may also help frame future

585   theoretical studies of stage-dependent multispecies interactions, as the larger task of identifying

586   the population and community-level ramifications of such interactions remains.

587

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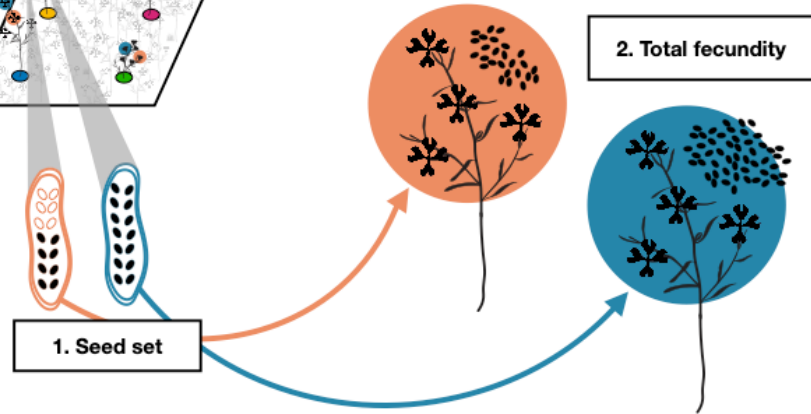
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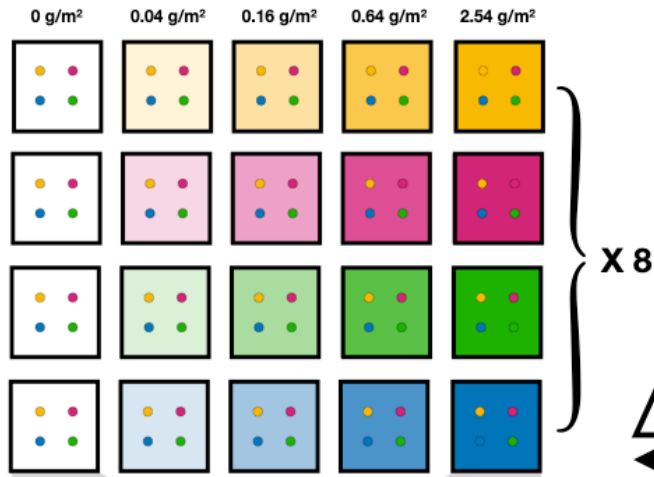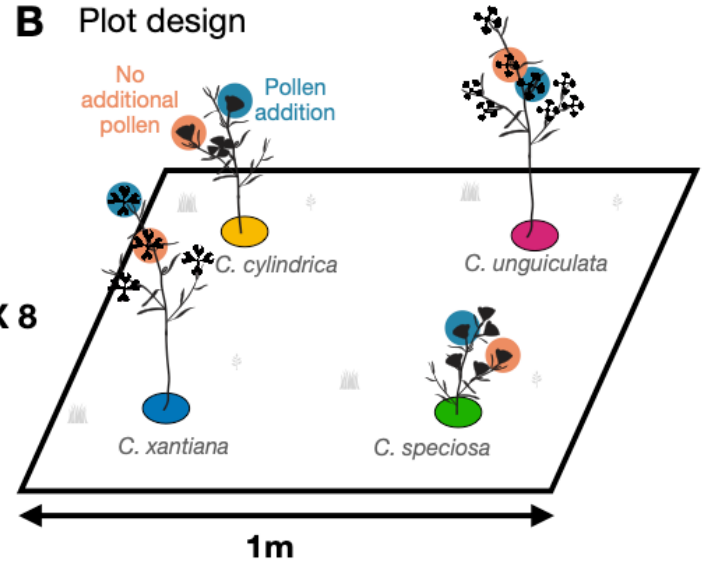
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735   Figure 1. Schematic of the pairwise interaction plot experiment. A. In experimental 1m x 1m

736   plots, seeds of one *Clarkia* species (yellow: *C. cylindrica*, green: *C. speciosa*, pink: *C.*

737   *unguiculata*, blue: *C. xantiana*) were sown in the background at a range of seeding rates from

738   0g/m2 to 2.54g/m2; 20 seeds of a focal *Clarkia* species were sown in one of the four cabone

739   rings secured in the four corners of the plot. Following germination, focal seedlings in the

740   cabone rings were thinned to a single individual. The schematic shows the range of

741   background treatments but does not depict the actual arrangement of plots in the field. Four

742   plots with a given background species and varying background seeding densities were grouped

743   into blocks. There were 8 replicate plots of each background species x background seeding

744   density. B. Depiction of pollination treatments on focal plants. In each plot, two pollination

745   treatments were applied to all focal plants that had 2 or more flowers. One flower was assigned

746   as the control and received no additional pollen while the second flower received additional

747   pollen from hand pollination. Pollen was collected from the appropriate *Clarkia* species from

748   plants growing at the site but outside of experimental plots. C. Two response variables were

749   measured on each focal plants 1) seed set equal to the ratio of filled seed to total ovules

750   (unfertilized ovules, aborted ovules and filled seed) in fruits from control and pollen-addition

751   flowers; 2) total fecundity equal to the product of fruit number, average total ovule number per

752   fruit, and average seeds per fruit in the two different pollination treatments.

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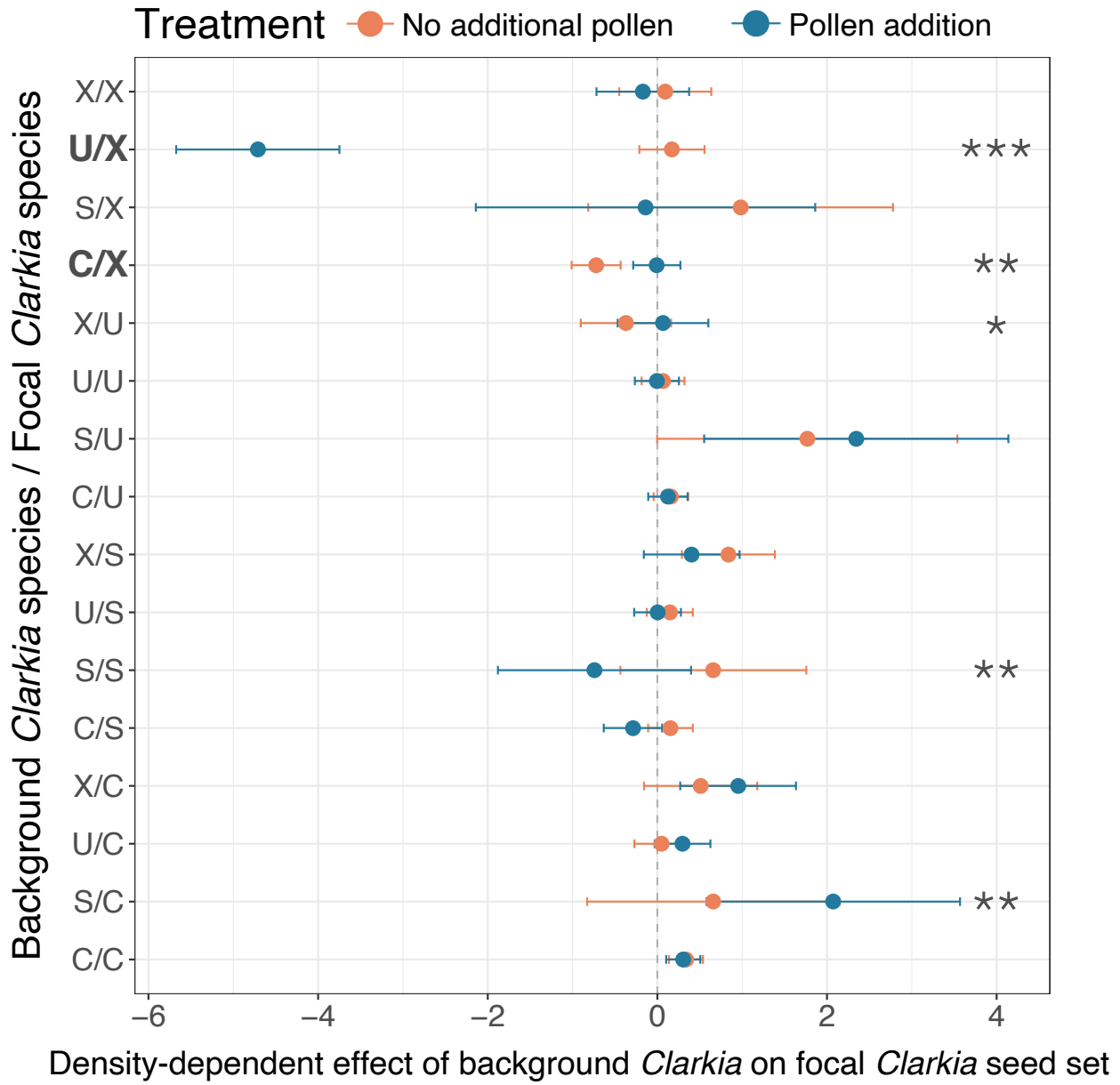
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756   Figure 2. The effect of increasing density of background *Clarkia* on the probability of an ovule

757   becoming a successful seed in focal *Clarkia*. The effect (slope) varies according to species pairs

758   and interactions over pollination. Each row is a different background/focal species combination.

759   Points indicate the estimated effect of increasing background species' density on the probability

760   of seed set for the focal species, and lines are standard errors. Negative values indicate the

761   probability of seed set declines with increasing background density (a competitive effect of

762   background *Clarkia*), whereas positive values mean that the probability of seed set increases

763   with background density (there is a facilitative effect of background *Clarkia*). Letters stand for

764   the first letter of the species name: C- *Clarkia cylindrica*; S- *C. speciosa*; U-*C. unguiculata*; and

765   X- *C. xantiana*. Blue points are the treatment where the effect of pollinators is removed (pollen

766   addition). Orange points are the treatment where the effect of pollinators is retained (no

767   additional pollen). Bolded combinations are those that include an interaction between

768   background density and pollination treatment that is significantly different from zero; stars

769   indicate a significant effect of pollination treatment on the interaction (*, $p<0.05$; **, $p<0.01$; ***,

770    $p<0.001$).

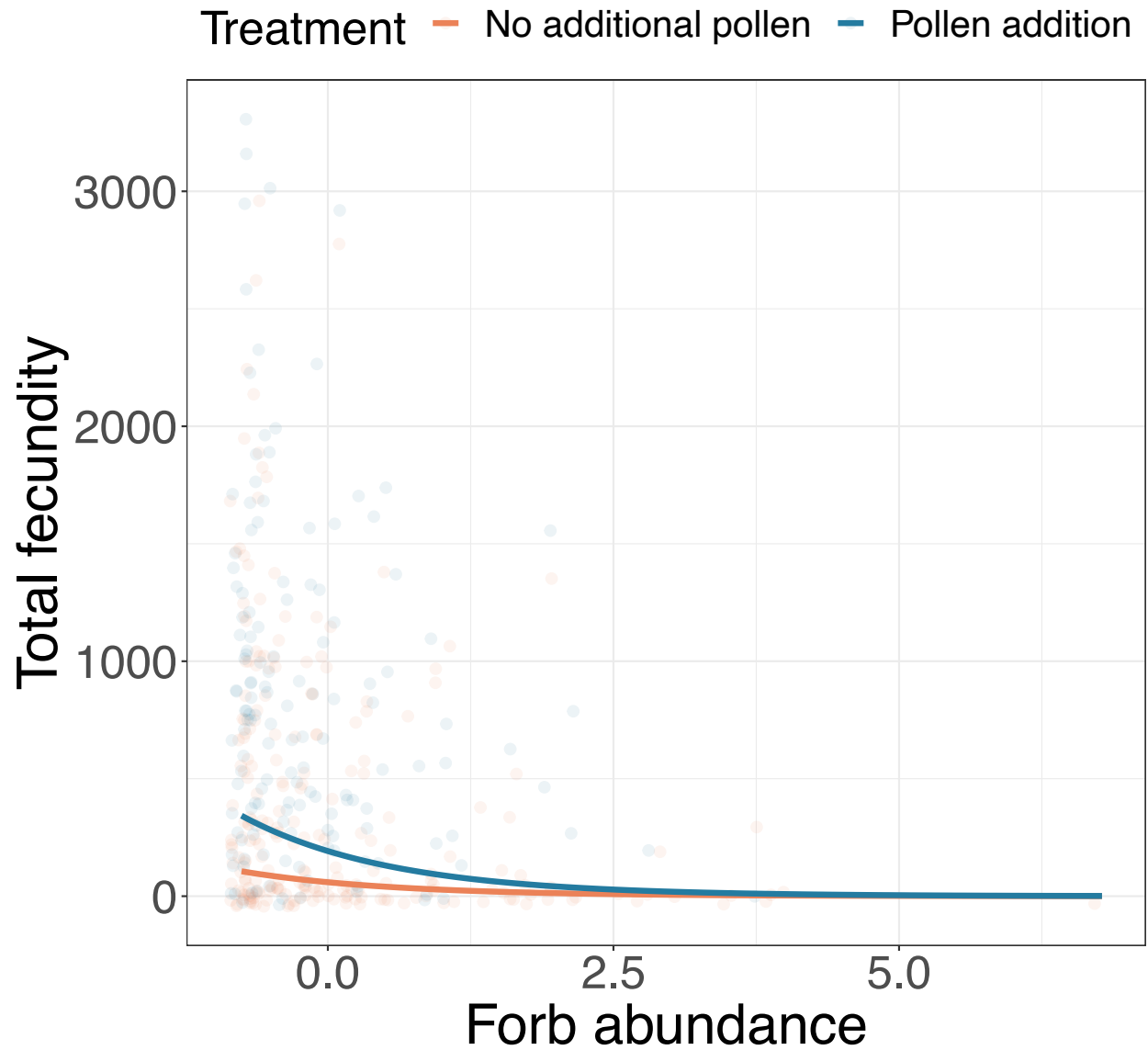771
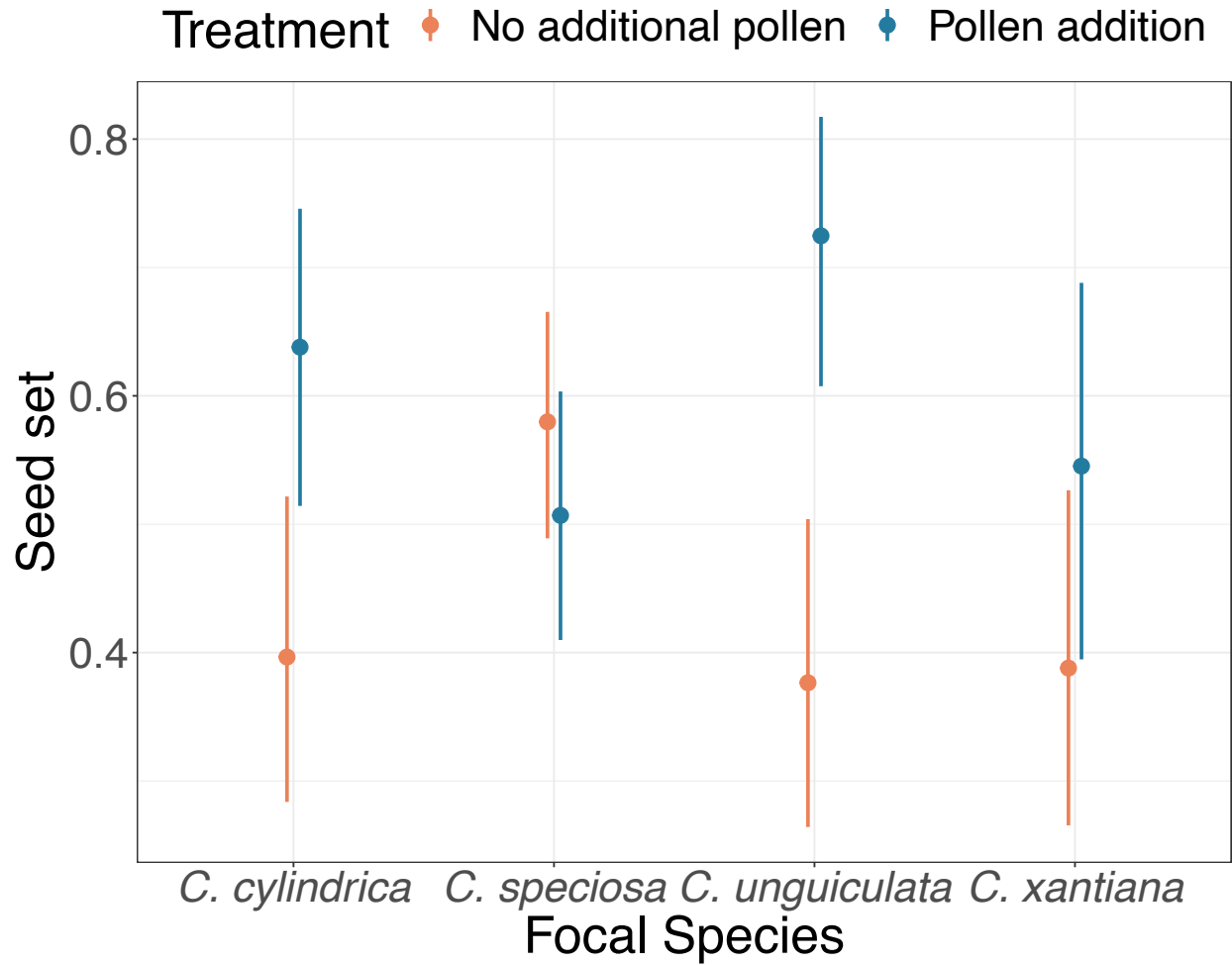
Figure 3. Species-specific probability of seed success in fruits for both pollination treatments. Points represent the marginal estimated average across all background species treatments at the mean background *Clarkia* density. Bars represent the 95% confidence interval for each estimate.
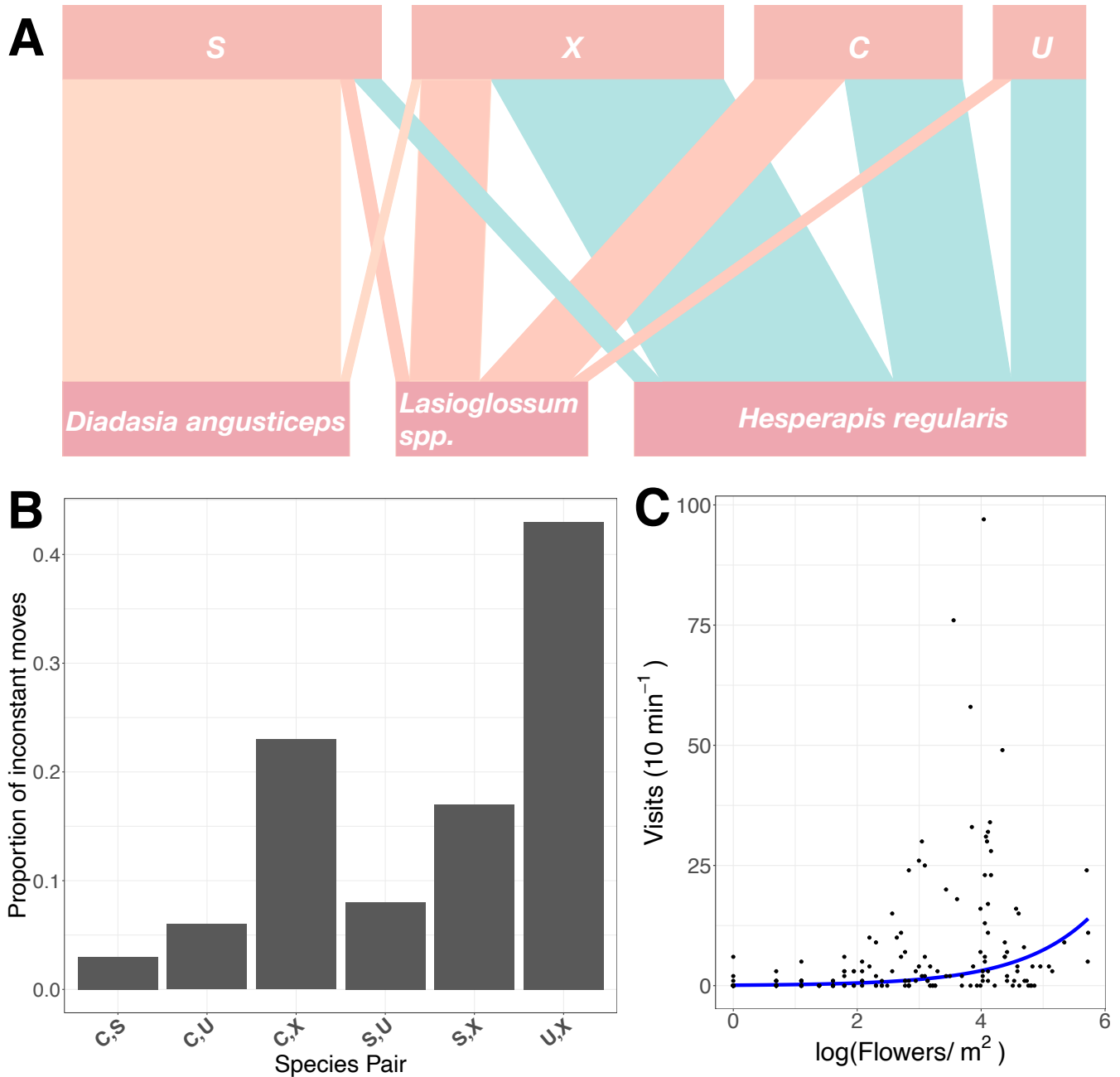
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Figure 4. Predicted full-plant seed set as a function of pollination treatment and the number of non-*Clarkia* forbs surrounding the focal as a seedling.

C: *C. cylindrica*; **S**: *C. speciosa*; **U**: *C. unguiculata*; **X**: *C. xantiana*

Figure 5. (A) The network of the plant and pollinator interactions observed during the pairwise interaction experiment. (B) The proportion of inconstant moves for each transition type between different *Clarkia* in the experimental arrays. (C) Rate of visitation as a function of floral abundance in the interaction plots.

787   Table 1. The effect of pollinators on seed set in the density dependent interactions between

788   *Clarkia* species (Figure 1), and the suggested explanation of the change in terms of observed

789   pollinator behaviors (Figure 3). Only statistically significant pairwise interactions are shown in

790   this table.

Background	Focal	Change in density dependent effect of background on focal ± SE	Interpretation	Behavioral Explanation	p-value
Clarkia unguiculata (U)	*Clarkia xantiana* (X)	4.88 ± 0.93	Pollinators alleviate the competitive effect of U on X	Joint attraction to higher densities, but pollinator preference for *C. xantiana*	< 0.001 (***)
Clarkia cylindrica (C)	*Clarkia xantiana* (X)	-0.72 ± 0.21	Pollinators exacerbate the competitive effect of C on X	Incompatible pollen transfer	0.0011 (**)
Clarkia xantiana (X)	*Clarkia unguiculata* (U)	-0.44 ± 0.21	Pollinators exacerbate the competitive effect of X on U	Pollinator preference for *C. xantiana* and incompatible pollen transfer	0.039 (*)

Clarkia speciosa (S)	*Clarkia speciosa* (S)	1.40 ± 1.48	Pollinators alleviate the competitive effect of S on S	Pollinator attraction to higher densities	0.0091 (**)
Clarkia speciosa (S)	*Clarkia cylindrica* (C)	-1.41 ± 0.53	Pollinators reduce the facilitative effect of S on C	Low pollinator overlap and therefore low pollinator service to C	0.0073 (**)

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