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10   Phenology and flowering overlap drive specialization in plant-pollinator networks

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54   **Abstract**

55   Variation in dietary specialization stems from fundamental interactions between species and their

56   environment. Consequently, understanding the drivers of this variation is key to understanding ecological

57   and evolutionary processes. Dietary specialization in wild bees has received attention due to their close

58   mutualistic dependence on plants, and because both groups are threatened by biodiversity loss. Many

59   principles governing pollinator specialization have been identified, but they remain largely unvalidated.

60   Organismal phenology has the potential to structure realized specialization by determining concurrent

61   resource availability and pollinator foraging activity. We evaluate this principle using mechanistic models

62   of adaptive foraging in pollinators within plant-pollinator networks. While temporal resource overlap has

63   little impact on specialization in pollinators with extended flight periods, reduced overlap increases

64   specialization as pollinator flight periods decrease. These results are corroborated empirically using

65   pollen load data taken from bees with shorter and longer flight periods across environments with high and

66   low temporal resource overlap.

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Introduction

The dietary specialization of an organism sits at the nexus of numerous fundamental processes in ecology and evolutionary biology. Dietary specialization helps define organismal niches (Kartzinel et al 2015), mediates migration and dispersal potential (Bommarco et al 2010; Boyle et al 2011), shapes inter- and intraspecific competition (Svanbäck & D.I. Bolnik 2007; deVries 2017), influences species persistence in the face of environmental disturbance (Wood et al 2019), and can affect rates of speciation and extinction (Thompson 1998). Even the simple assembly of the collection of organisms' dietary ranges in a community defines one of the major concepts in ecology, the food web. Therefore, identifying the drivers influencing dietary specialization provides fundamental steps towards understanding a multitude of essential biological questions.

Much of the progress in understanding dietary specialization in consumers comes from studies of herbivory (Kartzinel et al 2015), particularly on insects (Forister et al 2015). Using wild bees and plant-pollinator networks as our study system, we extend the scope of those studies to include mutualistic interactions. Mutualisms are ubiquitous ecological interactions in which participant species benefit each other (Bronstein 1994). Pollination, therefore, differs from other insect herbivory because of the reproductive benefit offered to both consumer and consumed species. Bees depend on removing pollen from flowers to rear their offspring, providing a pollination service at the same time (Westerkamp 1996). Pollination is also of particular interest given its role in supporting terrestrial biodiversity (Biesmeijer et al 2006) and agricultural output (Garibaldi et al 2013), a role threatened by widespread declines in both pollinators and insect pollinated plants (Biesmeijer et al 2006; Burkle et al 2013). Some studies have investigated 'specialization' in plant-pollinator networks, but based on floral visitation rather than the actual interaction of pollen collection (Dorado *et al*. 2011; King *et al*. 2013). Where pollen collection has been measured, it has often been in the context of building networks of pollen transfer (e.g. Lopezaraiza-Mikel et al. 2007; Alarón 2010), but these studies do not concurrently investigate or clarify the dietary niche of the pollinators themselves. In contrast, the pollen diets of wild bee pollinators have frequently been quantified, but often without a focus on the ecological drivers of dietary specialization (e.g. Wood & Roberts 2018). This knowledge gap emphasizes the need to investigate the biological processes explaining the realized specialization of pollinators within plant-pollinator networks that account for the actual interaction of pollen collection by pollinators.

Research on insect herbivores has largely focused on how adaptation to plant traits and defenses drives consumer concentration on specific phylogenetically related resources (Ali & Agrawal 2012; Hunter 2016). Though the imposition of a taxonomic hierarchy does not fully capture all similarities and

101   distances between host plants (Fordyce *et al*. 2016), grouping host plants by botanical family allows for

102   broad comparisons to be made between more and less generalized species (Forister *et al*. 2015). In

103   addition to phylogenetically inherent plant traits that are important for the dietary specialization of

104   herbivores, other drivers have been identified for consumers more generally (MacArthur & Pianka 1966;

105   Waser et al 1996, see Table 1, *Appendix S1.1*). Here, we expand on the fundamental effect of resource

106   density on a consumer's dietary specialization (MacArthur & Pianka 1966), not in a spatial context, but

107   temporally. This resource density is important in its interaction with consumer phenology. For long-lived

108   organisms (e.g., predatory vertebrates), opportunities to access a single resource type principally depend

109   on the resource's spatial distribution. If a single resource type is physically dense, then a predator can

110   specialize on it without needing to turn to alternatives, whereas if it is patchily distributed then a strategy

111   of specialization is less optimal. However, for a comparatively short-lived organism like a bee whose

112   adult flight period (its de facto lifespan in the context of resource gathering for reproductive investment)

113   can be measured in days, the distribution of a resource type in time is also a critically important

114   determinant of accessibility. A plant species that flowers for 30 days is a *de facto* dense, continuously

115   available resource for a co-occurring bee species whose flight period lasts for only 25 days. However, this

116   same plant species that flowers for 30 days can be considered to be sparse and patchily distributed for a

117   separate bee species which flies for 90 days. The temporal pattern of flowering can therefore be

118   considered analogous to resource density, variations in which will be acutely experienced by short-lived

119   organisms. These ideas have proven influential (e.g., Robinson & Wilson 1998; CaraDonna *et al*. 2017)

120   and aspects of phenology have been implemented in network models for the sake of other ecological

121   questions (e.g. Encinas-Viso et al 2012), but direct theoretical and empirical validation is required to

122   solidify our understanding of phenological drivers of diet breadth.

123   Expanding upon this idea of temporal density, we hypothesize that the degree of temporal overlap

124   in the availability of different resources (flowering overlap among co-occurring plant species) in

125   combination with the fundamental life-history phenologies of bees (adult flight period) can influence

126   realized dietary specialization (i.e. their actual choices made under real-world conditions). Applied to

127   plant-pollinator systems, we hypothesize that increased flowering overlap will reduce the dietary

128   specialization (i.e. increase generalization) of pollinators with short flight periods, but not necessarily

129   those with long flight periods (Fig. 1). Pollinators with short flight periods will experience markedly

130   different resource availability based on the degree of temporal overlap of co-flowering species. High

131   flowering overlap will allow pollinators with short flight periods access to a greater number of options

132   available concurrently while low overlap will restrict options. Pollinators with long flight periods are

133   nominally less constricted by the temporal overlap of co-occurring resources, theoretically having access

134   to the same number of options over the course of their flight periods regardless of the degree of overlap

135 on average (Fig. 1). Importantly, our hypothesis does not indicate that flight period will necessarily

136 correspond with and predict being more or less specialized *ceteris paribus*. Instead, it describes how

137 temporal resource overlap will influence dietary specialization as a function of pollinators' flight periods

138 when considered as an average response across a community.

139   We employed a multi-faceted approach to test our hypothesis. First, we leverage advances in

140 modeling adaptive foraging in ecological networks (Valdovinos et al 2013; 2016) to directly address the

141 phenological mechanism driving dietary specialization across different pollinator flight periods. Second,

142 we utilize our intercontinental pollen load dataset of bees with a short flight period (genus *Andrena*) and

143 bees with a long flight period (genus *Lasioglossum*) from both a highly seasonal and a less seasonal

144 environment which function as low and high temporal resource overlap treatments, respectively, to

145 empirically test the effects of overlap. Although the modelling and empirical approaches differ

146 quantitatively, qualitatively comparing their outputs allows for independent assessments of the

147 mechanism proposed in our hypothesis (Fig. 1).

148

149 **Methods**

150

151 **Model Development**

152   Plant-pollinator network models have two major components, the network structure and the

153 dynamics that occur on those networks. The networks used in this study were grouped into size classes

154 with plant-pollinator ratio based on an empirical pollination network (see *Appendix S1.2*). Before

155 simulations, networks were fully connected to give each pollinator population the maximum within-

156 model range of dietary options without a priori restrictions (Fig S1). Namely, the adjacency matrices were

157 filled entirely with 1's, indicating all potential interactions are initially considered possible (see *Appendix*

158 *S1.2*). The realized interactions within simulations emerge from the population, mutualistic, and adaptive

159 foraging dynamics occurring on the network structure which were implemented based on existing work

160 (Valdovinos et al 2013; 2016). In summary, the model mechanistically models pollination as a consumer-

161 resource interaction by separately accounting for vegetative density and floral rewards consumed by

162 pollinators. The model's time-dependent variables track the adaptive dynamics of each plant species'

163 population dynamics ($p(t)_i$), each animal pollinator species' population dynamics ($a(t)_j$), each plant

164 species' pool of floral rewards ($R(t)_i$), and the adaptive dynamics of the per-capita foraging effort

165 preferences of each pollinator species j for each plant species i ($\alpha(t)_{ij}$; henceforth referred to as foraging

166 effort). Visits of pollinator j to plant i (V_{ij}) are consumer interactions between pollinator j and plant i's

167 floral rewards. These visits (V_{ij}) result in mutual reproductive benefit, and pollinator effort for any given

168 plant changes dependent upon that benefit. Specifically, pollinator j's foraging effort on plant i (α_{ij})

169   increases whenever pollinator j's reward intake from plant i, $f_{ij}(R_i)$, is higher than its average reward

170   intake from all the plants (subset P_j) constituting its diet, $\sum_{k \in P_j} \alpha_{kj} f_{kj}(R_k)$. Please see the full description

171   of the underlying dynamic model in *Appendix S1.2.*

172   Temporal plasticity in network connectivity was implemented by incorporating time dependent

173   phenology functions to modify the rates controlling interactions between plants and pollinators in the

174   network. These functions are formed using modified sinusoidal wave functions which produce unique

175   phenologies for every plant i (T_{p_i}) and animal pollinator j (T_{a_j}). In flowering plant species, the phenology

176   function T_{p_i} (see *Appendix S1.3*) modifies the phenology of floral reward production (R_i). The T_{p_i}

177   function controls the flowering of plant i, such that plant i only produces floral rewards when $T_{p_i} > 0$ (the

178   flowering period), otherwise reward production is 0 during interceding periods of inactivity we dub

179   "break periods." Similarly, in animal pollinators, all visitation rates (V) are modified by the phenology

180   function T_{a_j} such that pollinators are only foraging during their flight period and not during interceding

181   break periods (see *Appendix S1.3*). The T_{a_j} function also modifies α_{ij} such that foraging effort

182   preferences only change during active flight periods. With this framework, any active flying pollinator

183   and flowering plant can only potentially interact during phenological co-occurrence (Fig. 2). Note that

184   even overlapping phenologies between pollinators and plants only produce potential interactions as

185   adaptive foraging drives pollinator foraging choices among possible resources.

186   Scaling up this framework to multiple interactions introduces temporal plasticity in network

187   topology through organismal phenology as unique potential interactions activate and deactivate across

188   time (Fig. S5). The phenology functions (T_{p_i} & T_{a_j}) were designed to be sufficiently malleable with only

189   simple user inputs that facilitate direct control over the temporal availability of specific resources and the

190   activity patterns of the animal pollinators over time in simulations (see *Appendix S1.4*, Fig. S1-S5). These

191   inputs are the duration of flowering/foraging periods and a parameter dictating the length of time

192   interceding between subsequent periods of flowering or foraging, i.e., the break periods (see Table S2 &

193   S3; Fig. 2, S4 & S5). With these inputs, we created a range of unique plant phenologies through different

194   combinations of durations for flowering periods and interceding non-flowering periods. These

195   combinations created a wide range of flowering overlap among the plant species against which to test our

196   hypothesis (see Fig. S12; *Appendix S1.8*). The quantitative degree of overlap in co-occurring floral

197   resources can be measured in simulations as the Total Resource Overlap (TRO) of the entire plant

198   community, and the Averaged Resource Overlap (ARO) per plant species by integrating overlapping

199   resource curves (R_i) within simulations (Fig. S12). See Metrics section and *Appendix S1.8* for complete

200   details. In animal pollinators, phenological activity patterns are set up to produce a range of different

201   flight period lengths separated by differing lengths in between flight periods.

202   Each flowering (flight) period and intervening period of inactivity between repeating flowering
203   (flight) periods is of equal and constant duration per plant (pollinator) per single simulation. In other
204   words, all plants share flowering period and break period lengths and all pollinators share flight period
205   lengths per simulation. Spacing on the timeline is as dictated in *Appendix S1.3*. Additionally, all plants
206   and the inherent phenologies of pollinators and plants do not change within simulations, only between
207   simulations as different phenology parameters are used to create different phenological conditions.
208   Simulations use three fully connected bipartite network frameworks across 2072 combinations of plant
209   and pollinator phenologies to produce 62160 unique networks used to model over 22 million plant-
210   pollinator interactions (see *Appendix S1.4*).

211

212   **Choice of model bee genera & regions for empirical study**

213   The two bee genera *Andrena* and *Lasioglossum* were selected as two contrasting models for this
214   study (*Appendix S1.5*). They are the two largest bee genera by number of described species (Ascher and
215   Pickering 2021), and are well-represented in Holarctic bee communities, allowing for comparison across
216   biogeographical regions within and between two distinct lineages each with a shared evolutionary history.
217   Restricting the analysis to two large bee genera controls for potentially confounding effects of
218   phylogenetic position (Resende *et al*. 2007) while retaining statistical power through the potentially large
219   sample size deriving from the high generic richness. The majority of *Andrena* and *Lasioglossum* species
220   generally lack morphological adaptations for pollen harvesting and therefore favor shallow, open, and
221   radially symmetrical flowers, and within each genus have similar dispersal abilities, controlling for the
222   effects of resource accessibility and the cost of travel (see *Appendix S1.5* for additional detail). However,
223   the genera pursue different life history strategies, with *Andrena* following a solitary lifecycle with a short
224   foraging period typically lasting a few weeks (Westrich 1989; Else & Edwards 2018). *Lasioglossum*
225   species contain a mixture of solitary and social species (Brady et al 2006), but both types have longer
226   foraging periods, typically lasting several months (Westrich 1989; Else & Edwards 2018). *Andrena* and
227   *Lasioglossum* can therefore be considered to have functionally 'short' and 'long' foraging periods,
228   respectively (*Appendix S1.7*).

229   *Andrena* and *Lasioglossum* were collected from two biogeographical regions, Britain and
230   Michigan, USA. These regions are both found in the Holarctic and so have broadly similar floral
231   communities composed of the same major botanical families (Stace 2010; Voss & Reznicek 2012).
232   Importantly, they differ noticeably in their levels of temporal flowering resource overlap. The highly
233   seasonal continental climate of Michigan (Beck et al 2018) produces lower degrees of overlap and highly
234   seasonal flowering communities, while the more mild oceanic climate of the British Isles and its

235 consistent temperatures produces longer, overlapping flowering times among plant species (see *Appendix*

236 *S1.6* for additional detail and justification).

237   Restricting the analysis to the same two bee genera across two biogeographical regions that differ

238 most strongly in their temporal resource overlap rather than botanical composition, therefore, controls for

239 possible effects of phylogenetic structuring at both the bee and the plant level. This allows us to evaluate

240 the relative importance of foraging period and environmental seasonality in structuring a generalized

241 foraging response in wild bees.

242

243 **Selection and standardization of pollen load data**

244   Pinned *Andrena* and *Lasioglossum* specimens with pollen loads were selected from museum and

245 contemporary non-standardized collections, with the majority (81.9%) collected between 2013-2018.

246 Specimens were collected from 265 Michigan sites and 289 UK sites (see *Appendix S1.7*). Because of the

247 high variability in occurrence between bee species in wild communities in general (Williams *et al.* 2001)

248 and plant-pollinator networks specifically (Burkle & Alarcón 2011; Jordano 2016), capturing an

249 equivalent number of specimens for each species from a similar number of sites within a similar time

250 period is functionally unfeasible for all but the most abundant species. In order to maximize species-level

251 replication and taxonomic representation, an approach favouring the greatest number of samples was

252 adopted without restrictions based on collection locality or date. A total of 2,609 suitable specimens from

253 118 species (21.9±3.8 samples per species) were analysed, representing between 30-63% of the genus-

254 level fauna of each region. Pollen was removed from specimens and analyzed following standard

255 methodology (Wood & Roberts 2018). Pollen was identified to the lowest possible taxonomic level using

256 light microscopy, in most cases to genus (see *Appendix S1.7* for additional detail). A minimum sample

257 size of five pollen loads was selected as the cut-off for inclusion in the study.

258

259 **Metrics**

260   Within the model, temporal resource overlap between any two flowering plant species p_1 and p_2

261 in a simulation is defined as the shared area under their respective resource curves R_1 and R_2 during the

262 simulation. This was quantified as both the sum of all overlap across the entire plant community for total

263 resource overlap (TRO) and average resource overlap (ARO) per individual plant species (see *Appendix*

264 *S1.8*). Note that resource overlap is not necessarily synonymous with the length of flowering periods. Per

265 unit time, overlap can emerge regardless of flowering period length, so long as flowering periods co-

266 occur in time.

267   Dietary specialization was calculated using two metrics, Deviation from Generalism (DFG) and

268 the Coefficient of Variation (CV). Both metrics are calculated at the level of pollinator species due to

269 potentially unrepresentative effects of flower constancy that make calculation at an individual level

270 unrepresentative of species-level preference (see Appendix S1.8). When used for simulated pollinators,

271 both metrics take measurement of relative allocation of foraging effort (α_{ij}) per pollinator species across

272 all potential resource options as input to produce a per pollinator species dietary specialization score. The

273 DFG metric is the normalized summation of all pairwise differences of pollinator foraging effort on

274 potential floral resources (*Appendix S1.8*, Table S4). It ranges from 0 (perfect generalist) to 1 (perfect

275 specialist), regardless of botanical species richness. When used for pollen load data, the quantity of pollen

276 collected from each resource (grouped by either botanical family or botanical genus) is used in place of

277 the foraging effort, under the assumption that greater quantities of pollen collected from any particular

278 plant group correspond to higher foraging effort on that group. Importantly, the algorithm used to

279 calculate our DFG score is a holistic accounting for every possible interaction and compares all possible

280 interactions among each other to accumulate a score. This means that for each bee species, their realized

281 collection patterns are compared to all resources collected by all bees in either the Michigan or UK

282 datasets, therefore geographically partitioning the comparison between regions. Specifically, *Andrena* and

283 *Lasioglossum* (combined) collected from 44 and 37 botanical families in Michigan and the UK,

284 respectively, and 91 botanical genera in both Michigan and the UK (see Table S8). We investigate the

285 effects of organismal phenology and flowering resource overlap by comparing realized collection patterns

286 to all plant taxa in the dataset, some of which will only be available during specific time periods and

287 access to which is affected by flight period length.

288 The DFG metric may not be the best option in all circumstances. It functions best when available

289 data can convincingly represent all possible foraging options because DFG calculates specialization

290 considering all potential foraging options. This functions especially well in the model, but it is not

291 necessarily guaranteed in empirical surveys. Therefore, we also employed the CV as our second metric of

292 specialization (also termed the Species Specialization Index; Julliard et al 2006). This well-known

293 summary statistic was applied to our model's output foraging effort (α_{ij}) per individual pollinator

294 population, whereas in the empirical data we take the CV of the percentage of pollen loads collected

295 across plant groups per region (as for DFG). Higher CV values occur with values for specific plant taxa

296 that deviate most strongly from other values, indicating specialization (Fig. S13). As a metric of

297 specialization, the CV will increase when there are a limited number of extreme values. It performs the

298 same whether or not the full range of possible resource options for foraging pollinators is known and it

299 can function as a means of inter-regional comparison given the similar number of resource options

300 between our sampling regions. The relationship between the two metrics is positive monotonic but non-

301 linear (Fig. S13) showing that the two metrics relate to the measurement of specialization differently as

302 desired. With model results, both DFG and CV were applied to final foraging levels at the end of

303   simulations (DFG_{End} & CV_{End}), as well as to the average foraging levels across the last 1000 time steps (

304   DFG_{Avg} & CV_{Avg}; see *Appendix S1.8* for additional details). In contrast, for the empirical pollen load data,

305   metrics were applied categorically by bee genus and region.

306

307   **Statistics**

308   Statistical analysis was conducted in R 3.3.2. Regression analysis on model diet breadth results

309   was done using the lm function and measured with traditional R^2 metric when working with DFG_{End}

310   results or with beta regressions (betareg package in R) and the pseudo R^2 metric when working with DF

311   G_{Avg}. When measuring diet breadth results with CV_{End} or CV_{Avg}, log-linked gamma regressions were

312   completed with the mgcv package and the amount of deviance accounted for by the regression was

313   measured with the D^2 metric. Due to deeply non-normal data, differences in the metrics generated from

314   the empirical dataset were tested using Kruskal-Wallis one-way analysis of variance tests. Confidence

315   intervals in Figure 5 were calculated using the resampling process outlined in Desharnais *et al*. (2015).

316

317   **Results**

318   **Model Results**

319   Our simulation results (Figs. 3, 4) support our hypothesis (Fig. 1) demonstrating strong effects of

320   temporal resource overlap on the dietary specialization of pollinators with short but not long flight

321   periods. Fig. 3 shows an example of results from one network as an illustration of how resource overlap

322   explains variation in the dietary specialization of pollinators with shorter flight periods (Fig. 3a, c), but

323   does little to explain the dietary specialization of pollinators with longer flight periods (Fig. 3b, d). The

324   different measurable ranges in resource overlap for long flight period bees (Fig. 3) stem from the fact that

325   long flight period bees tend to extract more resources than short flight period bees over the course of their

326   full flight period, all else (e.g., resource extraction rates) being roughly equal in the model. This is the

327   case whether overlap is measured in aggregate (TRO) or on average (ARO) due to their strong correlation

328   in our results. The transition from high explanatory power to low explanatory power for temporal

329   resource overlap is apparent as pollinator flight period length increases, regardless of whether

330   specialization was measured at the end of simulations or averaged across the last 1000 model time steps

331   (visual depiction in Fig. 4). This result is consistent across varying lengths of time between pollinator

332   flight periods (i.e., break periods) using either the DFG or CV metric across all networks tested (Fig. S14-

333   S16). As predicted, low levels of resource overlap drive pollinators with short flight periods to specialize

334   because potential resource options are limited at any given moment in time. As temporal resource overlap

335   increases, potential options increase resulting in greater generalization (Fig. 3a, c). Bees with long flight

336   periods, on the other hand, do not experience the same limitation of potential options due to temporal

337 resource overlap, because they are active most of the entire flowering season and can potentially access

338 most or all of the flowering plants. Results were consistent regardless of whether resource overlap was

339 measured as total resource overlap (TRO) or average resource overlap (ARO).

340

341 **Pollen data results**

342 　　Our empirical results support our hypothesis, showing more specialized diets for bees with short

343 flight periods in more seasonal environments (Michigan) with lower flowering overlap than in less

344 seasonal environments (UK) with higher flowering overlap. Additionally, Michigan presents more single

345 family specialists than the UK (Fig. S17). Dietary specialization between bee genera and regions varied

346 significantly at both the level of botanical family ($\chi2=30.1$, $p<0.001$, Fig. 5a) and genus ($\chi2=27.3$,

347 $p<0.001$, Fig. 5b). In accordance with our hypothesis, there was an effect of region at the botanical family

348 level, but only for the short flight period *Andrena* where species in Michigan were significantly more

349 specialized than their British counterparts. In contrast, there were no significant differences for the long

350 flight period *Lasioglossum*. *Lasioglossum* species in the region with lower flowering overlap (MI) were

351 the most generalized of all studied groups, but this difference was non-significant. At the botanical genus

352 level, the same trend was more strongly expressed, as *Andrena* in Michigan were again significantly more

353 specialized than those in Britain, with the latter group showing no differences from *Lasioglossum* in

354 either Michigan or the UK. Results were consistent when analyzed using the DFG metric (Fig. S18).

355

356 **Discussion**

357 　　Our model results mechanistically demonstrate how differing phenologies interact with varying

358 degrees of temporal resource overlap to alter pollinator dietary specialization. Though nominally having

359 the possibility of affecting the realized specialization of pollinators with both long and short flight

360 periods, increasing temporal resource overlap was only found to increase the dietary generalization of

361 species with short flight periods. This same qualitative result was found in our empirical pollen load

362 datasets, which presents the first empirical validation of this specific benchmark theory on

363 phenologically-mediated adaptive foraging by consumers in general (MacArthur & Pianka 1966) and

364 pollinators in particular (Waser et al 1996). In addition to our approach detailed here, regional differences

365 in dietary breath are also apparent using established analysis methods (Fig. S17), and our metrics

366 correlate well with well-known measures (Appendix S1.8), helping corroborate our results.

367 　　The lack of a meaningful dietary response by long flight period bees to temporal resource overlap

368 in both the model and empirical datasets, suggests that increased temporal resource overlap does not

369 functionally change the resources available to this group. Waser et al (1996) suggests that longer

370 flowering periods are necessary for long flight period bees to co-occur with a resource and develop a

371   specialized foraging relationship. While long flowering periods may seem intuitively linked to high

372   resource overlap, high resource overlap in and of itself does not necessitate long flowering periods for

373   individual resources. Flowering periods may remain short but overlapped with other resources that are

374   also only available for a short period of time. It therefore follows that the absolute length of the flowering

375   period of individual resources influences specialization in long flight period pollinators, but not resource

376   overlap *per se*. In contrast, the absolute length of the flowering period of individual resources is almost

377   irrelevant for short flight period pollinators because they are active for such a restricted period of time; for

378   them, only the degree of overlap is what determines concurrently available resources.

379   It is important to set these findings within a wider context, specifically that of other known

380   drivers of dietary specialization. In addition to the impact of spatial and temporal resource density on

381   dietary specialization, fundamental research (MacArthur & Pianka 1966; Waser et al 1996) also points to

382   the constraining impacts of differing resource quality, the cost of travel, and morphological limitations

383   (Table 1). These factors are strong enough to shape realized foraging niches. For example, the

384   consumption of certain resources by foraging bees without physiological adaptations is strongly and

385   actively discouraged (Wang et al 2019; Brochu et al 2020). Through selecting the regions of the UK and

386   Michigan, efforts were made to control for these additional factors in order to focus specifically on and

387   test for the effects of varying bee phenology and flowering period overlap in isolation, *ceteris paribus*

388   (see Appendix S1.5). However, these should not be viewed as mechanisms that explain all aspects of

389   realized dietary breadth in and of themselves. The phenomenon of synchronous specialization can be

390   commonly observed in many bee communities, where at least two specialists are present at the same time,

391   each specializing on different resources. For example, specialists such as those of *Helianthus* (Asteraceae,

392   *A. helianthi*) and *Solidago*/*Symphyotrichum* (Asteraceae, *A. asteris*) and those of *Bryonia* (Cucurbitaceae,

393   *A. florea*) and Fabaceae (*A. wilkella*) can be found concurrently in Michigan and the UK, respectively.

394   Clearly, resource overlap cannot explain host choice itself where alternative mechanisms relating to

395   morphological or physiological adaptation may be more important (Danforth *et al.* 2019). Instead, the

396   level of temporal resource overlap should be viewed as a factor that affects the level of realized

397   specialization across a pollinator community, rather than a predictor of specialization of the level of the

398   individual species.

399   It should also be noted that total season length (the overarching flowering season for all flowers)

400   was not investigated in this study. The two regions and selected model genera were specifically chosen to

401   be as similar as possible, including total season length. It is here that care must be taken. It has long been

402   noted that deserts and arid regions with short and highly concentrated flowering periods play host not

403   only to species-rich bee communities, but also to bee communities that display the highest levels of

404   dietary specialization anywhere on earth (Moldenke 1979; Waser et al 1996; Danforth et al 2019). The

405 combination of high levels of specialization occurring during a short flowering period with considerable
406 flowering overlap (and hence many different resources available concurrently) further shows that the
407 explanatory principle of flowering resource overlap that we demonstrate here cannot be used in and of
408 itself to explain every aspect of dietary specialization. Instead, total season length (overarching flowering
409 season) may be a third factor affecting opportunities for an individual species to interact with available
410 resources in addition to flight period and flowering overlap. By restricting the resources available outside
411 a narrow flowering window, a short season may result in other factors such as interspecific competition or
412 morphological and physiological constraints to increase in relative importance despite the high resource
413 overlap. In future work, the relationships between these three phenological factors and their impact on
414 specialization could be clarified by leveraging our model's seasonality functions to more explicitly mimic
415 a variety of environmental flowering patterns and interrogate results with relevant empirical data from a
416 wider range of more extreme environments.

417 With future work in mind, our modeling developments provide a flexible operational basis going
418 forward. We showed that even high dimension network models can be further expanded to include the
419 dynamics of organismal phenology by focusing on simple inputs and tractability in developing a
420 functional phenology-modeling framework. Our framework provides the adaptability needed to mimic a
421 variety of different biomes' seasonal growth patterns (described above). Additionally, for more direct
422 comparisons to empirical networks in the future, work will need to be done integrating a variety of
423 phenologies among plant and pollinator species in single simulations. While model results matched our
424 theoretical expectations well, empirical results show some signs of complexity. A likely source of this
425 complexity is the fact that pollinator communities exist with many unique phenologies. Expanding the
426 model to study how well the effects of our described mechanism withstands a diversity of phenologies
427 (both at the consumer and resource level) will help to delimit the many factors driving species diet
428 breadth. This is particularly important when diet breadth exists as part of a larger ecological function like
429 pollination or seed dispersal and will indirectly influence diversity and distribution.

430 Our empirical approach was deliberately regional, and focused on comparing average responses
431 from sampled species in the empirical dataset. In adopting this regional approach and using this as a
432 categorical variable, no single bee individual actually experiences these overall regional environmental
433 conditions. The individual bee lives in a subset of the total area and thus is necessarily exposed to
434 conditions that may vary around the regional average. Because this approach gathers together samples
435 from disparate areas across bee species with different habitat specializations, it is possible that variation in
436 geographic sampling may influence the results. Future empirical studies could focus on specific locations
437 to characterize the degree of floral overlap specific to each site and quantify the dietary breadth of
438 selected taxa through repeated sampling for increased precision. This would allow an assessment of the

439 degree of variation in dietary specialization within both regions and individual species, in addition to the

440 comparisons between regions that were made here. However, a more localized sampling strategy is still

441 constrained by the difficulty of standardizing measurements (such as analysis of collected pollen from a

442 set number of individuals) across multiple pollinator taxa. Due to their high inherent variability in

443 occurrence (Williams et al. 2001; Burkle & Alarcón 2011; Jordano 2016) this would potentially limit the

444 number of taxa that can be compared between sites or regions. The same constraint applies to temporal

445 standardization. Many pollinator taxa appear sporadically thus limiting the number of individuals and

446 species that can be captured for analysis. Such future studies could test the scalability of the results

447 presented here. In the face of our changing climate, both scalability and range of effect will be important

448 elements in future investigations involving the phenological drivers of pollinator diets.

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471 **Code Availability:** Simulation code and simulation data (Fig. 3 & Fig. 4) are available at the repository:

472 https://github.com/fsvaldovinos/Phenology. Phenology parameters used in the simulation portion of our

473 study are available in Table S10.

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623 **Tables & Figures**

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625

626 **Table 1:** Factors favoring specialization in foraging as detailed in MacArthur & Pianka (1966) and their

627 corresponding construction in Waser et al's (1996**)** study on factors favoring generalization in foraging.

628 The third column describes the common factor in each treatment. The factor noted in green highlights the

629 work which helped inspire our study.

Drivers of specialized diet (MacArthur and Pianka 1966)	Drivers of generalized diet (Waser et al. 1996)	Common factor
Greater density of a specific resource	**Long foraging period relative to availability of specific resources**	**Resource density, either spatially or temporally**
Travel is easy for forager	Travel is costly for forager	Cost associated with travelling to resources
High degree of distinction between resource options	High degree of similarity between resource options	Inherent differences in resource quality
Increased difficultly in resource procurement and utilisation	Minor constraints of behaviour and morphology	Inherent difficulty in accessing different resources

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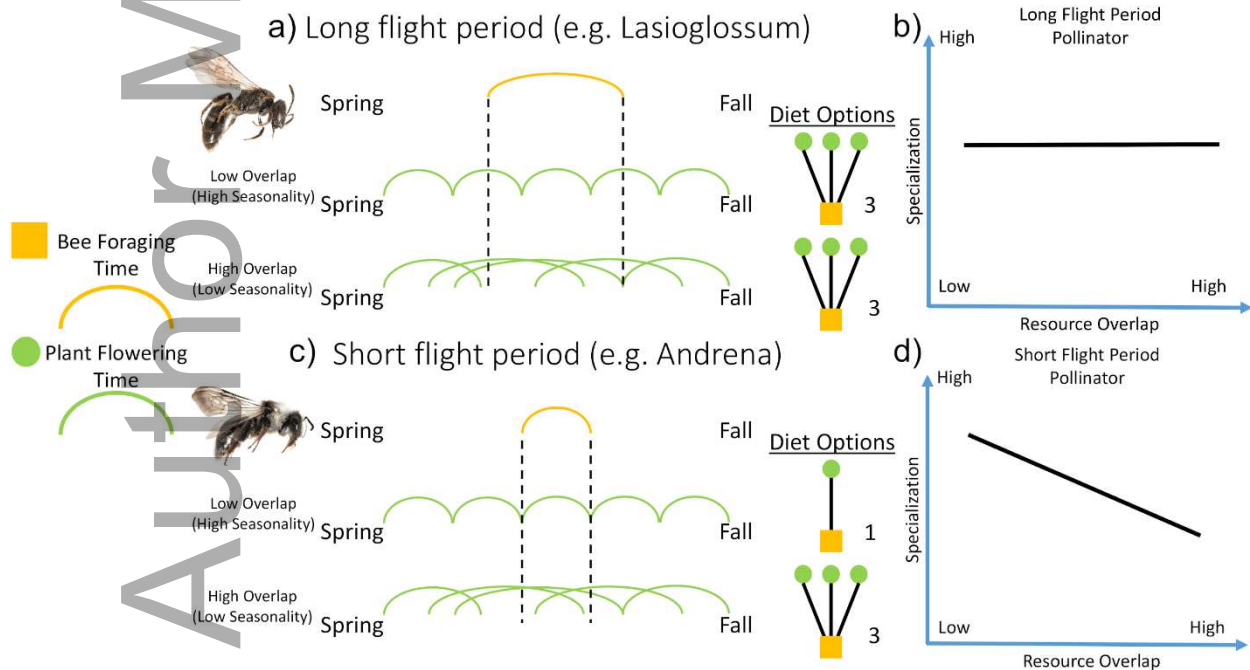
Figure 1: Graphical diagram of our hypothesis. Our hypothesis stems from the temporal overlap of flowering resources available to pollinators. Highly seasonal delimitations between different flowering populations create low levels of temporal overlap among different flowering resources. On the other hand,

644   fewer seasonal delimitations between different flowering populations create higher levels of temporal

645   overlap among different flowering resources. a) In long flight-period pollinators (e.g. *Lasioglossum*),

646   differing levels of temporal resource overlap have a weaker average effect on the degree of diet options

647   available to the pollinator. b) This is predicted to lead to a non-significant relationship between overlap

648   and specialization among long flight period pollinators. c) In short flight-period pollinators (e.g.

649   *Andrena*), low and high temporal resource overlap can limit or expand pollinator diet options

650   respectively. d) This is predicted to lead to a significant relationship between overlap and specialization in

651   short flight-period pollinators.

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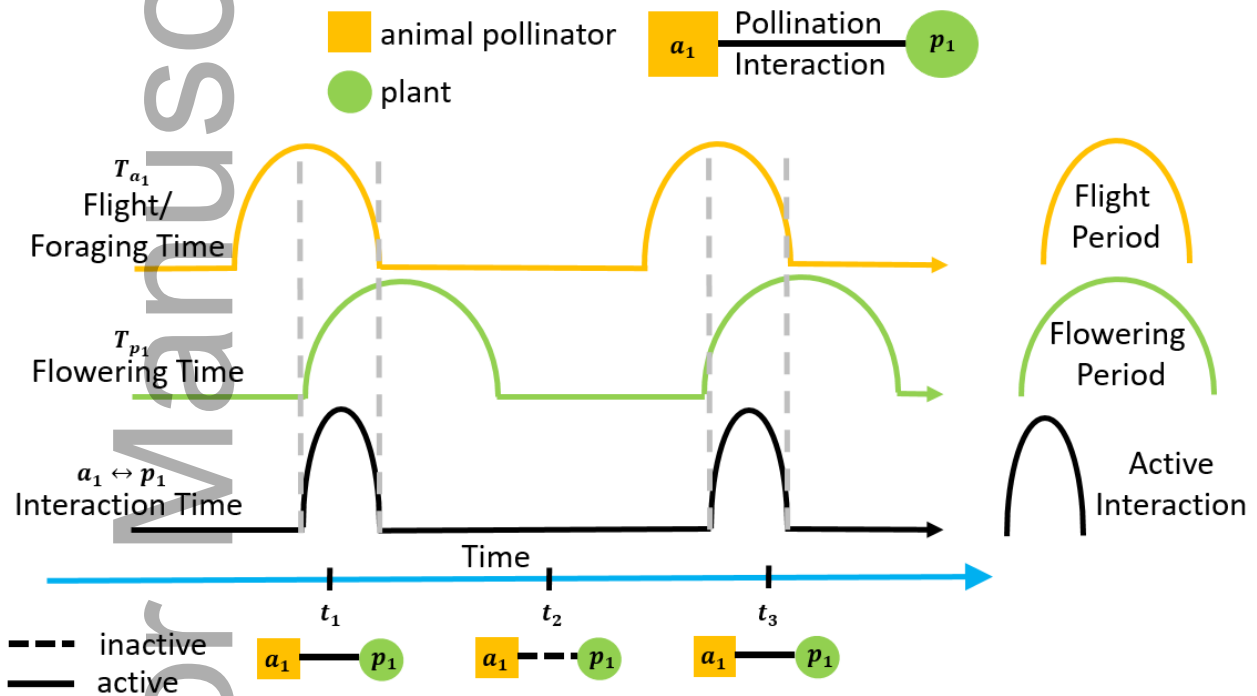
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654   **Figure 2: Diagram of phenologically mediated pollination interactions.** Our model framework

655   simulates pollination interactions over time by controlling key biological rates via phenology functions.

656   Flight/foraging in pollinators is mediated by the function T_{a_j} and flowering in plants is mediated via the

657   function T_{p_i}. Foraging and rewards production are only active during the flight period and flowering

658   period, respectively. The length of these periods and the time interceding each period is set by the user.

659   See Appendix S1.3. Any possible interaction between plants and pollinators is only active during

660   phenological overlap. Otherwise the interaction is inactive in the pollination network.
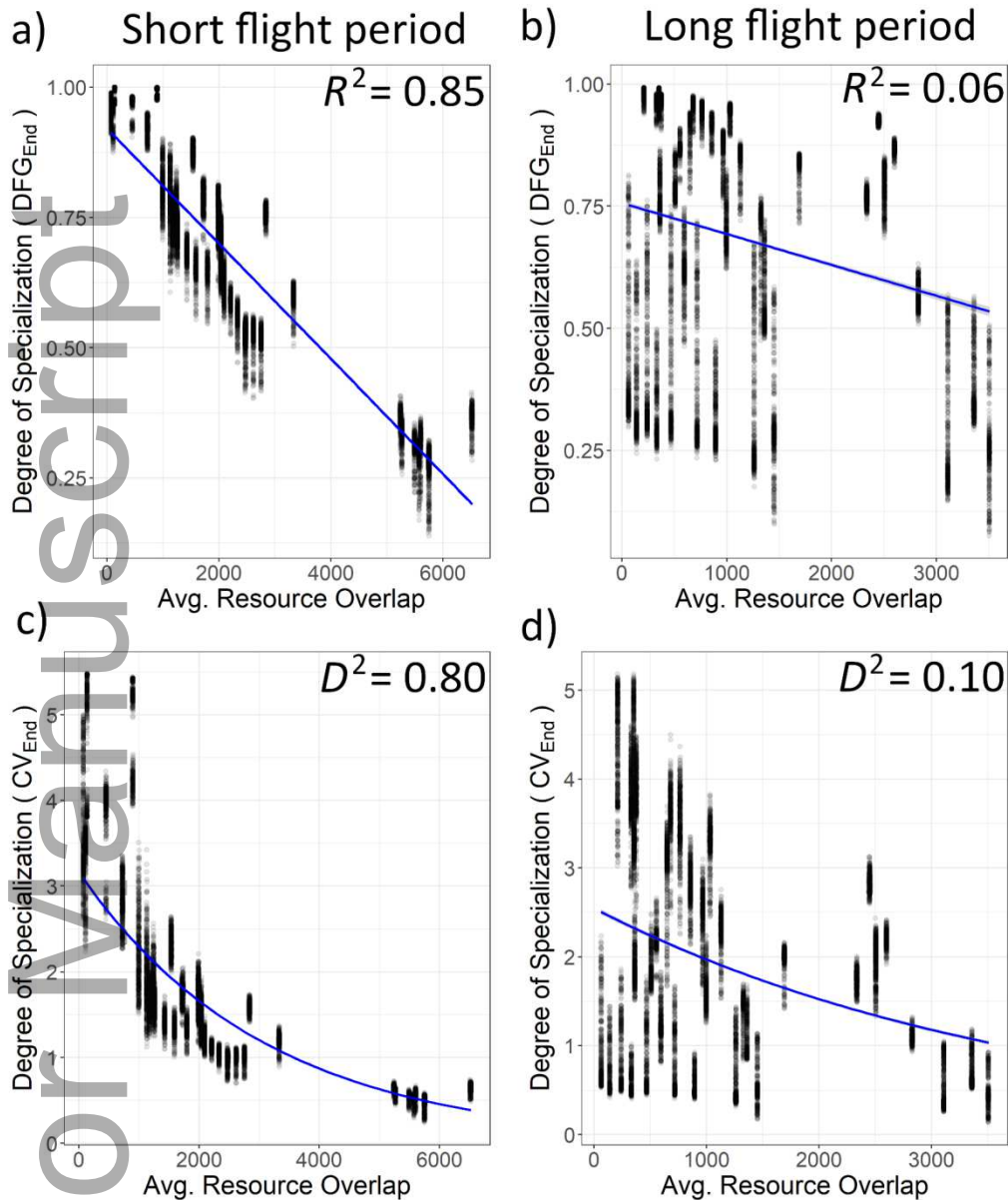
Figure 3: Temporal resource overlap drives specialization more strongly in short flight period than long flight period pollinators. Example model output on pollinator specialization taken across average plant overlap (ARO) for a short flight period (flight period = 20 time steps) and a long flight period pollinator (flight period = 300 time steps). Each dot represents the dietary specialization metric of a single pollinator population based on their foraging effort per plant species. Dietary specialization was measured at the end of simulations using a) DFG in a short flight period bee, $\beta = $ -1.1e^{-4}, F-statistic: 1.05e+05 on 1 and 18498 DF, p-value: < 2.2e^{-16}, b) DFG in a long flight period bee, $\beta = $ -6.3e^{-5}, F-statistic: 1089 on 1 and 18498 DF, p-value: < 2.2e^{-16}, c) CV in a short flight period bee, $\beta = $ 3.2e^{-4}, Residual deviance: 671.94 on 18498 degrees of freedom, d) CV in a long flight period bee, $\beta = $ -2.6e^{-4}, Residual deviance: 8244.4 on 18498 degrees of freedom. Example data taken from a network framework with 30 plant and

672   50 pollinator species. Higher values of both DFG and CV metrics indicate higher levels of specialization
673   while lower values indicate greater generalization.

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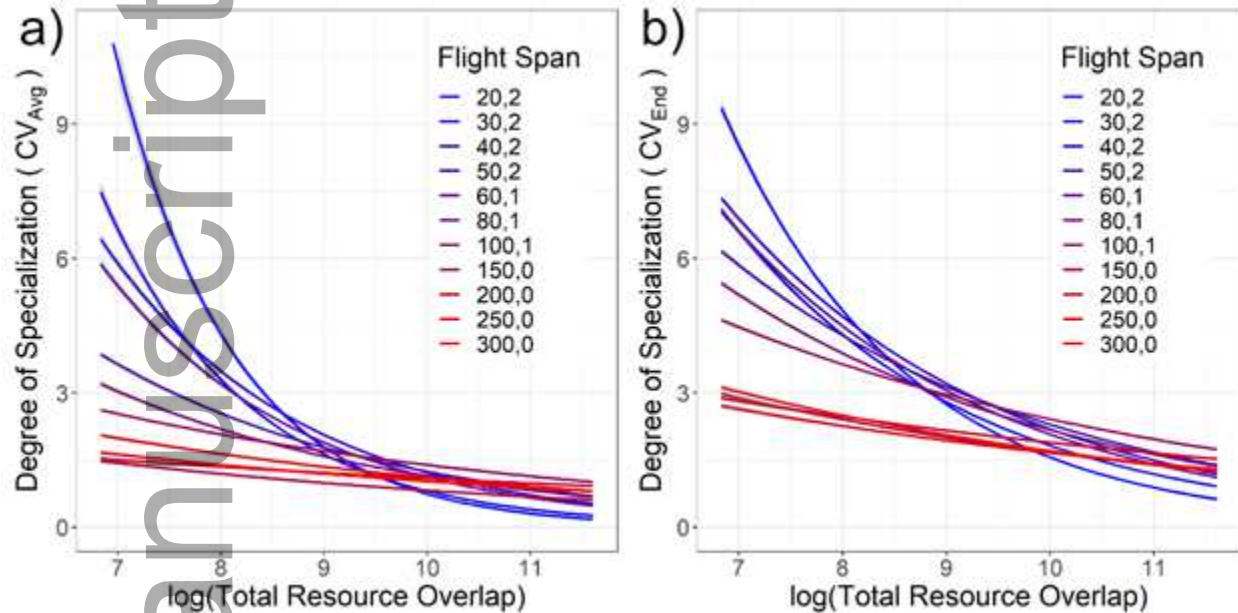
Figure 4: Interactive effect of temporal resource overlap and pollinator flight period on pollinator
dietary specialization. Representative sample of generalized linear models (Gamma distribution with log
link functions) showing change in effect of Total Resource Overlap (TRO) on pollinator dietary
specialization in model simulations. Flight period labels indicate the length of the flight period and the
number of phenology cycles between subsequent flight periods (see Supplementary Methods). Dietary
specialization is shown as the degree of specialization measured by the CV of pollinator foraging effort
per plant species a) averaged across the last 1000 time steps and b) taken at the end of simulations. Higher
CV values correspond with a higher level of specialization while lower CV values indicate greater
generalization. Example data taken from a network framework with 30 plant and 50 pollinator species.

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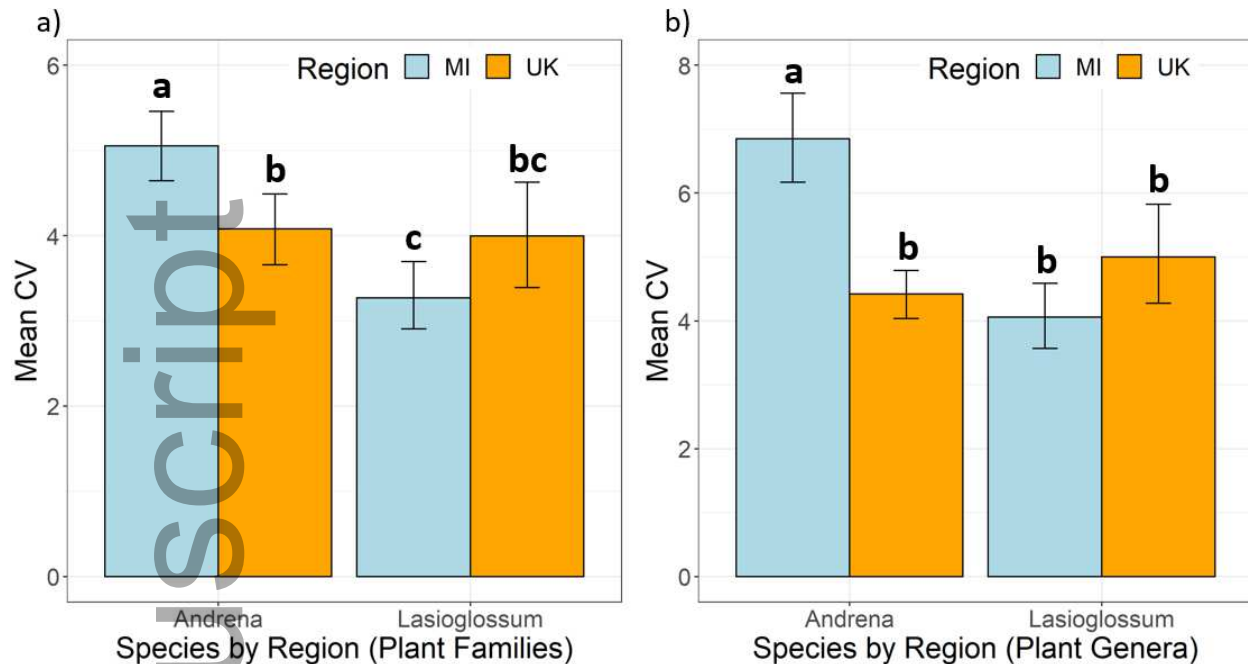
Figure 5: Empirical measures of dietary specialization. Short flight period *Andrena* bees show higher levels of specialization in highly seasonal (Michigan) compared to the weakly seasonal (UK), with no differences for long flight period *Lasioglossum* bees using the CV metric. Moreover, only in Michigan is there a difference in specialization between the two bee genera, showing a minimal impact of flight period in weakly seasonal environments. Effects are consistent at both the (a) botanical family and (b) botanical genus level. Bars headed by different letters were found to be significantly different via Dunn post-hoc test (a): $p<0.05$, DF=3, $\eta^2=0.21$, (b): ($p<0.05$, DF=3, $\eta^2=0.20$). Error bars show 95% confidence intervals created via the resampling process outlined in Desharnais *et al*. (2015).
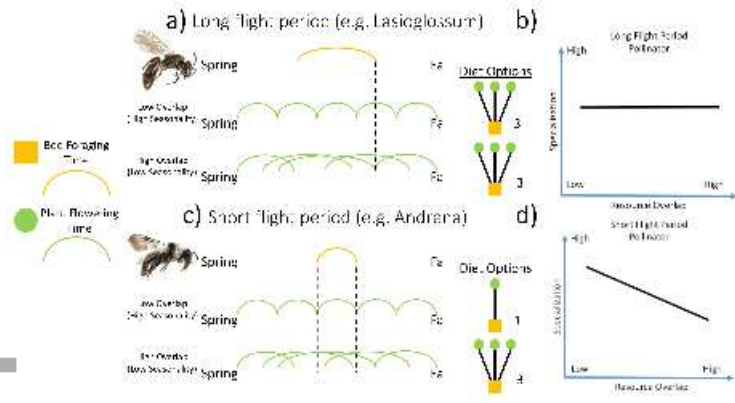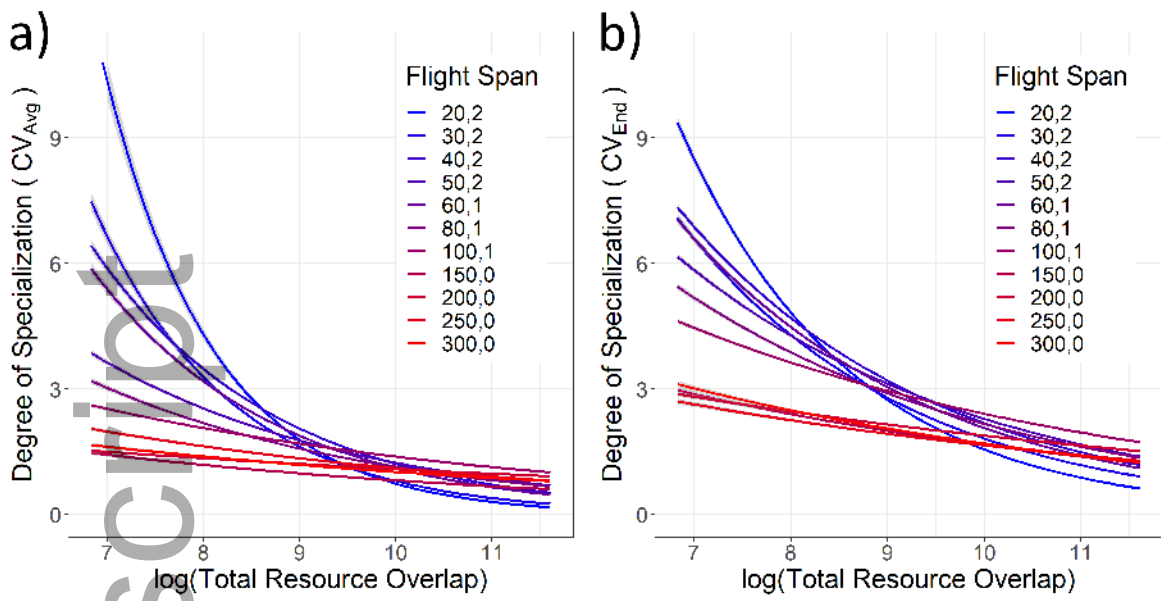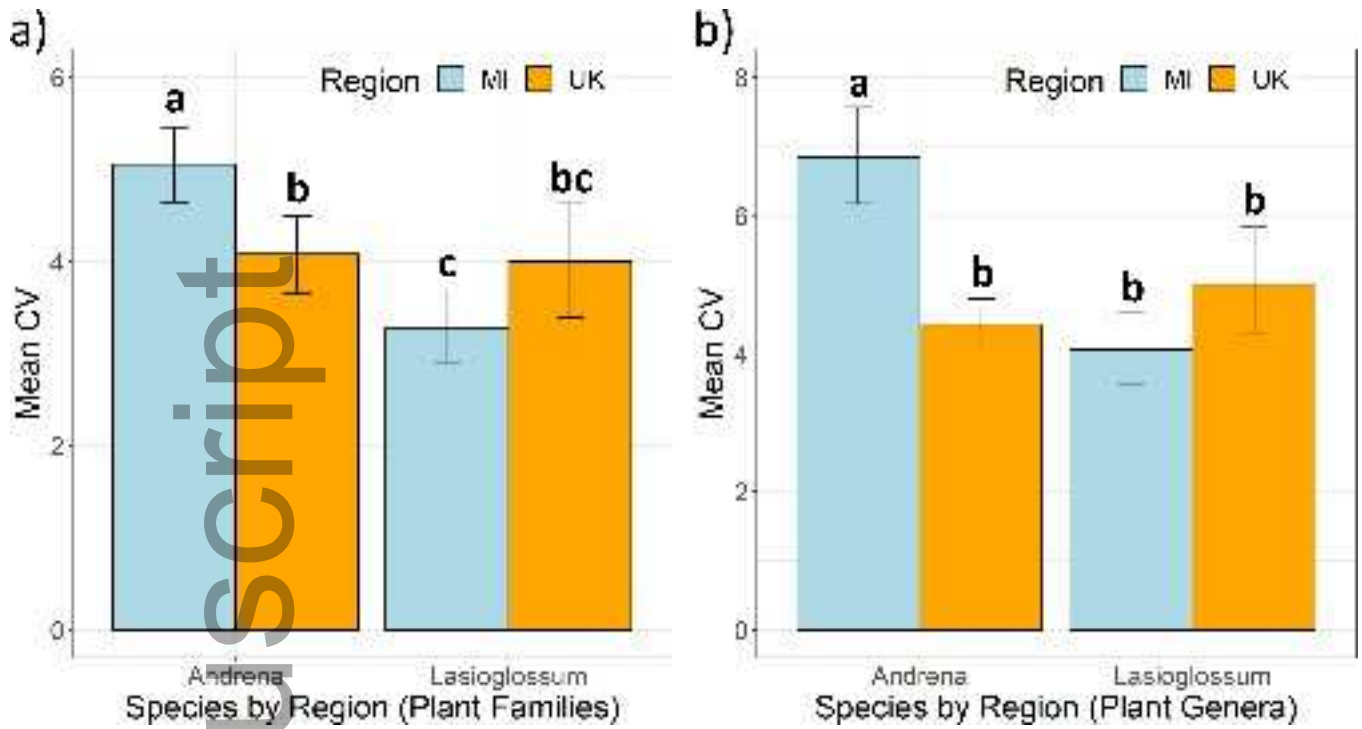
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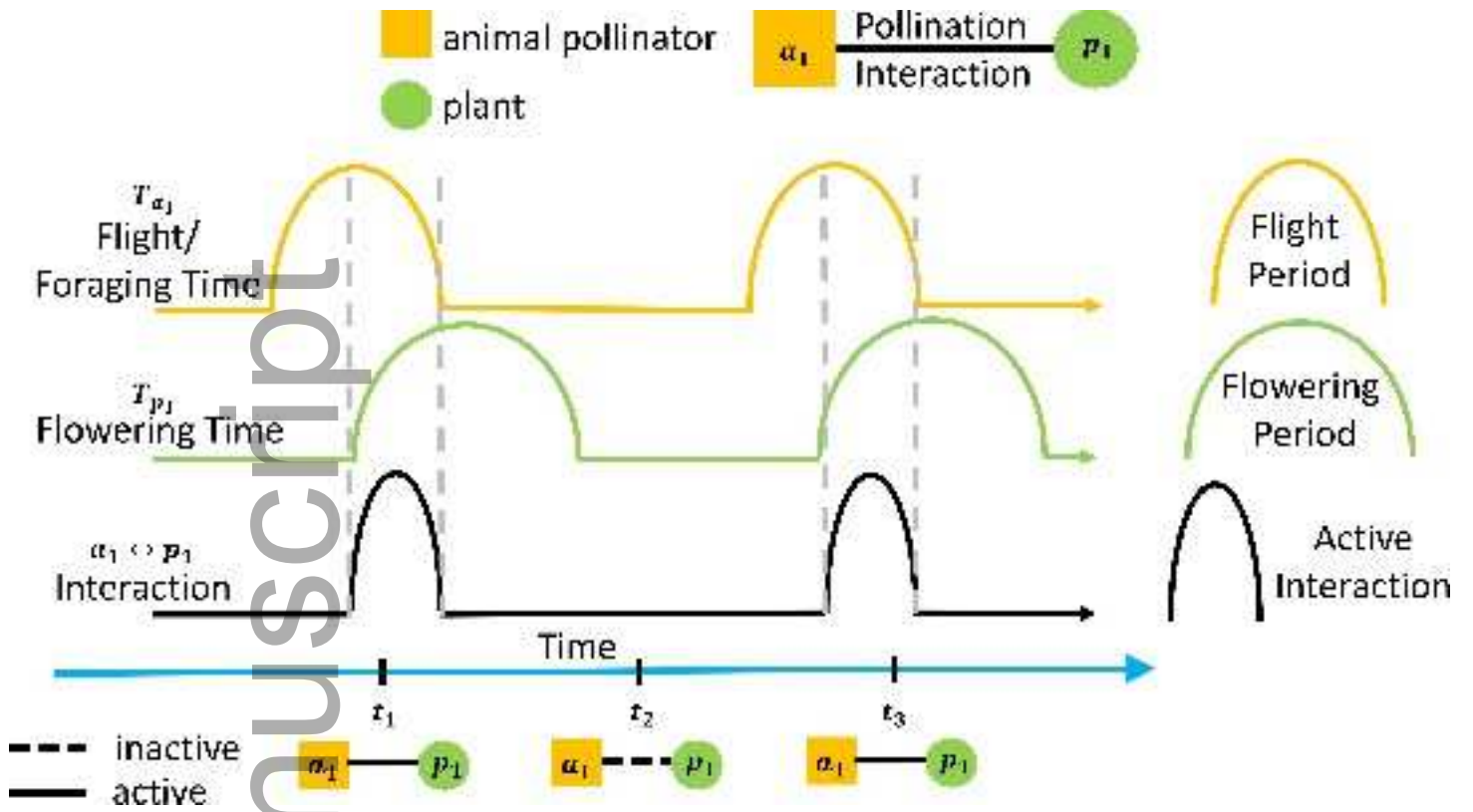
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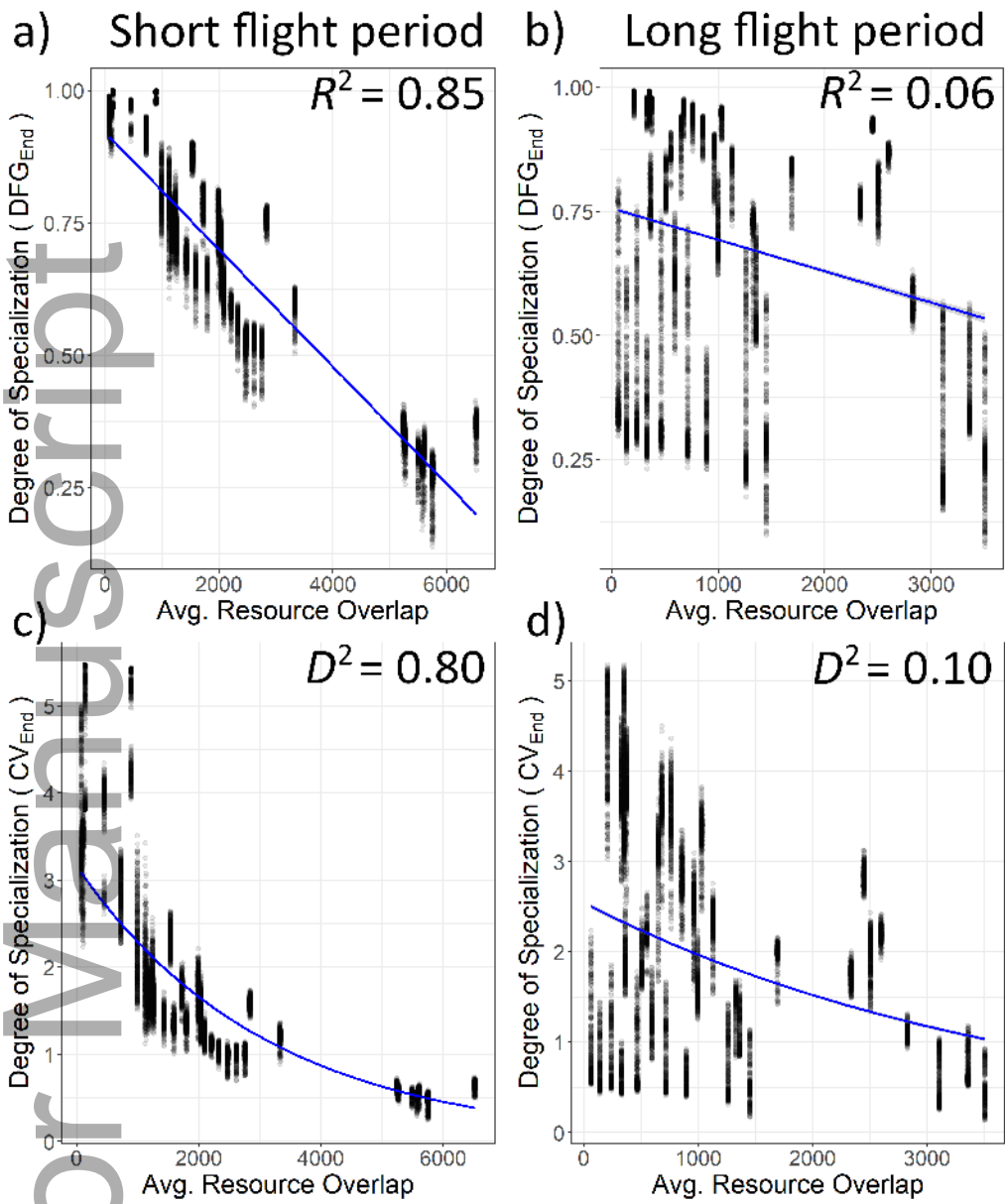
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