

**Resource overlap and dilution effects shape host plant use
in a myrmecophilous butterfly**

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13

14

15 ABSTRACT

- 16 1. The effects of consumers on fitness of resource organisms are a complex function of the
17 spatio-temporal distribution of the resources, consumer functional responses and trait
18 preferences, and availability of other resources.
- 19 2. The ubiquitous variation in the intensity of species interactions has important
20 consequences for the ecological and evolutionary dynamics of natural populations.
21 Nevertheless, little is known about the processes causing this variation and their
22 operational scales. Here, we examine how variation in the intensity of a consumer-
23 resource interaction is related to resource timing, resource density and abundance of other
24 resources.
- 25 3. Using the butterfly consumer *Phengaris alcon* and its two sequential resources, the host
26 plant *Gentiana pneumonanthe* and the host ants *Myrmica* spp., we investigated how
27 butterfly egg-laying depended on focal host plant phenology, density and phenology of
28 neighboring host plants and host ant abundance.
- 29 4. Butterflies preferred plants that simultaneously maximized the availability of both larval
30 resources in time and space, i.e., they chose early-flowering plants that were of higher
31 nutritional quality for larvae where host ants were abundant. Both the probability of
32 oviposition and the number of eggs were lower in plant individuals with a high neighbor
33 density than in more isolated plants, and this dilution effect was stronger when neighbors
34 flowered early.
- 35 5. Our results show that plant-herbivore interactions simultaneously depend on the spatio-
36 temporal distribution of a focal resource, and on the small-scale spatial variation in the

37 abundance of other herbivore resources. Given that consumers have negative effects on
38 fitness and prefer certain timing of the resource organisms, this implies that processes
39 acting at the levels of individuals, populations and communities simultaneously
40 contribute to variation in consumer-mediated natural selection.

41

42 Keywords: butterflies, flowering phenology, myrmecophily, plant-herbivore interactions,
43 resource use, spatial variation

44

45 INTRODUCTION

46 Resource-consumer interactions often have important effects on the performance of both partners
47 and the distribution and abundance of consumers is expected to match the spatio-temporal
48 distribution of their resources. Resource use by insect herbivores is often conditioned by
49 oviposition site selection by females. As larval stages usually show low mobility, insect
50 oviposition preferences are predicted to match the spatial and temporal distribution of host plants
51 suitable for offspring development (Gripenberg, Mayhew, Parnell, & Roslin, 2010; Jaenike,
52 1978; Scheirs & De Bruyn, 2002). The suitability of host plants, in turn, might depend on factors
53 such as host plant nutritional quality (Chen, Lin, Wang, Yeh, & Hwang, 2004), size (Rabasa,
54 Gutiérrez, & Escudero, 2005), microclimatic conditions (Eilers, Pettersson, & Öckinger, 2013) or
55 enemy-free space (Ballabeni, Włodarczyk, & Rahier, 2001). Most consumers depend on multiple
56 resources throughout their life cycle, e.g. different sources of food, shelter and resting sites
57 (Dennis, Shreeve, & Van Dyck, 2003, 2006). The availability of one resource might thus
58 influence the use of other resources. For example, the availability of nectar resources for adults
59 (Öckinger, 2008) or secondary hosts for larvae (Wynhoff, Bakker, Oteman, Arnaldo, & van
60 Langevelde, 2015) might determine host plant choices in butterflies.

61 The quantitative relationship between the abundance of consumers and the abundance of
62 resource organisms, and thus resource exploitation, will depend both on the birth and death
63 processes and on consumer behavior. Consumer behavior may specifically cause consumer
64 density and resource exploitation to increase (cf. resource concentration hypothesis, e.g.
65 Hambäck & Englund, 2005; Root, 1973; Stephens & Myers, 2012) or decrease (cf. resource
66 dilution, e.g. Otway, Hector, & Lawton, 2005) with increasing patch size and resource

67 abundance. Observed differences in the relationships between resource exploitation and patch
68 size or patch density among different consumers have been suggested to be the result of
69 differences in how emigration and immigration rates depend on patch size and patch density, and
70 on the scale of consumer selection (Andersson, Löfstedt, & Hambäck, 2013; Hambäck &
71 Englund, 2005). For example, a strong negative relationship between consumer density and
72 patch area observed in visual searchers like butterflies might be the result of that immigration is
73 diameter-dependent while emigration is perimeter-dependent. Not only should the abundance of
74 the resource organism be important for consumer responses, but also its timing and the temporal
75 matching with the activity period of the consumer. For example, in herbivores that depend on a
76 specific developmental stage of their host plant, the density of plants that are in suitable
77 developmental stages at the time when the herbivore is active, rather than the overall density, is
78 expected to influence host use. Although the effects of resource density on plant-insect
79 interactions (Kim & Underwood, 2015; Kula, Castillo, Dudash, & Fenster, 2014; Verschut,
80 Becher, Anderson, & Hambäck, 2016; Yamamura, 2002) are well studied, the role of resource
81 timing and the effects of the availability of other resources have rarely been considered in these
82 studies. Moreover, while the ecological and evolutionary effects of variation in consumer-
83 resource interaction intensities have been documented for many systems (e.g. Chamberlain,
84 Bronstein, & Rudgers, 2014; Kolb, Ehrlén, & Eriksson, 2007; Vanhoenacker, Ågren, & Ehrlén,
85 2013), the simultaneous effects of factors at different levels: individuals (e.g. timing),
86 populations (e.g. resource density), and communities (e.g. availability of other resources) have
87 rarely been explored. This is particularly true for small spatial scales, such as variation in the
88 intensity of herbivory among individuals within plant populations.

89 Myrmecophilous butterflies of the genus *Phengaris* need two sequential hosts to
90 complete their development: the caterpillars are predispersal seed predators during their first
91 instars and parasitize ant nests (*Myrmica* spp.) during later stages. Butterflies are very specific
92 regarding both host plant and host ant species and the developmental stage and phenology of
93 host plants (G. W. Elmes et al., 1998; Thomas & Elmes, 2001; Valdés & Ehrlén, 2017). Female
94 butterflies oviposit preferentially on buds in early phenological stages, probably because these
95 constitute higher-quality food for the caterpillars; the developing seeds might become tougher,
96 drier and more difficult to digest as buds develop into flowers and fruits (Arnaldo, Gonzalez,
97 Oliveira, Langevelde, & Wynhoff, 2014). In some species, host plant flowering time determines
98 oviposition and individuals flowering early in the season receive more eggs because the presence
99 of the preferred bud developmental stages overlaps more with the period of butterfly oviposition
100 in early- than in late-flowering plants (Valdés & Ehrlén, 2018). Moreover, the mobility of
101 caterpillars after leaving their host plants is low (Hayes, 2015), and further development is
102 possible only if the foraging range of suitable host ants is sufficiently close to the host plant
103 individual (usually a few meters). Butterflies are therefore expected to oviposit on host plants in
104 suitable development stages only if plants occur at micro-sites where ant hosts are present
105 (Wynhoff, Grutters, & Langevelde, 2008; Wynhoff & van Langevelde, 2017).

106 In this study, we investigated how the phenology, in terms of the developmental stage of
107 the reproductive structures, of one resource, the focal host plant *Gentiana pneumonanthe*, the
108 density and phenology of neighboring conspecific plants, and the abundance of host ants
109 influence resource use, in terms of egg-laying, by the consumer butterfly *Phengaris alcon*. We
110 used an extensive field data set to test two hypotheses: (1) Effects of plant phenology and ant

111 abundance on egg distribution patterns are interdependent: butterflies choose plants for
112 oviposition that simultaneously maximize the availability of both resources, i.e. they have a
113 stronger preference for early-flowering host plants where host ants are abundant, and (2) The
114 probability of a plant receiving at least one egg, as well as the number of eggs in oviposited
115 plants, decreases with increasing conspecific neighbor density (i. e. a dilution effect), and this
116 decrease is stronger when neighbors show the preferred phenology (i.e. flower early).

117 MATERIALS AND METHODS

118 Study system

119 The marsh gentian (*Gentiana pneumonanthe* L.) is a rare, long-lived perennial herb, occurring in
120 open habitats, such as wet heathlands and grasslands (Simmonds, 1946). Plants can have one to
121 many, up to 45 cm high, shoots and produce deep blue flowers that are pollinated by
122 bumblebees. The species is self-compatible and flowers in July and August in the study area (SW
123 Sweden). Fruits are capsules containing a high number of minute, wind-dispersed seeds (mean
124 seed number per fruit \pm SD = 490 ± 243 , mean seed weight = 0.041 mg, authors' unpublished
125 data). *Gentiana pneumonanthe* is the host plant of the Alcon Blue butterfly (*Phengaris alcon*), a
126 specialist predispersal seed predator which oviposits on young flower buds in July and August
127 (Appelqvist & Bengtsson, 2007). During an oviposition event, adult female butterflies usually
128 lay more than one egg on the same plant and even on the same bud, and there is no evidence of
129 avoiding plants that already carry eggs (Van Dyck & Regniers, 2010). The caterpillars feed
130 inside the capsule until they reach the fourth instar, when they drop to the ground to be picked up
131 by *Myrmica* ants. Caterpillars mimic the surface chemistry of the ant brood (Nash, Als, Maile,
132 Jones, & Boomsma, 2008) and the acoustic signals of queen ants (Sala, Casacci, Balletto,

133 Bonelli, & Barbero, 2014), and these features cause ants to carry them to their nest, where they
134 spend the rest of their larval period as brood parasites. Females of *Phengaris* detect host ant
135 presence through plant chemicals produced by ants or by plants in response to root tissue damage
136 caused by ants (Patricelli et al., 2015; van Dyck et al., 2000; Wynhoff & van Langevelde, 2017).
137 Contrary to the majority of *Phengaris* species, which prey on ant brood, *P. alcon* is a “cuckoo”
138 species (Als et al., 2004), and caterpillars feed primarily on regurgitants from ant workers,
139 trophic eggs (i.e. nutritious, infertile eggs which are fed to the queens and ant larvae) and prey
140 items brought to the nest by ants. Only ants belonging to *Myrmica* sp. can act as hosts of *P.*
141 *alcon*. In Sweden, *M. rubra* is considered to be the most common host ant species (Graham W.
142 Elmes et al., 1994), although *M. ruginodis* has also been reported as a host (Nash & Andersen,
143 2015).

144 Data collection

145 The study was carried out in a population of *G. pneumonanthe*, where the butterfly *P.*
146 *alcon* was present, located in Tånga Hed nature reserve in the county of Västra Götaland, SW
147 Sweden (58°01'40.0"N 12°49'47.0"E). Field work was conducted between 9 July and 3
148 September 2016. The plant population occupies a fenced meadow that is grazed by cattle at the
149 end of the summer every year. A study plot measuring 69 m × 45 m was established in the
150 meadow. This plot was further divided into a grid comprising 345 3 m × 3 m subplots with
151 corners permanently marked by wooden poles (Fig. 1A). In 154 of the subplots where *G.*
152 *pneumonanthe* was present, all reproductive shoots of *G. pneumonanthe* were mapped (Fig. 1B),
153 and their phenology and the number of eggs of *P. alcon* were recorded between 29 July and 5
154 August (18 additional occupied subplots were not possible to fully survey due to time

155 constraints). Shoots were mapped by recording their coordinates within subplots. We mapped
156 shoots rather than plant individuals (that may have one or several shoots) because we judged that
157 individual shoots are the relevant unit for the butterfly to assess the timing of the food resource,
158 and because individual shoots act as the unit of attraction for butterfly females. For each shoot,
159 phenology was recorded as the developmental stage of the most advanced bud, according to six
160 ordinal categories: (1) the sepals covering the bud completely, (2) bud becoming visible, (3) bud
161 growing over the sepals, (4) bud turning blue, (5) flower opening, and (6) flower showing signs
162 of wilting (Valdés & Ehrlén, 2017). Each stage corresponds to a time interval of flower
163 development, with higher values indicating a more advanced floral development at the day of
164 recording, i.e. an earlier flowering phenology. The number of eggs was counted on the whole
165 shoot.

166 The ant community was sampled at each corner of the occupied subplots (a total of 254
167 points) at two occasions, 14 July and 3 September (Fig. 1B). Baits consisted of a 50-ml plastic
168 tube in which we placed a sugar cube. The tubes were left open on the ground in the evening, and
169 collected the next morning. Ants collected were transferred to 70° ethanol and the number of ants
170 of different *Myrmica* species were counted in the lab (using Douwes, Abenius, Cederberg, &
171 Wahlstedt, 2012 for identification). Ants belonging to other genera where not identified to
172 species, but counted as “other ants”.

173 **Interpolations of ant abundances**

174 We also incorporated the locations of the 254 points where the ant community was sampled into
175 the GIS. We used inverse distance weighted interpolation (Pebesma, 2004) based on the values at
176 the sampling points to generate values of the abundance of ant species over the surface of all

177 occupied subplots. A maximum distance of 3 m was used because it represents the ground
178 foraging distance of most investigated *Myrmica* species (G. W. Elmes et al., 1998). From these
179 interpolated surfaces (see Figs. S1-S5), we extracted values of abundance of the different ant
180 species for each of the mapped shoots.

181 **Calculation of neighborhood measures**

182 Field maps were digitized using a Geographic Information System (GIS) created with
183 ArcGIS 10.3.1, assigning relative coordinates to each recorded reproductive shoot of *G.*
184 *pneumonanthe* (Fig. 1B). For each shoot, we defined a buffer zone with a 3-m radius, centered at
185 the focal shoot (see example in Fig. 1B), and calculated the number of reproductive shoots of *G.*
186 *pneumonanthe* per m² within this buffer zone (hereafter, “neighbor density”) as well as the mean
187 phenology of these shoots (hereafter, “neighbor phenology”), excluding in each case the focal
188 shoot.

189 **Statistical analyses**

190 The effects of shoot phenology, host ant abundance, neighbor density and neighbor phenology on
191 *P. alcon* egg distribution were examined using two Generalized Linear Models (GLMs). Effects
192 on the probability of a shoot having at least one egg were evaluated using a binomial GLM, and
193 effects on the number of eggs in shoots with at least one egg were evaluated using a negative
194 binomial GLM. Both models included also the effects of three interactions. First, we included the
195 interaction between shoot phenology and ant abundance in order to test if the effects of the two
196 resources on egg distribution patterns are interdependent. Second, we included the interaction
197 between neighbor density and neighbor phenology in order to test if the effect of host plant
198 density depends on phenology of neighboring host plants. Third, we included the interaction

199 between shoot phenology and neighbor phenology to account for the fact that the relationship
200 between egg distribution and phenology of the focal plant might depend on the phenology of
201 neighboring host plants. As a measure of host ant abundance, we used the abundance of *M. rubra*
202 (hereafter, “ant abundance”). *M. rubra* is considered to be the most common host ant species of
203 *P. alcon* in Sweden (Graham W. Elmes et al., 1994), although *M. ruginodis* has also been
204 reported as a host in areas near our study site (Nash & Andersen, 2015). As we have no direct
205 information on host ant use from our study site (no nests have been opened), we cannot exclude
206 any of these two species as being used as hosts by *P. alcon*. Our decision to use the abundance of
207 only *M. rubra* in our models was based on that it was the only species that showed positive
208 effects on the probability of host plants receiving eggs and the number of eggs in plants with at
209 least one egg (*M. ruginodis* had in fact a negative effect, Table S1). However, as we have no
210 conclusive evidence that *M. rubra* serves as the only or main host at our site, we also performed
211 alternative analyses using the abundance of *M. ruginodis* and the summed abundances of both *M.*
212 *rubra* and *M. ruginodis* (Table S2).

213 All predictors were standardized by subtracting the mean and dividing by the standard
214 deviation before the analyses. We checked for spatial autocorrelation in the residuals of models
215 by plotting spatial correlograms and by calculating global Moran's I with a permutation test
216 (1000 random permutations). Moran's I was calculated based on a connectivity matrix of
217 pairwise Euclidean distances among the shoots up to a distance of 30 m. Residual spatial
218 autocorrelation could lead to biased model estimates and invalid statistical inference (Dormann
219 et al., 2007). A significant spatial autocorrelation was found in the residuals of the binomial
220 GLM, but not for the negative binomial GLM (global Moran's I = 0.0148, $p < 0.001$ and global

221 Moran's I = -0.0013, p = 0.479, respectively, Figs. S6-S7). We therefore applied Moran's
222 eigenvector mapping (MEM), which translates the spatial arrangement of data points into
223 explanatory variables (eigenvectors) that capture spatial effects, to the binomial model
224 examining effects on the probability of a shoot having at least one egg (Dray, Legendre, & Peres-
225 Neto, 2006; Thayn & Simanis, 2013). The model was refitted including two eigenvectors issued
226 from MEM as spatial predictors, and this strongly reduced the residual spatial autocorrelation
227 (global Moran's I = 0.0004, p = 0.004, Fig. S6). Although residual spatial autocorrelation was
228 still significant, the low value of Moran's I and visual inspection of the spatial correlogram (Fig.
229 S6) indicated that almost all of the residual spatial autocorrelation was removed by the spatial
230 predictors. The results of this model were similar to the results of the binomial GLM not
231 including the spatial predictors (Table S3). Statistical analyses were carried out in R 3.4.0 (R
232 Core Team 2017).

233 RESULTS

234 Eggs of *P. alcon* were found on 731 (8.3%) of 8848 reproductive shoots of *G.*
235 *pneumonanthe* recorded in 154 subplots. On shoots with at least one egg, the mean number of
236 eggs was 5.03 ± 0.20 SE.

237 The effects of shoot phenology and ant abundance on *P. alcon* oviposition were
238 interdependent. The probability of a shoot of *G. pneumonanthe* having at least one egg increased
239 with an earlier phenology (i.e. with a more advanced floral development at the day of recording,
240 Table 1, Fig. 2A). This increase was stronger in shoots where *M. rubra* was more abundant (the
241 effect of the interaction shoot phenology \times ant abundance being significant in the model without
242 spatial predictors and marginally significant after including the spatial predictors, Table S3, Fig.

243 2A, Table 1). In analyses based on the abundance of *M. ruginodis* or the summed abundance of
244 *M. rubra* and *M. ruginodis*, the probability of a shoot of *G. pneumonanthe* having at least one
245 egg instead decreased with a higher ant abundance (Table S2). The number of *P. alcon* eggs on
246 individuals with at least one egg increased with an earlier shoot phenology and with a higher host
247 ant abundance, and the effect of the interaction between phenology and ant abundance was
248 marginally significant and in the same direction as in the model for the probability of having
249 eggs (Table 1, Fig. 2B and C).

250 High densities of host plant shoots resulted in a dilution effect, and the strength of this
251 effect depended on the quality of neighboring plants. Both the probability of having at least one
252 egg and the number of eggs on shoots with at least one egg decreased with the overall density of
253 neighboring host plant shoots (Table 1, Fig. 3). In both cases, the decrease was stronger when
254 neighboring host plants showed the preferred phenology, i.e. had an earlier phenology
255 (significant effect of the interaction neighbor density × neighbor phenology, Table 1, Fig. 3).

256 DISCUSSION

257 The results of this study show that resource use in the myrmecophilous butterfly *P. alcon*
258 is shaped by both the spatial overlap of the two key larval resources and by a dilution effect.
259 Specifically, we found that butterflies tend to prefer to oviposit on early-flowering plants that
260 have a high abundance of potential host ants, that plants surrounded by many conspecific
261 neighbors receive fewer eggs, and that the dilution effect is stronger when neighbors show the
262 preferred phenology.

263 We found that both the probability of *P. alcon* butterflies laying at least one egg on a host
264 plant as well as the number of eggs increased with an earlier phenology of its host plant *G.*

265 *pneumonanthe*. This agrees with previous studies showing that insects usually prefer plants with
266 a particular phenology (Elzinga et al., 2007), and more specifically, that antagonists
267 preferentially attack early-flowering plants (König, Wiklund, & Ehrlén, 2015; Parachnowitsch &
268 Caruso, 2008; Valdés & Ehrlén, 2017, 2018). Interestingly, in our study the strength of this
269 preference for an early plant phenology did depend on the abundance of a possible second
270 resource for the antagonist, i.e. the ant species *Myrmica rubra*. The preference of *P. alcon* for
271 early-flowering host plants tended to be stronger at locations where *M. rubra* was more
272 abundant. For example, the probability of a shoot with the earliest possible phenology receiving
273 at least one egg was 0.07 at sites where *M. rubra* was absent, and 0.62 at sites with the maximum
274 *M. rubra* abundance observed ($n = 34$ ants). This suggests that the butterflies are able to
275 simultaneously track the distribution of the two resources, and to preferentially oviposit on plants
276 where both the availability of high-quality food for the caterpillars and the probability of
277 adoption by a suitable species of *Myrmica* are higher. When suitable host ants were absent or
278 very scarce, host plant phenology did not seem to affect egg-laying, and the probability that
279 early-flowering plants should receive eggs was very low. Our use of abundance of *M. rubra* as a
280 measure of host ant abundance was not based on actual host identification but on correlations
281 between abundance and occurrence and number of eggs. Although the other *Myrmica* species
282 investigated had a negative effect on egg occurrence (Table S2), we cannot completely rule out
283 the possibility that these species act as hosts in our study site, and that the correlations with *M.*
284 *rubra* abundance are due to the effect of some unmeasured environmental variable, rather than to
285 butterflies directly tracking the abundance of this ant species. However, in combination with
286 previous evidence of *M. rubra* being the most common host ant species of *P. alcon* in Sweden

287 (Graham W. Elmes et al., 1994), the results of our analyses suggest that *M. rubra* serves as a host
288 species at our study site.

289 Spatial overlap between the distribution of host plants and host ant nests at larger scales
290 has previously been shown to increase the density and population persistence of the congeneric
291 species *P. arion* (Casacci et al., 2011; Thomas, Simcox, & Clarke, 2009). Other studies with
292 *Phengaris* butterflies have demonstrated effects of host plant phenology (Thomas & Elmes,
293 2001; Valdés & Ehrlén, 2017, 2018), host ant presence (van Dyck et al., 2000; Wynhoff et al.,
294 2008; Wynhoff & van Langevelde, 2017) or both of these factors (Casacci et al., 2011) for
295 oviposition site selection. Our study suggests that the spatial overlap between these two
296 resources also at the scale of the host plant individual is associated with butterfly oviposition
297 preference, and that the effects of plant phenology and ant abundance are interactive. An
298 important general implication of these findings is that differences in availability of a resource
299 over very small spatial scales might influence the use of other resource by consumers that
300 depend on multiple resources. The results also suggest that the effects of factors at the levels of
301 the individual (plant phenology) and the community (availability of the ant resource) on small-
302 scale spatial variation in consumer-resource interactions are interactive.

303 Our results show both that there is a dilution effect of local host plant density on butterfly
304 resource use, and that the strength of this effect depends on the phenology of neighboring plants.
305 Higher densities of neighboring host plants were associated with both a decreasing probability of
306 a focal plant receiving at least one egg and a lower number of eggs in plants with eggs, i.e. a
307 lower consumer pressure. The results of previous studies with this species (Van Dyck &
308 Regniers, 2010) suggest that females usually lay more than one egg on the same plant, and that

309 they do not avoid oviposition on plants that already carry eggs. If this is true also in our study,
310 then the eggs observed on an individual plant correspond to the offspring of either a single or
311 several females (but this is something we cannot determine because oviposition was not directly
312 observed in this study). Because we cannot be sure whether the lower number of eggs was the
313 result of fewer females visiting the plant, or of each visiting female laying fewer eggs, it is more
314 appropriate here to talk about “consumer pressure” than about “consumer abundance”. In any
315 case, the observed negative relationship between consumer pressure and overall resource
316 abundance was stronger when the surrounding plants flowered early in the season, i.e. they had
317 buds in early developmental stages during the period of butterfly oviposition. In other words, at a
318 given conspecific density more eggs were found in *G. pneumonanthe* plants surrounded by non-
319 attractive neighbors (i.e. late-flowering plants). In our study, plant phenology thus appears to
320 influence butterfly oviposition not only because the phenology of a focal plant interacts with host
321 ant availability to determine plant suitability for oviposition, but also because the phenology of
322 neighbors modulates the strength of host plant density effects on oviposition. Therefore, not only
323 factors at the levels of individuals and communities, but also at the level of the plant population,
324 drive variation in resource use.

325 Our results suggest that oviposition decisions in myrmecophilous butterflies are taken at
326 two levels. When flying over an area populated with host plants, females might primarily use
327 visual cues (Van Dyck & Regniers, 2010) to evaluate host plant availability (i.e. density) and
328 identify host plants with the preferred phenology (i.e. early-flowering). When butterflies
329 approach host plants, or after alighting on a plant, females may use both visual cues to evaluate
330 plant phenology and chemical cues to detect ant presence (Patricelli et al., 2015; Wynhoff et al.,

331 2015; Wynhoff & van Langevelde, 2017), thereby evaluating the spatial overlap of the two
332 resources needed by their offspring. If females use plant developmental stage as a cue indicating
333 the availability of high-quality food for the caterpillars, host plants surrounded by late-flowering
334 neighbors would be more attractive to butterflies than host plants surrounded by early-flowering
335 neighbors. Negative density-dependence in antagonists has been documented also in other
336 systems, where egg clumping on plants with few conspecific neighbors was explained by a
337 disproportionate attraction of insect herbivores to more isolated host plants (Hasenbank &
338 Hartley, 2015; Shea, Smyth, Sheppard, Morton, & Chalimbaud, 2000). For herbivores feeding on
339 several plant species, associational effects linked to the surrounding plant community have been
340 documented more frequently (e.g. Bergvall, Rautio, Kesti, Tuomi, & Leimar, 2006; Hjältén,
341 Danell, Lundberg, & Hjalten, 1993). Our study shows that associational effects are present also
342 for a specialized herbivore using a single host species, and that the strength of these density-
343 dependent effects depends on the phenology of conspecific neighboring host plants.

344 Our results are important to understand the factors causing variation in the intensity of
345 interactions between consumers and their resources. Given that consumers often have important
346 effects on fitness in the consumed organisms and that they show preferences for timing of the
347 resource organisms, identifying the factors that influence the intensity of interactions is also
348 important to understand the mechanisms underlying variation in natural selection. In our study
349 system, the butterfly seed predator has strong negative effects on plant fitness and shows a
350 preference for plants with an early flowering phenology, leading to butterfly-mediated selection
351 for later flowering (Valdés & Ehrlén, 2017). The results of the current study strongly suggest that
352 the strength of butterfly preferences for early-flowering plants is influenced by both population

353 context, in terms of population density and the trait distribution with the population, and by
354 community context in terms of the abundance of the ant species that function as the second host
355 of butterfly caterpillars. Taken together, these findings illustrate that observed spatial variation in
356 intensities of interactions and consumer-mediated selection on traits of the resource organisms
357 can be the result of processes acting at the levels of individuals, populations and communities.

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Table 1: Results of the GLMs of the effects on the probability of a flowering shoot of *Gentiana pneumonanthe*

365 receiving at least one egg from the butterfly *Phengaris alcon* (binomial GLM)
 366 and the number of eggs in shoots with at least one egg (negative binomial GLM), of shoot
 367 phenology, ant abundance (measured as abundance of *Myrmica rubra*), neighbor density and
 368 neighbor phenology, as well as three two-way interactions of these predictors. In the binomial
 369 GLM, two eigenvectors issued from Moran's eigenvector mapping (MEM) are also included as
 370 predictors, in order to reduce residual spatial autocorrelation (see details in the text).

	Probability of having at least one egg (n = 8848, R ² = 0.45)			Number of eggs (n = 731, R ² = 0.23)		
	Estimate	SE	P	Estimate	SE	P
Shoot phenology	1.476	0.079	<0.001	0.251	0.036	<0.001
Ant abundance	-0.028	0.051	0.588	0.117	0.067	<0.001
Neighbor density	-1.673	0.101	<0.001	-0.351	0.067	<0.001
Neighbor phenology	-1.154	0.123	<0.001	-0.105	0.040	0.009
Shoot phenology × Ant abundance	0.116	0.064	0.071	0.057	0.031	0.062
Shoot phenology × Neighbor phenology	0.100	0.072	0.163	0.002	0.034	0.943
Neighbor density × Neighbor phenology	-0.480	0.087	<0.001	-0.089	0.042	0.034
MEM Vector 1	0.281	0.030	<0.001			
MEM Vector 2	0.356	0.050	<0.001			

FIGURE LEGENDS

Figure 1: Sampling design. A) Study plot ($69 \times 45 \text{ m}^2$), comprising 345 3 m^2 subplots. B) Detail of several occupied subplots with reproductive shoots of *Gentiana pneumonanthe* and sampling points for ants. Shoots are represented by points, and colored according to shoot phenology. Numbers indicate the number of *Phengaris alcon* eggs found on the shoot. An example of a 3-m buffer used for neighbor measures on a focal shoot (represented by a star) is shown.

Figure 2: Effects of shoot phenology and host ant abundance on the distribution of *Phengaris alcon* eggs on its host plant *Gentiana pneumonanthe*. A) Effects on the probability of a shoot having at least one egg, the relationship between the probability of having at least one egg and shoot phenology shown for different ant abundances. B) Effects of shoot phenology on the number of eggs in shoots with at least one egg. Higher values of shoot phenology indicate earlier flowering. C) Effects of ant abundance on the number of eggs in shoots with at least one egg. In A), binomial GLM fit lines are represented with a color gradient for a continuous increment in ant abundance within the range of observed values. In B) and C), negative binomial GLM fit lines and confidence intervals are shown.

Figure 3: Effects of the interaction between neighbor density and neighbor phenology on the probability of a flowering shoot of *Gentiana pneumonanthe* having at least one egg of the butterfly *Phengaris alcon* (A) and the number of eggs in shoots with at least one egg (B). The relationships with neighbor density are shown for different values of neighbor phenology. Binomial (A) or negative binomial (B) GLM fit lines are represented with a color gradient for a continuous increment in neighbor phenology within the range of observed values. Higher values of neighbor phenology indicate earlier flowering.

Figure 1

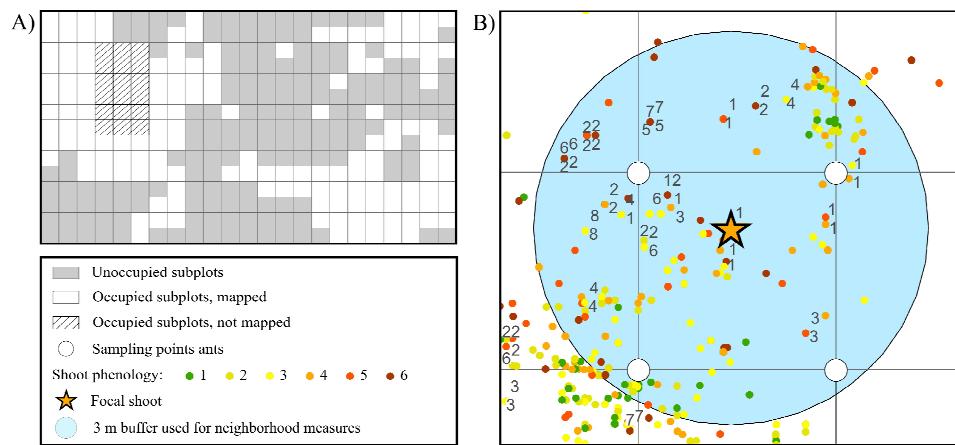


Figure 2

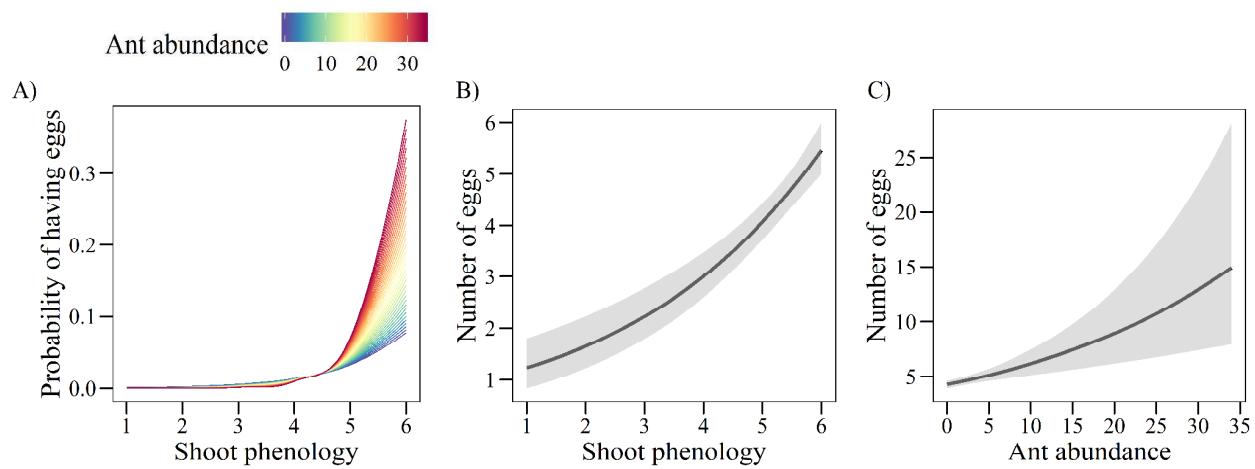
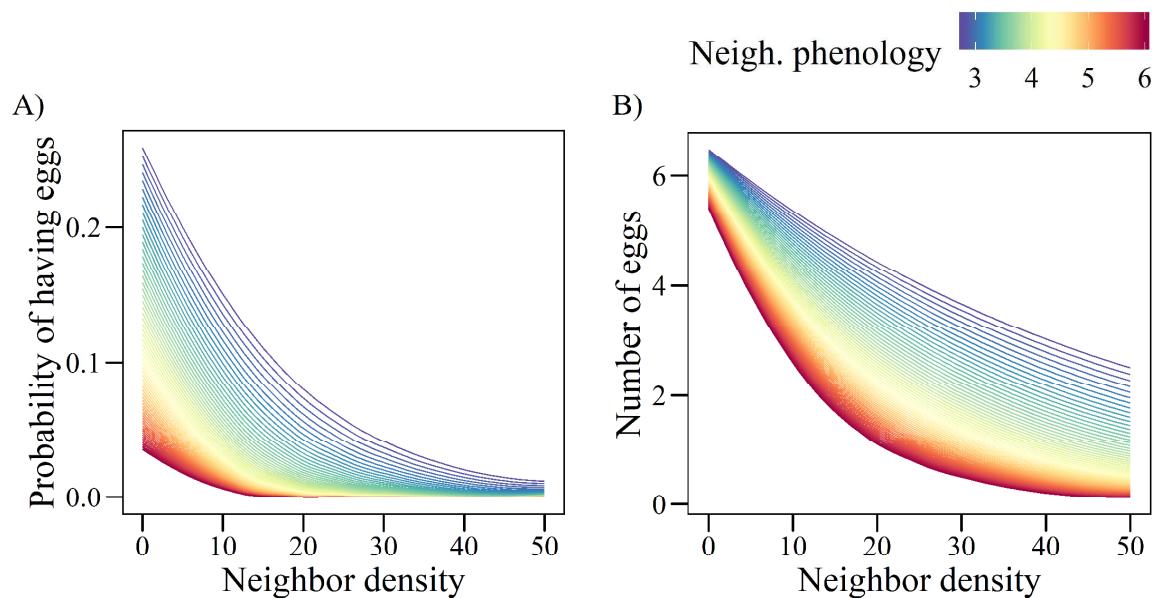


Figure 3



Supporting Information

Table S1: Coefficients from univariate GLMs relating the probability of having eggs (A, binomial model) and the number of eggs in plants with at least one egg (B, negative binomial model) to the abundance of different ant species that might act as hosts of *P. alcon* in the study site.

	A) Probability of having eggs (n = 8848)			B) Number of eggs (n = 731)		
	Estimate	SE	P	Estimate	SE	P
<i>M. rubra</i>	0.174	0.029	<0.001	0.137	0.031	<0.001
<i>M. ruginodis</i>	-0.215	0.046	<0.001	-0.016	0.033	0.620
<i>M. rubra + M. ruginodis</i>	-0.101	0.042	0.015	0.043	0.032	0.180

Table S2: Results of the GLMs of the effects on the probability of a flowering shoot of *Gentiana pneumonanthe* receiving at least one egg from the butterfly *Phengaris alcon* (binomial GLM) and the number of eggs in shoots with at least one egg (negative binomial GLM), of shoot phenology, ant abundance, neighbor density and neighbor phenology, as well as three two-way interactions of these predictors. Ant abundance was measured as abundance of *Myrmica ruginodis* in A) and as the summed abundance of *M. rubra* and *M. ruginodis* in B). In the binomial GLMs, two eigenvectors issued from Moran's eigenvector mapping (MEM) are also included as predictors, in order to reduce residual spatial autocorrelation (see details in the text).

	Probability of having at least one egg (n = 8848, R ² = 0.45)			Number of eggs (n = 731, R ² = 0.20)		
	Estimate	SE	P	Estimate	SE	P
A) Shoot phenology	1.486	0.081	<0.001	0.250	0.036	<0.001
Ant abundance	-0.211	0.086	0.014	-0.030	0.032	0.349
Neighbor density	-1.698	0.104	<0.001	-0.394	0.068	<0.001
Neighbor phenology	-1.173	0.127	<0.001	-0.110	0.041	0.007
Shoot phenology × Ant abundance	0.044	0.085	0.603	0.013	0.039	0.744
Shoot phenology × Neighbor phenology	0.109	0.071	0.124	0.004	0.034	0.906
Neighbor density × Neighbor phenology	-0.484	0.090	<0.001	-0.111	0.043	0.010
MEM Vector 1	0.328	0.032	<0.001			
MEM Vector 2	0.337	0.050	<0.001			
B) Shoot phenology	1.489	0.081	<0.001	0.251	0.036	<0.001
Ant abundance	-0.219	0.085	0.010	0.019	0.031	0.554
Neighbor density	-1.704	0.104	<0.001	-0.381	0.068	<0.001
Neighbor phenology	-1.187	0.127	<0.001	-0.105	0.041	0.010
Shoot phenology × Ant abundance	0.088	0.085	0.302	0.027	0.037	0.459
Shoot phenology × Neighbor phenology	0.105	0.071	0.137	0.005	0.034	0.885
Neighbor density × Neighbor phenology	-0.498	0.090	<0.001	-0.105	0.043	0.014
MEM Vector 1	0.326	0.032	<0.001			

MEM Vector 2

0.348 0.050 <0.001

Table S3: Results of the binomial GLM ($n = 8848$, $R^2 = 0.42$) relating the probability of a shoot of *G. pneumonanthe* having eggs of *P. alcon* to shoot phenology, ant abundance, neighbor density and neighbor phenology, and to three different two-way interactions of these predictors.

	Estimate	SE	P
Shoot phenology	1.401	0.076	<0.001
Ant abundance	0.044	0.050	0.383
Neighbor density	-1.954	0.091	<0.001
Neighbor phenology	-0.982	0.118	<0.001
Shoot phenology x Ant abundance	0.123	0.061	0.044
Shoot phenology x Neighbor phenology	-0.002	0.068	0.971
Neighbor density x Neighbor phenology	-626	0.083	<0.001

***P < 0.001; **P < 0.01; *P < 0.05

Figure S1: Result of the inverse distance weighted interpolation for abundance of *Myrmica rubra* based on abundance values (sum of individuals collected in 2 sampling sessions) at 254 sampling points. The color scale indicates the interpolated abundance values.

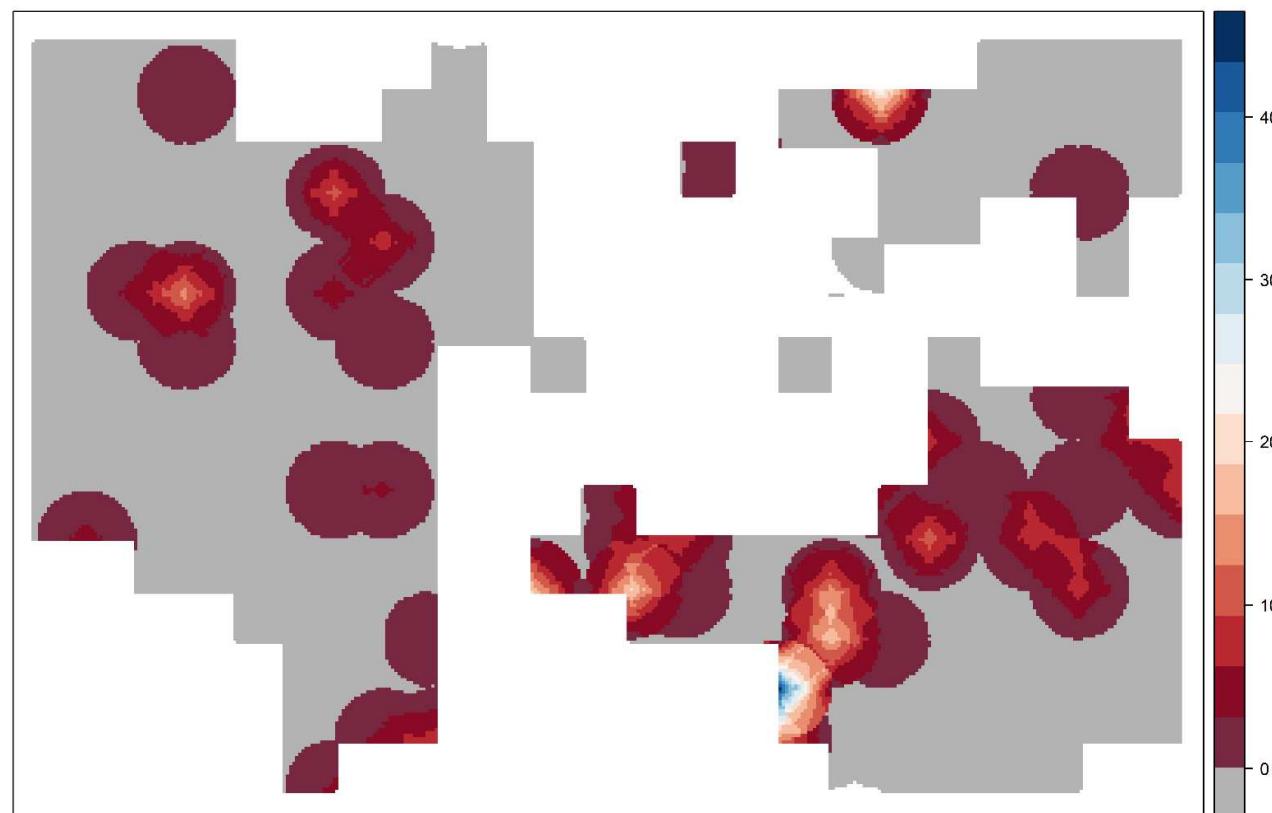


Figure S2: Result of the inverse distance weighted interpolation for abundance of *Myrmica scabrinodis* based on abundance values (sum of individuals collected in 2 sampling sessions) at 254 sampling points. The color scale indicates the interpolated abundance values.

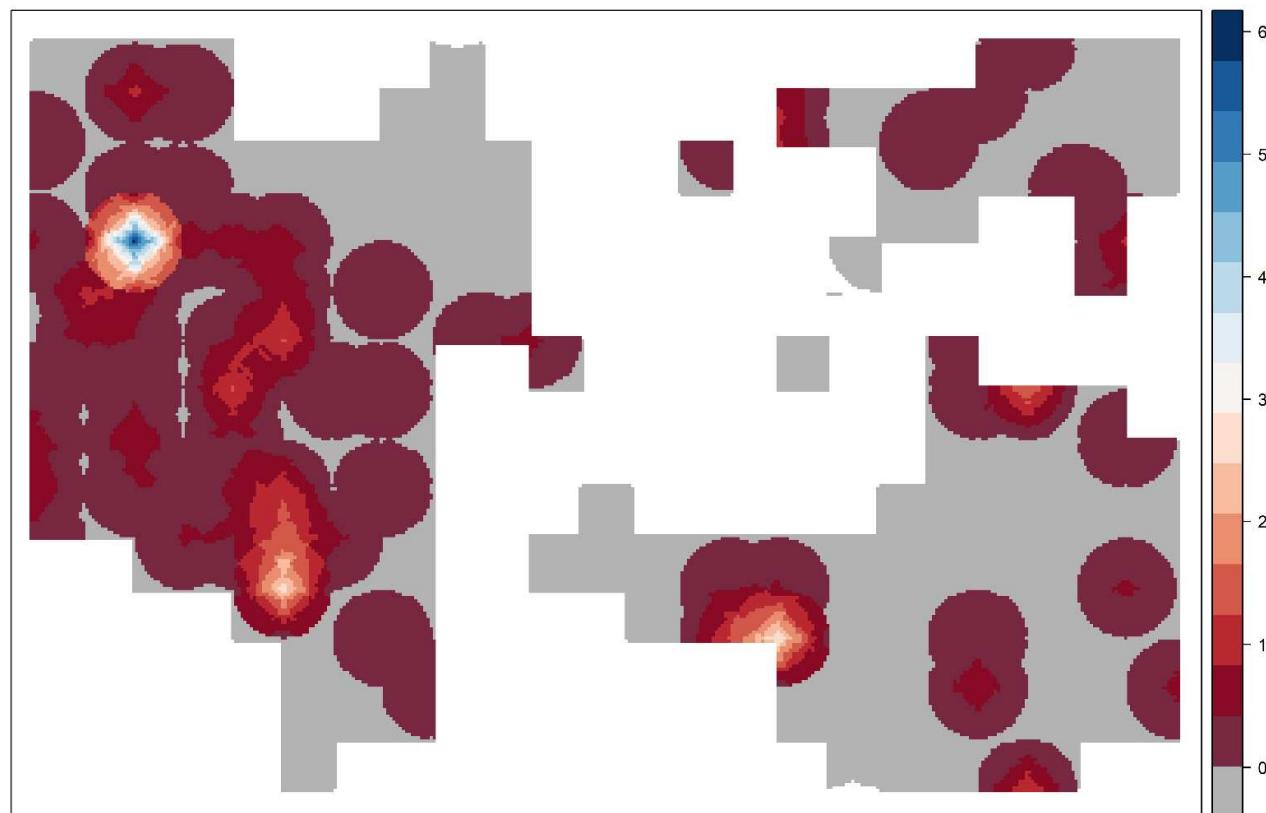


Figure S3: Result of the inverse distance weighted interpolation for abundance of *Myrmica ruginodis* based on abundance values (sum of individuals collected in 2 sampling sessions) at 254 sampling points. The color scale indicates the interpolated abundance values.

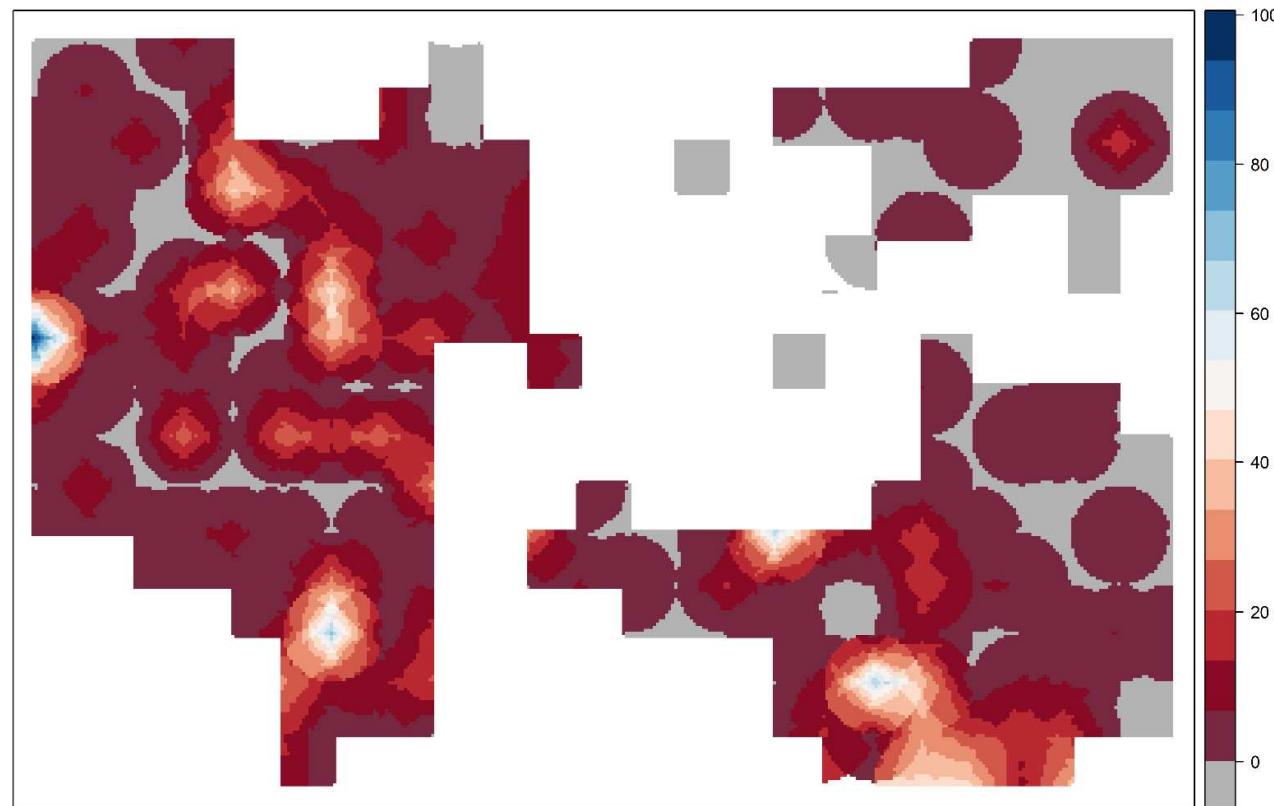


Figure S4: Result of the inverse distance weighted interpolation for abundance of *Myrmica schencki* based on abundance values (sum of individuals collected in 2 sampling sessions) at 254 sampling points. The color scale indicates the interpolated abundance values.

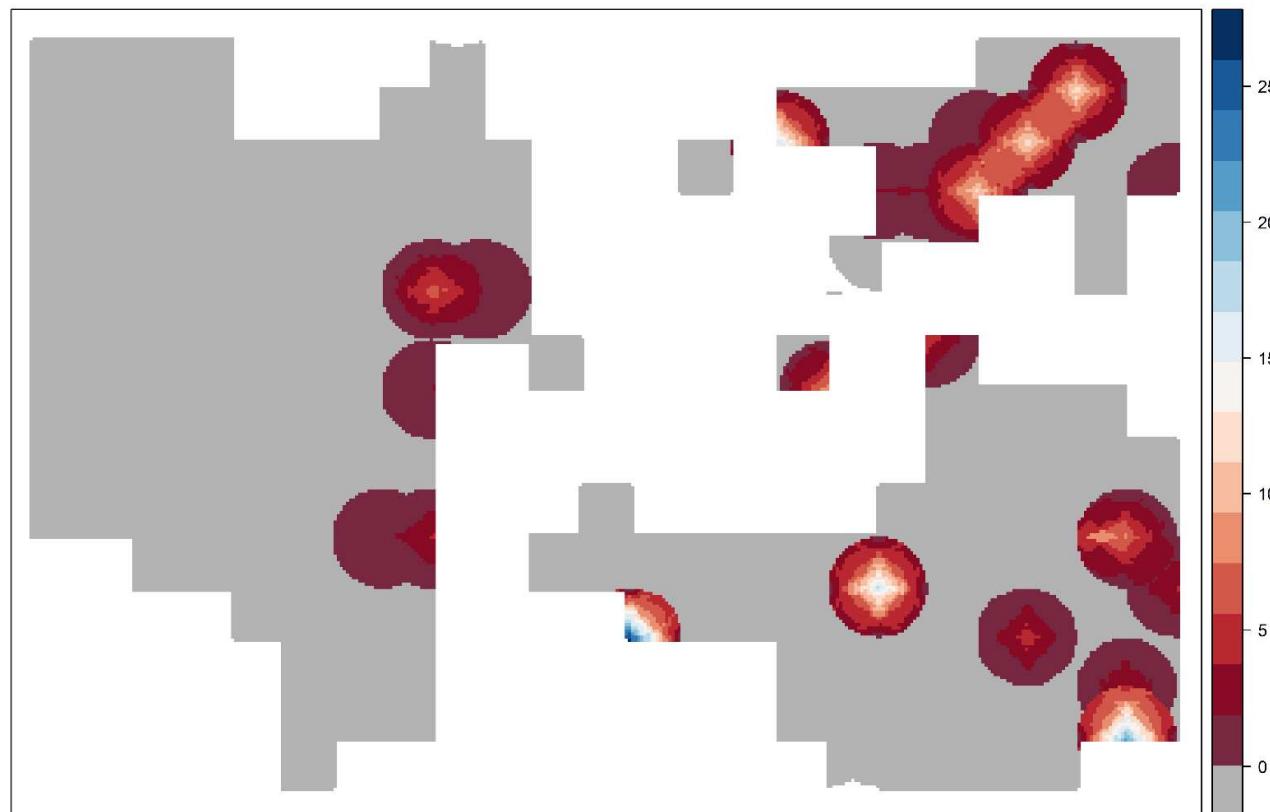


Figure S5: Result of the inverse distance weighted interpolation for abundance of non-*Myrmica* ants based on abundance values (sum of individuals collected in 2 sampling sessions) at 254 sampling points. The color scale indicates the interpolated abundance values.

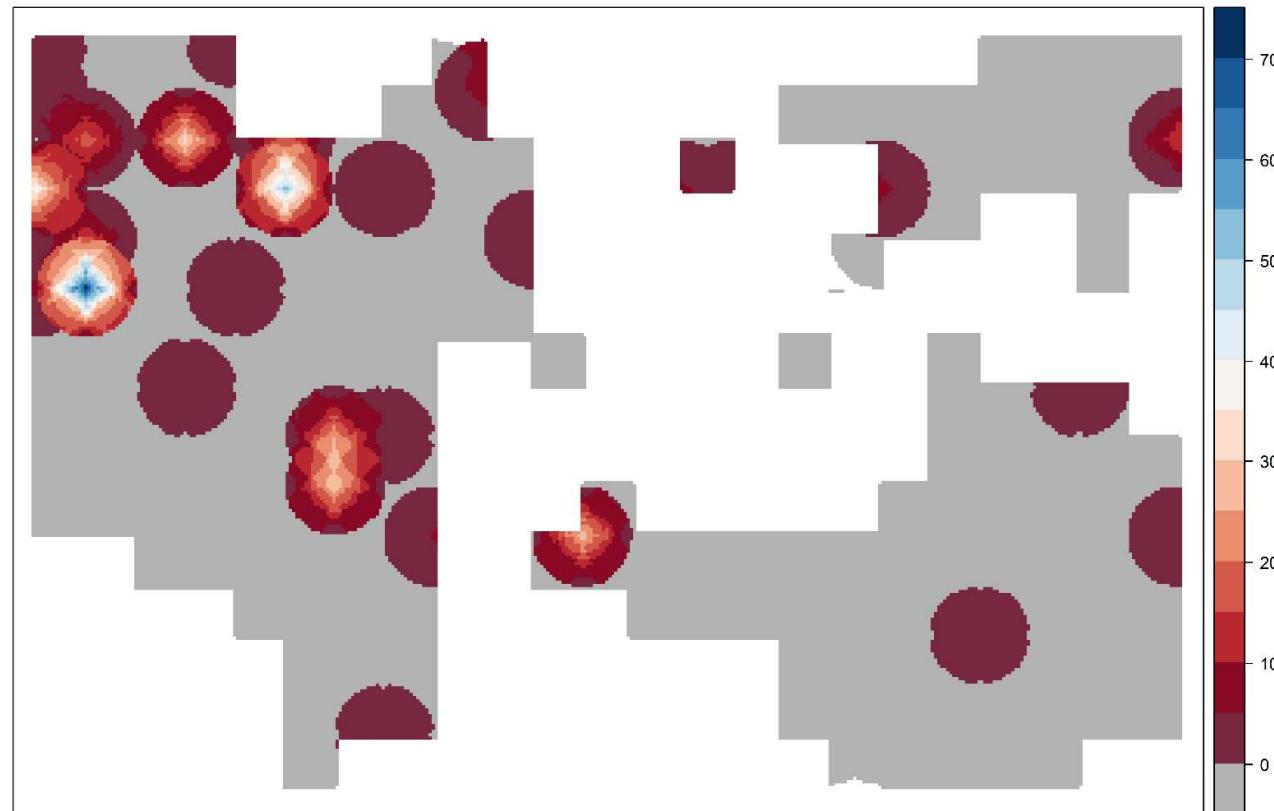


Figure S6: Spatial correlogram of the residuals of the binomial GLMs for the probability of a shoot having eggs before (red) and after (blue) including the two eigenvectors issued from MEM.

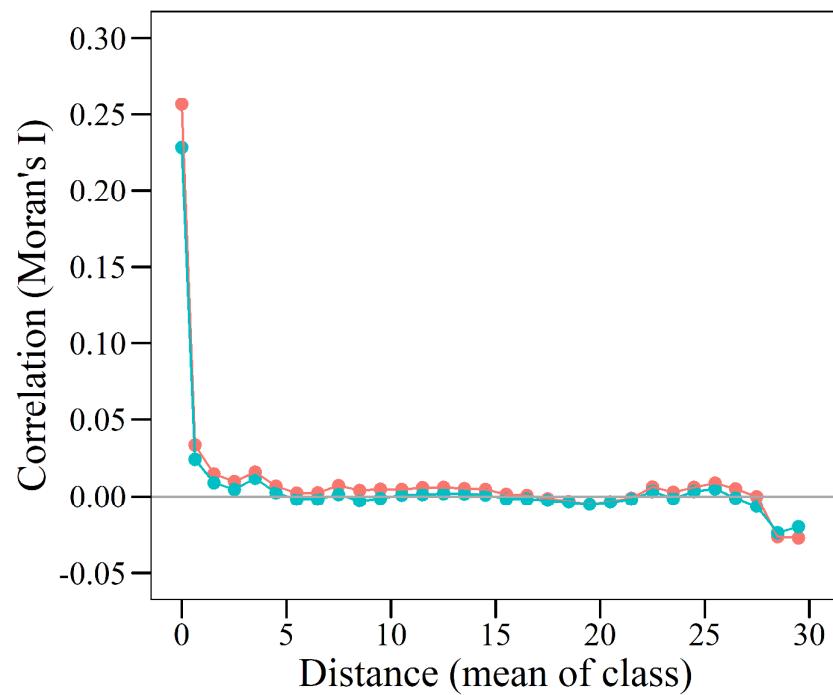


Figure S7: Spatial correlogram of the residuals of the negative binomial GLM for the number of eggs in shoots with at least one egg.

