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2   TITLE: Resource overlap and dilution effects shape host plant use in a myrmecophilous

3   butterfly

4   SHORT TITLE: Resource use in a myrmecophilous butterfly

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14   data with inputs from JE. AV and JE wrote the manuscript.

15

16 ABSTRACT

17 The effects of consumers on fitness of resource organisms are a complex function of the

18 spatio-temporal distribution of the resources, consumer functional responses and trait

19 preferences, and availability of other resources. Using the butterfly *Phengaris alcon* and

20 its two sequential hosts, the plant *Gentiana pneumonanthe* and *Myrmica* ants, we

21 investigated how butterfly egg-laying depended on focal host plant quality, density and

22 quality of neighboring host plants and host ant abundance. Butterflies preferred plants

23 that simultaneously maximized the availability of both larval resources, i.e., they chose

24 higher-quality early-flowering plants where host ants where abundant. Both the

25 probability of oviposition and the number of eggs were lower in plant individuals with a

26 high neighbor density than in more isolated plants, and this dilution effect was stronger

27 when neighbors were of high quality (i.e. flowered early). Our results show that plant-

28 herbivore interactions simultaneously depend on the spatio-temporal distribution of a

29 focal resource, and on the small-scale spatial variation in the abundance of other

30 herbivore resources. Given that consumers have negative effects on fitness and prefer

31 certain traits of the resource organisms, this implies that processes acting at the levels of

32 individuals, populations and communities simultaneously contribute to variation in

33 consumer-mediated natural selection.

34 SIGNIFICANCE STATEMENT

35 Variation in the intensity of species interactions is an important driver of ecological and

36 evolutionary dynamics of natural populations. Still, little is known about the processes

37 causing this variation and the spatial scales at which they operate. We show that the

38 intensity of a plant-butterfly interaction is determined by processes acting at the levels

39 of individuals, populations and communities. Variation in butterfly egg-laying was

40   associated with focal host plant quality, density and quality of neighboring plants, and

41   abundance of ant hosts for caterpillars. We conclude that processes acting at multiple

42   organizational levels simultaneously and interactively determine the intensity of

43   consumer-resource interactions, and suggest that variation in all these processes can

44   drive spatial variation in consumer-mediated natural selection.

45

46   INTRODUCTION

47   Resource-consumer interactions often have important effects on the performance of

48   both partners and the distribution and abundance of consumers is expected to match the

49   spatio-temporal distribution of their resources. Resource use by insect herbivores is

50   often conditioned by oviposition site selection by females. As larval stages usually show

51   low mobility, insect oviposition preferences are predicted to match the spatial and

52   temporal distribution of host plants suitable for offspring development (1–3). The

53   suitability of host plants, in turn, might depend on factors such as host plant nutritional

54   quality (4), size (5), microclimatic conditions (6) or enemy-free space (7). Most

55   consumers depend on multiple resources throughout their life cycle, e.g. different

56   sources of food, shelter and resting sites (8, 9), and the availability of one resource

57   might thus influence the use of other resources. For example, the availability of nectar

58   resources for adults (10) or secondary hosts for larvae (11) might determine host plant

59   choices in butterflies.

60   The quantitative relationship between the abundance of consumers and the

61   abundance of resource organisms, and thus resource exploitation, will depend both on

62   the birth and death processes and on the consumer behavior. Consumer behavior may

63   specifically cause consumer density and resource exploitation to increase (cf. resource

64   concentration hypothesis, e.g. (12–14)) or decrease (cf. resource dilution, e.g. (15)) with

65   increasing patch size and resource abundance. Observed differences in the relationships

66   between resource exploitation and patch size or patch density among different

67   consumers have been suggested to be the result of differences in how emigration and

68   immigration rates depend on patch size and patch density, and on the scale of consumer

69   selection (13, 16). For example, a strong negative relationship between consumer

70   density and patch area observed in visual searchers like butterflies might result from the

71 fact that immigration is diameter-dependent while emigration is perimeter-dependent.

72 Not only should the abundance of the resource organism but also its quality be

73 important for consumer responses. For example, in herbivores that depend on a specific

74 developmental stage of their host plant, the density of plants in suitable developmental

75 stages rather than the overall density is expected to influence host use. While many

76 studies have explored the effects of resource density on plant-insect interactions (17–

77 19), these studies have rarely considered also the role of resource quality and the effects

78 of the availability of other resources.

79   Myrmecophilous butterflies of the genus *Phengaris* need two sequential hosts to

80 complete their development: the caterpillars are predispersal seed predators during their

81 first instars and parasitize ant nests (*Myrmica* spp.) during later stages. Butterflies are

82 very specific regarding both host plant and host ant species and the developmental stage

83 of host plants (20–22). Female butterflies oviposit preferentially on buds in early

84 phenological stages, probably because these constitute higher-quality food; the

85 developing seeds might become tougher, drier and more difficult to digest as buds

86 develop into flowers and fruits (23). In some species, the presence of the preferred bud

87 developmental stages has been shown to overlap more with the period of butterfly

88 oviposition in early- than in late-flowering plants, and individuals flowering early in the

89 season receive more eggs (24). Moreover, the mobility of caterpillars after leaving their

90 host plants is low (25), and further development is possible only if the foraging range of

91 suitable host ants is sufficiently close to the host plant individual (usually a few meters).

92 Butterflies are therefore expected to oviposit on host plants in suitable development

93 stages only if plants occur at micro-sites where ant hosts are present (26, 27).

94   In this study, we investigated how the quality of the focal host plant *Gentiana*

95 *pneumonanthe* (in terms of the developmental stage of the reproductive structures), the

96   density and quality of neighboring conspecific plants, and the abundance of host ants

97   influence egg-laying by the butterfly *Phengaris alcon.* We used an extensive field data

98   set to test two hypotheses: (1) Effects of plant quality and ant abundance on egg

99   distribution patterns are interdependent: butterflies choose plants for oviposition that

100   simultaneously maximize the availability of both resources, i.e. they have a stronger

101   preference for high-quality early-flowering host plants where host ants are abundant,

102   and (2) The probability of a plant receiving at least one egg, as well as the number of

103   eggs in oviposited plants, decreases with increasing conspecific neighbor density (i. e.

104   dilution effect), and this decrease is stronger when neighbors are of high quality.

105   RESULTS

106   Eggs of *P. alcon* were found on 731 (8.3%) of 8848 reproductive shoots of *G.*

107   *pneumonanthe* recorded in 154 subplots. On shoots with at least one egg, the mean

108   number of eggs was 5.03 ± 0.20 SE.

109   The effects of shoot phenology and ant abundance on *P. alcon* oviposition were

110   interdependent. The probability of a shoot of *G. pneumonanthe* having at least one egg

111   increased with an earlier phenology (i.e. with a more advanced floral development at the

112   day of recording, Table 1, Fig. 2A). This increase was stronger in shoots where host

113   ants were more abundant (significant effect of the interaction shoot phenology $\times$ ant

114   abundance, Table 1, Fig. 2A). The number of *P. alcon* eggs on individuals with at least

115   one egg increased with an earlier shoot phenology and with a higher host ant

116   abundance, but there was no significant effect of the interaction between phenology and

117   ant abundance (Table 1, Fig. 2B and C).

118   High densities of host plant shoots resulted in a dilution effect, and the strength

119   of this effect depended on the quality of neighboring plants. Both the probability of

120 having at least one egg and the number of eggs on shoots with at least one egg

121 decreased with the overall density of neighboring host plant shoots (Table 1, Fig. 3). In

122 both cases, the decrease was stronger when neighboring host plants were of higher

123 quality, i.e. had an earlier phenology (significant effect of the interaction neighbor

124 density × neighbor phenology, Table 1, Fig. 3).

125 DISCUSSION

126   The results of this study show that resource use in the myrmecophilous butterfly

127 *P. alcon* is shaped by both the spatial overlap of the two key larval resources and by a

128 dilution effect. Specifically, we found that butterflies prefer to oviposit on early-

129 flowering plants that have a high abundance of host ants, that plants surrounded by

130 many conspecific neighbors receive fewer eggs, and that the dilution effect is stronger

131 when neighbors are of a high quality.

132   We found that both the probability of *P. alcon* butterflies laying at least one egg

133 on a host plant as well as the number of eggs increased with an earlier phenology of its

134 host plant *G. pneumonanthe*. This agrees with previous studies showing that insects

135 usually prefer plants with a particular phenology (28), and more specifically, that

136 antagonists preferentially attack early-flowering plants (22, 24, 29, 30). Interestingly, in

137 our study the strength of this preference for an early plant phenology did depend on the

138 abundance of the antagonist's second resource, i.e. the two host ant species *Myrmica*

139 *rubra* and *M. schencki*. The preference of *P. alcon* for early-flowering host plants was

140 stronger at locations where the host ants were more abundant. For example, the

141 probability of a shoot with the earliest possible phenology receiving at least one egg

142 was 0.07 at sites where host ants were absent, and 0.40 at sites with the maximum ant

143 abundance observed (n = 34 ants). This indicates that the butterflies are able to

144   simultaneously track the distribution of the two resources, and to preferentially oviposit

145   on plants where both the availability of high-quality food for the caterpillars and the

146   probability of adoption by the right species of *Myrmica* are higher. When suitable host

147   ants were absent or very scarce, host plant phenology did not seem to affect egg-laying,

148   and the probability that early-flowering plants should receive eggs was very low. Spatial

149   overlap between the distribution of host plants and host ant nests at larger scales has

150   previously been shown to increase the density and population persistence of the

151   congeneric species *P. arion* (31, 32). Other studies with *Phengaris* butterflies have

152   demonstrated effects of host plant phenology (21, 22, 24), host ant presence (26, 27, 33)

153   or both of these factors (34) for oviposition site selection. Our study shows that the

154   spatial overlap between these two resources also at the scale of the host plant individual

155   is associated with butterfly oviposition preference, and that the effects of plant

156   phenology and ant abundance are interactive. A general implication of our findings is

157   that differences in availability of a resource over very small spatial scales can influence

158   the use of other resource by consumers that depend on multiple resources.

159   Our results show both that there is a dilution effect of local host plant density on

160   butterfly resource use, and that the strength of this effect depends on the quality of

161   neighboring plants. Higher densities of neighboring host plants were associated with

162   both a decreasing probability of a focal plant receiving at least one egg and a lower

163   number of eggs in plants with eggs. Based on our results we are not able to say whether

164   the lower number of eggs was the result of fewer females visiting the plant, or of each

165   visiting female laying fewer eggs. The observed negative relationship between

166   consumer density and overall resource abundance was stronger when the neighbors

167   represented high-quality resources during the period of butterfly flight, i.e. when

168   surrounding plants flowered early in the season. In other words, at a given conspecific

169   density more eggs were found in *G. pneumonanthe* plants surrounded by non-attractive,

170   low-quality neighbors (i.e. late-flowering plants). In our study, plant phenology thus

171   influences butterfly oviposition not only because the phenology of a focal plant interacts

172   with host ant availability to determine plant suitability for oviposition, but also because

173   the phenology of neighbors modulates the strength of host plant density effects on

174   oviposition. Our results suggest that oviposition decisions in myrmecophilous

175   butterflies are taken at two levels. When flying over an area populated with host plants,

176   females might primarily use visual cues (35) to evaluate host plant availability (i.e.

177   density) and identify high-quality (i.e. early-flowering) host plants. When butterflies

178   approach host plants, or after alighting on a plant, females may use both visual cues to

179   evaluate plant quality and chemical cues to detect ant presence (11, 27, 36), thereby

180   evaluating the spatial overlap of the two resources needed by their offspring. If females

181   use plant developmental stage as a cue indicating plant quality, host plants surrounded

182   by low-quality neighbors would be more attractive to butterflies than host plants

183   surrounded by high-quality neighbors. Negative density-dependence in antagonists has

184   been documented also in other systems, where egg clumping on plants with few

185   conspecific neighbors was explained by a disproportionate attraction of insect

186   herbivores to more isolated host plants (37, 38). For herbivores feeding on several plant

187   species, associational effects linked to the surrounding plant community have been

188   documented more frequently (e.g. (39, 40)). Our study shows that associational effects

189   are present also for a specialized herbivore using a single host species, and that the

190   strength of these density-dependent effects depends on the quality of conspecific

191   neighboring host plants.

192   Our results are important to understand the factors causing variation in the

193   intensity of interactions between consumers and their resources. Given that consumers

194   often have important effects on fitness in the consumed organisms and that they show

195   preferences for traits of the resource organisms, identifying the factors that influence the

196   intensity of interactions is also important to understand the mechanisms underlying

197   variation in natural selection. In our study system, the butterfly seed predator has strong

198   negative effects on plant fitness and shows a preference for plants with an early

199   flowering phenology, leading to butterfly-mediated selection for later flowering (22).

200   The results of this study show that the strength of butterfly preferences for early-

201   flowering plants is influenced by both population context, in terms of population density

202   and the trait distribution with the population, and by community context in terms of the

203   abundance of the ant species that function as the second host of butterfly caterpillars.

204   Taken together, these findings illustrate that observed spatial variation in intensities of

205   interactions and consumer-mediated selection on traits of the resource organisms can be

206   the result of processes acting at the levels of individuals, populations and communities.

207   MATERIALS AND METHODS

208   **Study system**

209   The marsh gentian (*Gentiana pneumonanthe* L.) is a rare, long-lived perennial herb,

210   occurring in open habitats, such as wet heathlands and grasslands (41). Plants can have

211   one to many, up to 45 cm high, shoots and produce deep blue flowers that are pollinated

212   by bumblebees. The species is self-compatible and flowers in July and August in the

213   study area (SW Sweden). Fruits are capsules containing a high number of minute, wind-

214   dispersed seeds (mean seed number per fruit $\pm$ SD = 490 $\pm$ 243, mean seed weight =

215   0.041 mg, authors' unpublished data). *Gentiana pneumonanthe* is the host plant of the

216   Alcon Blue butterfly (*Phengaris alcon*), a specialist predispersal seed predator which

217   oviposits on young flower buds in July and August (42). During an oviposition event,

218   adult female butterflies usually lay more than one egg on the same plant and even on the

219   same bud, and there is no evidence of avoiding plants that already carry eggs (35). The

220   caterpillars feed inside the capsule until they reach the fourth instar, when they drop to

221   the ground to be picked up by *Myrmica* ants. Caterpillars mimic the surface chemistry

222   of the ant brood (43) and the acoustic signals of queen ants (44), and these features

223   cause ants to carry them to their nest, where they spend the rest of their larval period as

224   brood parasites. Females of *Phengaris* detect host ant presence through plant chemicals

225   produced by ants or by plants in response to root tissue damage caused by ants (27, 33,

226   36). Contrary to the majority of *Phengaris* species, which prey on ant brood, *P. alcon* is

227   a "cuckoo" species (45), and caterpillars feed primarily on regurgitants from ant

228   workers, trophic eggs (i.e. nutritious, infertile eggs which are fed to the queens and ant

229   larvae) and prey items brought to the nest by ants. Only ants belonging to *Myrmica* sp.

230   can act as hosts of *P. alcon*. In Sweden, *M. rubra* is considered to be the most common

231   host ant species (46).

232   **Data collection**

233   The study was carried out in a population of *G. pneumonanthe*, where the

234   butterfly *P. alcon* was present, located in Tånga Hed nature reserve in the county of

235   Västra Götaland, SW Sweden (58°01'40.0"N 12°49'47.0"E). Field work was conducted

236   between 9 July and 3 September 2016. The plant population occupies a fenced meadow

237   that is grazed by cattle at the end of the summer every year. A study plot measuring 69

238   m × 45 m was established in the meadow. This plot was further divided into a grid

239   comprising 345 3 m × 3 m subplots with corners permanently marked by wooden poles

240   (Fig. 1A). In 154 of the subplots where *G. pneumonanthe* was present, all reproductive

241   shoots of *G. pneumonanthe* were mapped (Fig. 1B), and their phenology and the

242   number of eggs of *P. alcon* were recorded between 29 July and 5 August (18 additional

243   occupied subplots were not possible to fully survey due to time constraints). Shoots

244   were mapped by recording their coordinates within subplots. We mapped shoots rather

245   than plant individuals (that may have one or several shoots) because we judged that

246   individual shoots are the relevant unit for the butterfly to assess the food resource

247   quality and because individual shoots act as the unit of attraction for butterfly females.

248   For each shoot, phenology was recorded as the developmental stage of the most

249   advanced bud, according to six ordinal categories: (1) the sepals covering the bud

250   completely, (2) bud becoming visible, (3) bud growing over the sepals, (4) bud turning

251   blue, (5) flower opening, and (6) flower showing signs of wilting (22). Each stage

252   corresponds to a time interval of flower development, with higher values indicating a

253   more advanced floral development at the day of recording, i.e. an earlier flowering

254   phenology. The number of eggs was counted on the whole shoot.

255   The ant community was sampled at each corner of the occupied subplots (a total

256   of 254 points) at two occasions, 14 July and 3 September (Fig. 1B). Baits consisted of a

257   50-ml plastic tube in which we placed a sugar cube. The tubes were left open on the

258   ground in the evening, and collected the next morning. Ants collected were transferred

259   to 70º ethanol and the number of ants of different *Myrmica* species were counted in the

260   lab (using (47) for identification). Ants belonging to other genera where not identified

261   to species, but counted as "other ants".

262   **Calculation of neighborhood measures**

263   Field maps were digitized using a Geographic Information System (GIS) created

264   with ArcGIS 10.3.1, assigning relative coordinates to each recorded reproductive shoot

265   of *G. pneumonanthe* (Fig. 1B). For each shoot, we defined a buffer zone with a 3-m

266   radius, centered at the focal shoot (see example in Fig. 1B), and calculated the number

267   of reproductive shoots of *G. pneumonanthe* per m^2 within this buffer zone (hereafter,

268   "neighbor density") as well as the mean phenology of these shoots (hereafter, "neighbor

269   phenology"), excluding in each case the focal shoot.

270   **Interpolations of ant abundances**

271   We also incorporated the locations of the 254 points where the ant community was

272   sampled into the GIS. We used inverse distance weighted interpolation (48) based on

273   the values at the sampling points to generate values of the abundance of ant species over

274   the surface of all occupied subplots. A maximum distance of 3 m was used because it

275   represents the ground foraging distance of most investigated *Myrmica* species (Elmes *et*

276   *al.* 1998). From these interpolated surfaces (see Figs. S1-5 in Supporting Information),

277   we extracted values of abundance of the different ant species for each of the mapped

278   shoots.

279   **Statistical analyses**

280   The effects of shoot phenology, host ant abundance, neighbor density and neighbor

281   phenology on *P. alcon* egg distribution were examined using two Generalized Linear

282   Models (GLMs). Effects on the probability of a shoot having at least one egg were

283   evaluated using a binomial GLM, and effects on the number of eggs in shoots with at

284   least one egg were evaluated using a negative binomial GLM. Both models included

285   also the effects of three interactions. First, we included the interaction between shoot

286   phenology and ant abundance in order to test if the effects of the two resources on egg

287   distribution patterns are interdependent. Second, we included the interaction between

288   neighbor density and neighbor phenology in order to test if the effect of host plant

289   density depends on phenology of neighboring host plants. Third, we included the

290   interaction between shoot phenology and neighbor phenology to account for the fact

291   that the relationship between egg distribution and phenology of the focal plant might

292   depend on the phenology of neighboring host plants. As a measure of host ant

293   abundance, we used the summed abundances of *M. rubra* and *M. schencki* (hereafter,

294   "ant abundance"). *M. rubra* is considered to be the most common host ant species of *P.*

295   *alcon* in Sweden (46), and *M. schencki* has been cited as host in several places in

296   Europe (49). Our data agreed with this previous knowledge, as the combined abundance

297   of *M. rubra* and *M. schencki* had the strongest positive effect on the probability of host

298   plants receiving eggs (Supporting Information Table S1).

299   All predictors were standardized by subtracting the mean and dividing by the

300   standard deviation before the analyses. We checked for spatial autocorrelation in the

301   residuals of models by plotting spatial correlograms and by calculating global Moran's I

302   with a permutation test (1000 random permutations). Moran's I was calculated based on

303   a connectivity matrix of pairwise Euclidean distances among the shoots up to a distance

304   of 30 m. Residual spatial autocorrelation could lead to biased model estimates and

305   invalid statistical inference (50). A significant spatial autocorrelation was found in the

306   residuals of the binomial GLM, but not for the negative binomial GLM (global Moran's

307   I = 0.0150, p < 0.001 and global Moran's I = 0.0023, p = 0.613, respectively, Fig. S6

308   and S7 in Supporting Information). We therefore applied Moran's eigenvector mapping

309   (MEM), which translates the spatial arrangement of data points into explanatory

310   variables (eigenvectors) that capture spatial effects, to the binomial model examining

311   effects on the probability of a shoot having at least one egg (51, 52). The model was

312   refitted including two eigenvectors issued from MEM as spatial predictors, and this

313   strongly reduced the residual spatial autocorrelation (global Moran's I = 0.0003, p =

314   0.03297, Fig. S6 in Supporting Information). Although residual spatial autocorrelation

315   was still significant, the low value of Moran's I and visual inspection of the spatial

316 correlogram (Fig. S6) indicated that almost all of the residual spatial autocorrelation

317 was removed by the spatial predictors. The results of this model were similar to the

318 results of the binomial GLM not including the spatial predictors (Table S2 in

319 Supporting Information). Statistical analyses were carried out in R 3.4.0 (53).

320 ACKNOWLEDGEMENTS

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Table 1: 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. In the binomial GLM, 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 = 0.22)	
	Estimate	SE	Estimate	SE
Shoot phenology	1.462 ***	0.079	0.257 ***	0.036
Ant abundance	-0.017	0.052	0.089 **	0.031
Neighbor density	-1.691 ***	0.102	-0.368 ***	0.067
Neighbor phenology	-1.150 ***	0.124	-0.121 **	0.041
Shoot phenology × Ant abundance	0.132 *	0.062	0.004	0.031
Shoot phenology × Neighbor phenology	0.068	0.074	0.014	0.035
Neighbor density × Neighbor phenology	-0.500 ***	0.087	-0.100 *	0.042
MEM Vector 1	0.289 ***	0.030		
MEM Vector 2	0.324 ***	0.052		

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

464

FIGURE LEGENDS

Figure 1: Sampling design. A) Study plot (69×45 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.
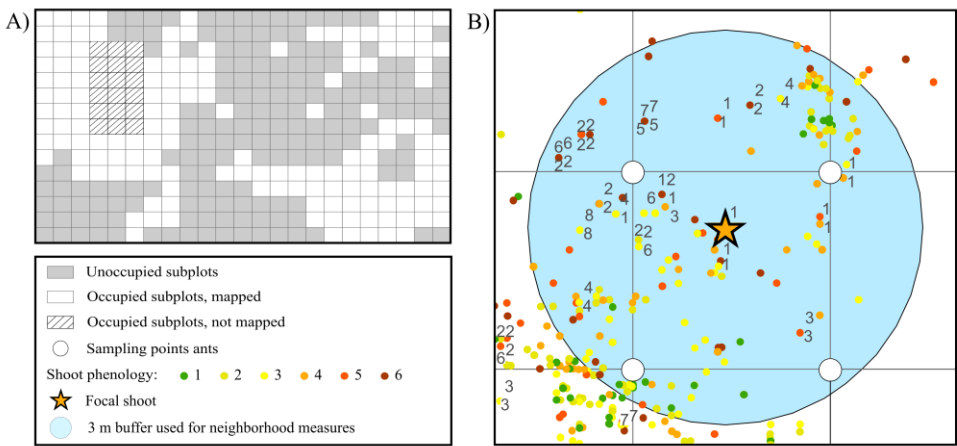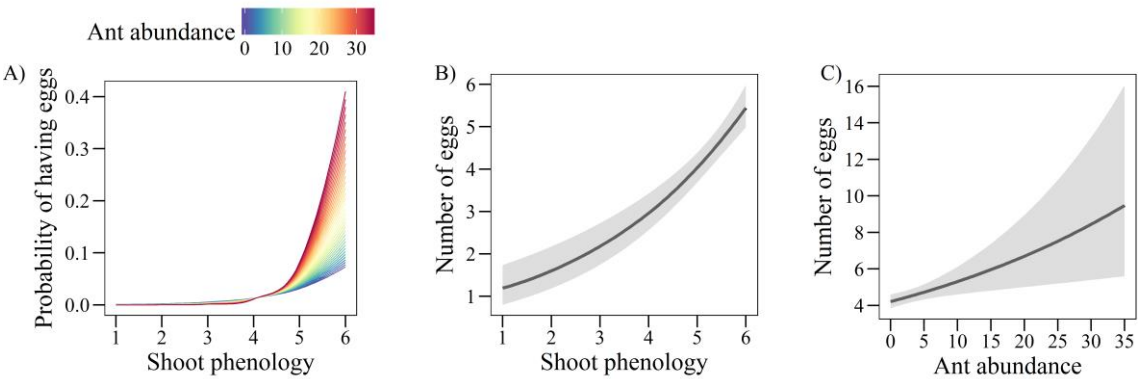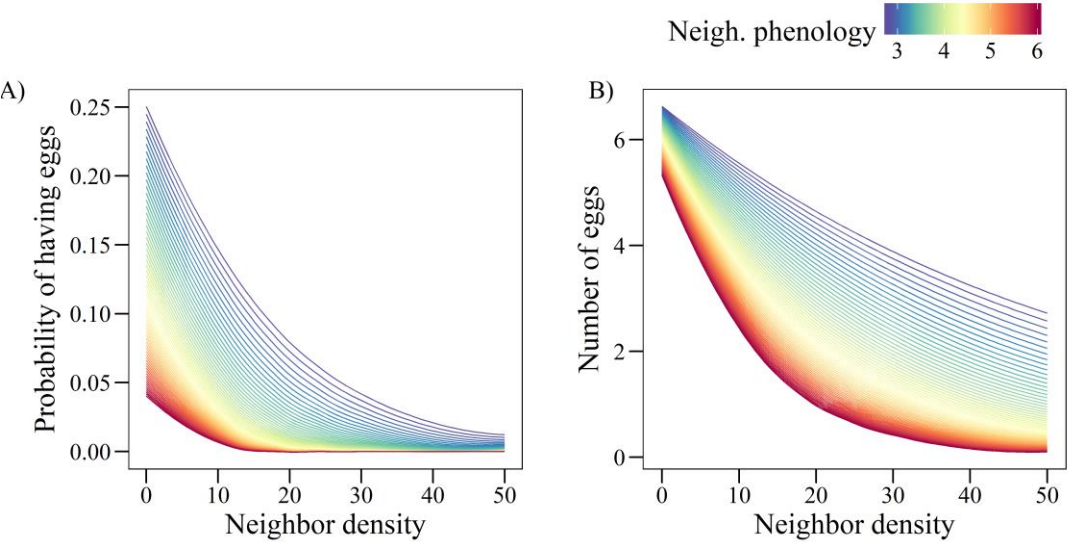
Figure 1

Figure 2

Figure 3

Supporting information

465   Table S1: Coefficients from univariate GLMs relating the probability of having eggs (A,

466   binomial model) and the number of eggs in plants with at least one egg (B, negative

467   binomial model) to the abundance of different ant species.

	A) Probability of having eggs (n = 8848)	B) Number of eggs (n = 731)
All *Myrmica*	-0.522 ***	-0.006
M. rubra	0.174 ***	0.137 ***
M. scabrinodis	-1.364 ***	-0.120 ***
M. ruginodis	-0.215 ***	-0.016
M. schencki	0.358 ***	0.006
Other ants	-0.403 ***	-0.061
M. rubra + M. schencki	0.360 ***	0.115 ***

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

468
469

470 Table S2: Results of the binomial GLM (n = 8848, R^2 = 0.42) relating the probability of

471 a shoot of *G. pneumonanthe* having eggs of *P. alcon* to shoot phenology, ant

472 abundance, neighbor density and neighbor phenology, and to three different two-way

473 interactions of these predictors.

	Estimate		SE
Shoot phenology	1.384	***	0.077
Ant abundance	0.061		0.051
Neighbor density	-1.943	***	0.092
Neighbor phenology	-1.014	***	0.120
Shoot phenology x Ant abundance	0.120	*	0.058
Shoot phenology x Neighbor phenology	-0.022		0.071
Neighbor density x Neighbor phenology	-0.650	*	0.084

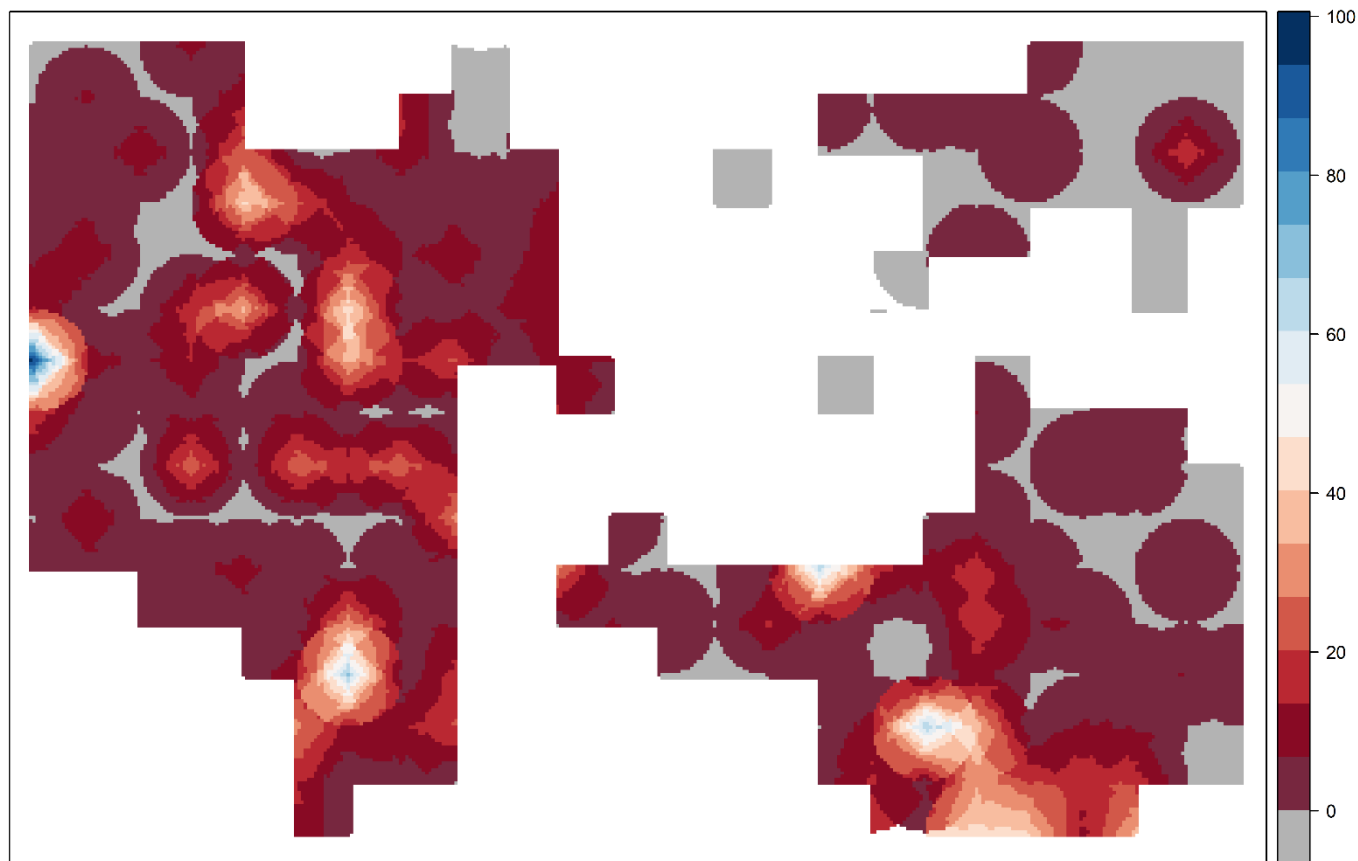***P < 0.001; **P < 0.01; *P < 0.05

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.
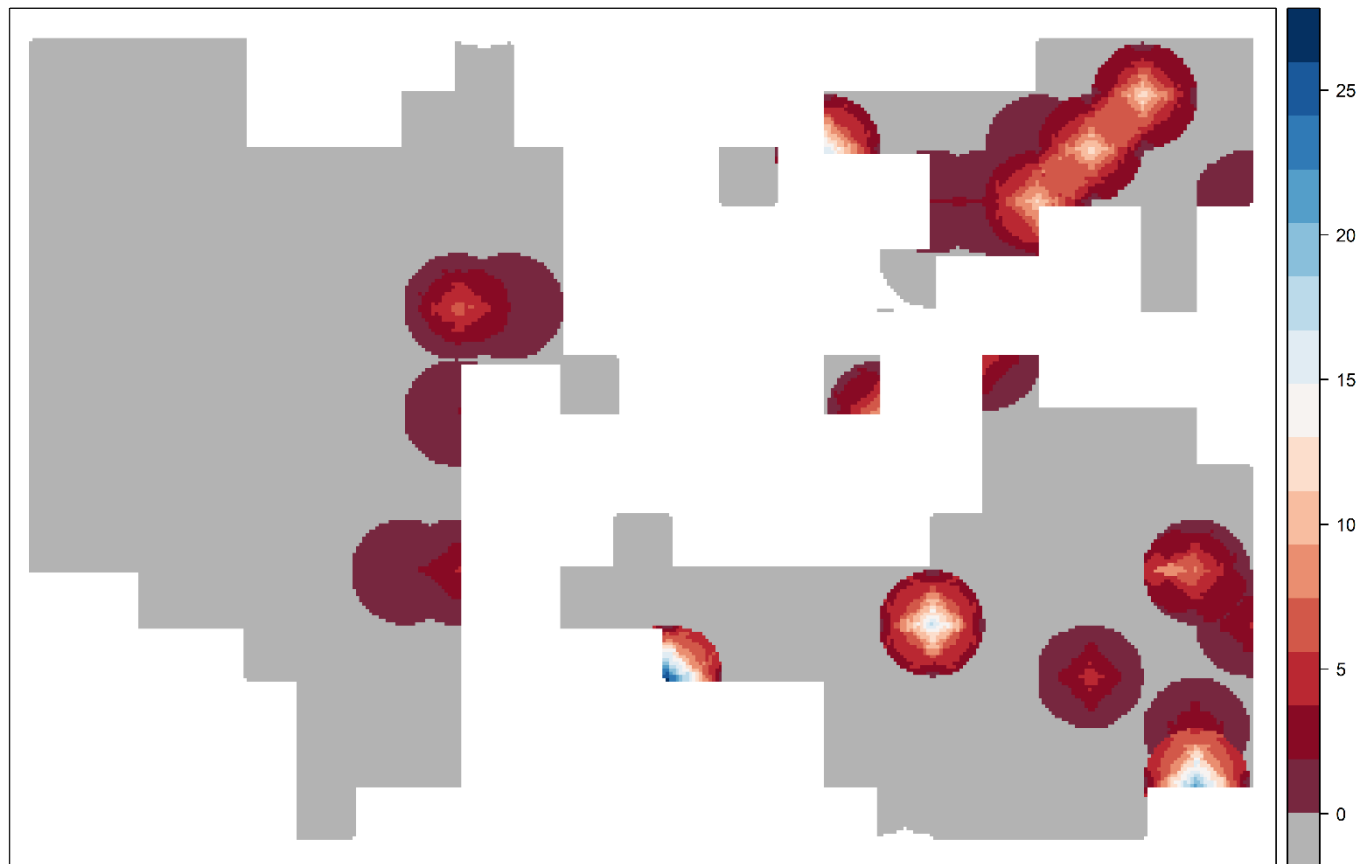

474
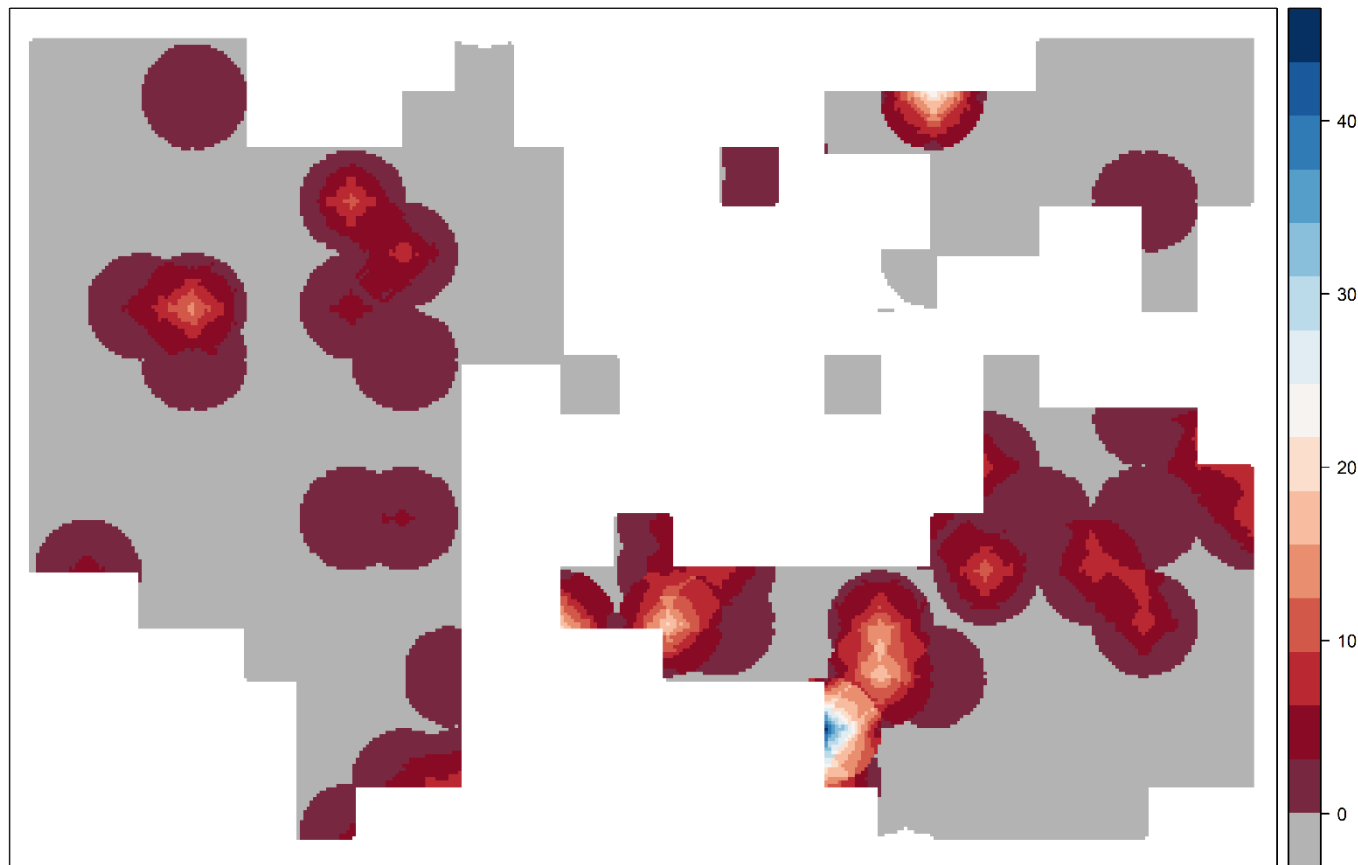
475   Figure S2: Result of the inverse distance weighted interpolation for abundance of *Myrmica scabrinodis* based on abundance values (sum of

476   individuals collected in 2 sampling sessions) at 254 sampling points. The color scale indicates the interpolated abundance values.

477
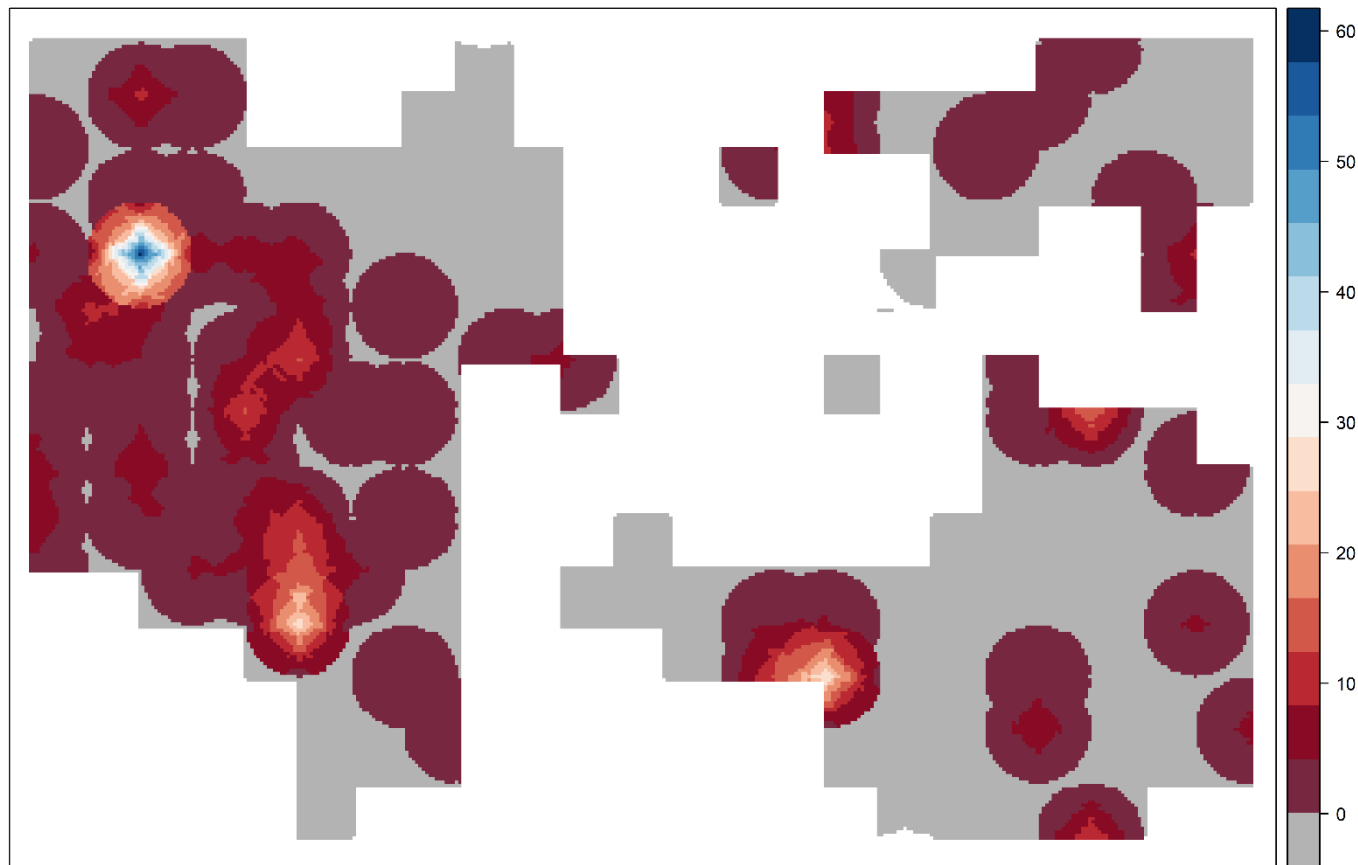
478   Figure S3: Result of the inverse distance weighted interpolation for abundance of *Myrmica ruginodis* based on abundance values (sum of

479   individuals collected in 2 sampling sessions) at 254 sampling points. The color scale indicates the interpolated abundance values.


480

481   Figure S4: Result of the inverse distance weighted interpolation for abundance of *Myrmica schencki* based on abundance values (sum of

482   individuals collected in 2 sampling sessions) at 254 sampling points. The color scale indicates the interpolated abundance values.


483

484   Figure S5: Result of the inverse distance weighted interpolation for abundance of non-*Myrmica* ants based on abundance values (sum of

485   individuals collected in 2 sampling sessions) at 254 sampling points. The color scale indicates the interpolated abundance values.
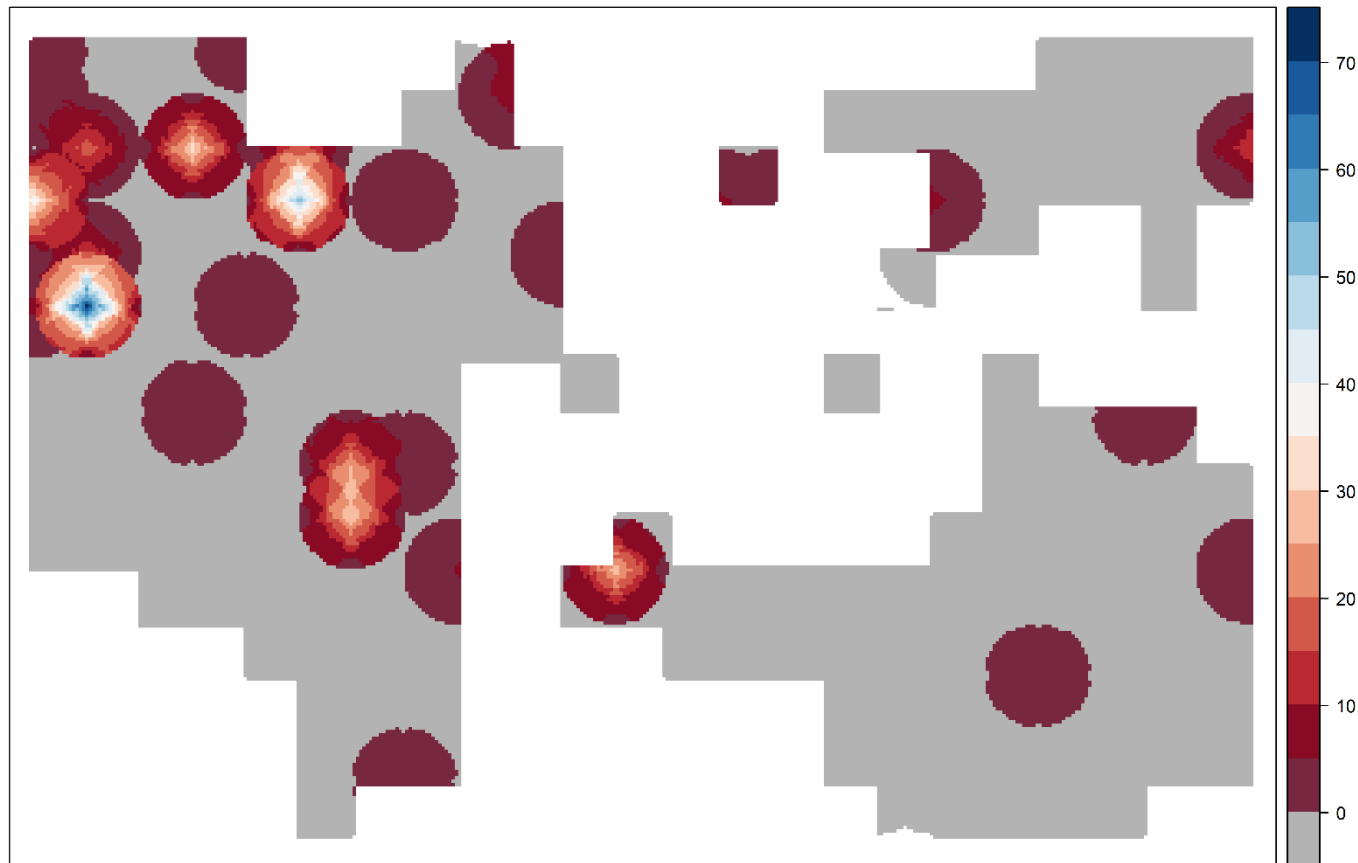
486

487   Figure S6: Spatial correlogram of the residuals of the binomial GLMs for the

488   probability of a shoot having eggs before (red) and after (blue) including the two

489   eigenvectors issued from MEM.
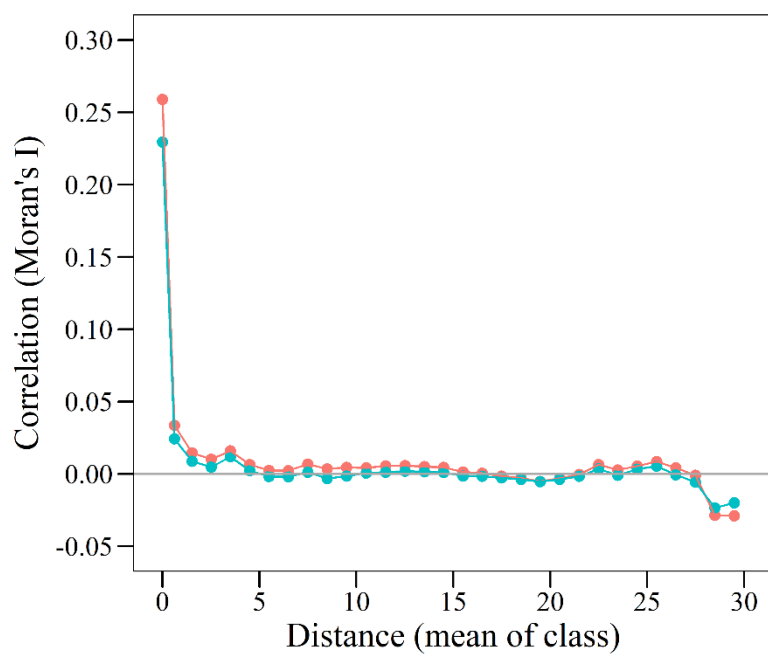
490

491   Figure S7: Spatial correlogram of the residuals of the negative binomial GLM for the

492   number of eggs in shoots with at least one egg.