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

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4 included at the end of the article.
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10 23 ABSTRACT
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13 24 The effects of consumers on resource organisms can depend on the spatio-temporal
14 distribution of the resources, functional responses and trait preferences in the consumer,
15 and availability of other resources. We investigated how egg-laying by the butterfly
16
17 27 *Phengaris alcon* was related to host plant quality, density and quality of neighboring
18 plants, and abundance of a second host, *Myrmica* ants. Butterflies preferred early-
19 flowering plants, and this preference was stronger where host ants were more abundant.
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21 29 Plant individuals with a high neighbor density received fewer eggs than more isolated
22 plants, and this dilution effect was stronger when neighbors flowered early. Our results
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24 30 show that plant-herbivore interactions simultaneously depend on the spatio-temporal
25 distribution of a focal resource, and on the abundance of other herbivore resources.
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27 34 Given negative fitness effects in the plant, they also suggest that spatial variation in
28 selection is the result of processes acting at the individual, population and community
29 level.
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2 37 INTRODUCTION
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5 38 Resource-consumer interactions often have important effects on the performance of
6 both partners and the distribution and abundance of consumers is expected to match the
7 spatio-temporal distribution of their resources. Resource use by insect herbivores is
8 often conditioned by oviposition site selection by females. As larval stages usually show
9 low mobility, insect oviposition preferences are predicted to match the spatial and
10 temporal distribution of host plants suitable for offspring development (Jaenike 1978;
11 Scheirs & De Bruyn 2002; Gripenberg *et al.* 2010). The suitability of host plants, in
12 turn, might depend on factors such as host plant nutritional quality (Chen *et al.* 2004),
13 size (Rabasa *et al.* 2005), microclimatic conditions (Eilers *et al.* 2013) or enemy-free
14 space (Kaminski *et al.* 2010). Most consumers depend on multiple resources throughout
15 their life cycle, e.g. different sources of food, shelter and resting sites (Dennis *et al.*
16 2003, 2006), and the availability of one resource might thus influence the use of other
17 resources. For example, the availability of nectar resources for adults (Öckinger 2008)
18 or secondary hosts for larvae (Wynhoff *et al.* 2015) might determine host plant choices
19 in butterflies.
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22 53 The quantitative relationship between the abundance of consumers and the
23 abundance of resource organisms, and thus resource exploitation, will depend both on
24 the birth and death processes and on the consumer behavior. Consumer behavior may
25 specifically cause consumer density and resource exploitation to increase (cf. resource
26 concentration hypothesis, e.g. Root 1973; Hambäck & Englund 2005; Stephens &
27 Myers 2012) or decrease (cf. resource dilution, e.g. Otway *et al.* 2005) with increasing
28 patch size and resource abundance. Observed differences in the relationships between
29 resource exploitation and patch size or patch density among different consumers have
30 been suggested to be the result of differences in how emigration and immigration rates
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2 depend on patch size and patch density, and on the scale of consumer selection
3 (Hambäck & Englund 2005; Andersson *et al.* 2013). For example, a strong negative
4 relationship between consumer density and patch area observed in visual searchers like
5 butterflies might result from the fact that immigration is diameter-dependent while
6 emigration is perimeter-dependent. Not only should the abundance of the resource
7 organism but also its quality be important for consumer responses. For example, in
8 herbivores that depend on a specific developmental stage of their host plant, the density
9 of plants in suitable developmental stages rather than the overall density is expected to
10 influence host use. While many studies have explored the effects of resource density on
11 plant-insect interactions (Yamamura 2002; Kula *et al.* 2014; Kim & Underwood 2015),
12 these studies have rarely considered also the role of resource quality and the effects of
13 the availability of other resources.
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16 Myrmecophilous butterflies of the genus *Phengaris* need two sequential hosts to
17 complete their development: the caterpillars are predispersal seed predators during their
18 first instars and parasitize ant nests (*Myrmica* spp.) during later stages. Butterflies are
19 very specific regarding both host plant and host ant species and the developmental stage
20 of host plants (Elmes *et al.* 1998; Thomas & Elmes 2001; Valdés & Ehrlén 2017).
21 Female butterflies oviposit preferentially on buds in early phenological stages, probably
22 because these constitute higher-quality food; the developing seeds might become
23 tougher, drier and more difficult to digest as buds develop into flowers and fruits
24 (Arnaldo *et al.* 2014). In some species, the presence of the preferred bud developmental
25 stages has been shown to overlap more with the period of butterfly oviposition in early-
26 than in late-flowering plants, and individuals flowering early in the season receive more
27 eggs (Valdés & Ehrlén 2017, *in press*). Moreover, the mobility of caterpillars after
28 leaving their host plants is low (Hayes 2015), and further development is possible only
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2 87 if the foraging range of suitable host ants is sufficiently close to the host plant individual
3 88 (usually a few meters). Butterflies are therefore expected to oviposit on host plants in
4 89 suitable development stages only if plants occur at micro-sites where ant hosts are
5 90 present (Wynhoff *et al.* 2008; Wynhoff & Langevelde 2017).

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12 91 In this study, we investigated how the quality of the focal host plant *Gentiana*
13 92 *pneumonanthe* (in terms of the developmental stage of the reproductive structures), the
14 93 density and quality of neighboring conspecific plants, and the abundance of host ants
15 94 influence egg-laying by the butterfly *Phengaris alcon*. We used an extensive field data
16 95 set to test two hypotheses: (1) Effects of plant quality and ant abundance on egg
17 96 distribution patterns are interdependent: butterflies choose plants for oviposition that
18 97 simultaneously maximize the availability of both resources, i.e. they have a stronger
19 98 preference for high-quality early-flowering host plants where host ants are abundant,
20 99 and (2) The probability of a plant receiving at least one egg, as well as the number of
21 100 eggs in oviposited plants, decreases with increasing conspecific neighbor density (i. e.
22 101 dilution effect), and this decrease is stronger when neighbors are of high quality.

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37 102 METHODS

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40 103 Study system

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42 104 The marsh gentian (*Gentiana pneumonanthe* L.) is a rare, long-lived perennial herb,
43 105 occurring in open habitats, such as wet heathlands and grasslands (Simmonds 1946).
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46 106 Plants can have one to many, up to 45 cm high, shoots and produce deep blue flowers
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48 107 that are pollinated by bumblebees. The species is self-compatible and flowers in July
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50 108 and August in the study area (SW Sweden). Fruits are capsules containing a high
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52 109 number of minute, wind-dispersed seeds (mean seed number per fruit \pm SD = 490 \pm
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54 110 243, mean seed weight = 0.041 mg, authors' unpublished data). *Gentiana*

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3 111 *pneumonanthe* is the host plant of the Alcon Blue butterfly (*Phengaris alcon*), a
4 112 specialist predispersal seed predator which oviposits on young flower buds in July and
5 113 August (Appelqvist & Bengtsson 2007). During an oviposition event, adult female
6 114 butterflies usually lay more than one egg on the same plant and even on the same bud,
7 115 and there is no evidence of avoiding plants that already carry eggs (Van Dyck &
8 116 Regniers 2010). The caterpillars feed inside the capsule until they reach the fourth
9 117 instar, when they drop to the ground to be picked up by *Myrmica* ants. Caterpillars
10 118 mimic the surface chemistry of the ant brood (Nash *et al.* 2008) and the acoustic signals
11 119 of queen ants (Sala *et al.* 2014), and these features cause ants to carry them to their nest,
12 120 where they spend the rest of their larval period as brood parasites. Females of *Phengaris*
13 121 detect host ant presence through plant chemicals produced by ants or by plants in
14 122 response to root tissue damage caused by ants (van Dyck *et al.* 2000; Patricelli *et al.*
15 123 2015; Wyhoffs & Langewelde 2017). Contrary to the majority of *Phengaris* species,
16 124 which prey on ant brood, *P. alcon* is a “cuckoo” species (Als *et al.* 2004), and
17 125 caterpillars feed primarily on regurgitants from ant workers, trophic eggs (i.e. nutritious,
18 126 infertile eggs which are fed to the queens and ant larvae) and prey items brought to the
19 127 nest by ants. Only ants belonging to *Myrmica* sp. can act as hosts of *P. alcon*. In
20 128 Sweden, *M. rubra* is considered to be the most common host ant species (Elmes *et al.*
21 129 1994).

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23 130 **Data collection**

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25 131 The study was carried out in a population of *G. pneumonanthe*, where the
26 132 butterfly *P. alcon* was present, located in Tånga Hed nature reserve in the county of
27 133 Västra Götaland, SW Sweden (58°01'40.0"N 12°49'47.0"E). Field work was conducted
28 134 between 9 July and 3 September 2016. The plant population occupies a fenced meadow
29 135 that is grazed by cattle at the end of the summer every year. A study plot measuring 69

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3 136 m × 45 m was established in the meadow. This plot was further divided into a grid
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5 137 comprising 345 3 m × 3 m subplots with corners permanently marked by wooden poles
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7 138 (Fig. 1A). In 154 of the subplots where *G. pneumonanthe* was present, all reproductive
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9 139 shoots of *G. pneumonanthe* were mapped (Fig. 1B), and their phenology and the
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11 140 number of eggs of *P. alcon* were recorded between 29 July and 5 August (18 additional
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13 141 occupied subplots were not possible to fully survey due to time constraints). Shoots
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15 142 were mapped by recording their coordinates within subplots. We mapped shoots rather
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17 143 than plant individuals (that may have one or several shoots) because we judged that
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19 144 individual shoots are the relevant unit for the butterfly to assess the food resource
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21 145 quality and because individual shoots act as the unit of attraction for butterfly females.
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24 146 For each shoot, phenology was recorded as the developmental stage of the most
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26 147 advanced bud, according to six ordinal categories: (1) the sepals covering the bud
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28 148 completely, (2) bud becoming visible, (3) bud growing over the sepals, (4) bud turning
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30 149 blue, (5) flower opening, and (6) flower showing signs of wilting (Valdés & Ehrlén
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32 150 2017). Each stage corresponds to a time interval of flower development, with higher
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34 151 values indicating a more advanced floral development at the day of recording, i.e. an
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36 152 earlier flowering phenology. The number of eggs was counted on the whole shoot.

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39 153 The ant community was sampled at each corner of the occupied subplots (a total
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41 154 of 254 points) at two occasions, 14 July and 3 September (Fig. 1B). Baits consisted of a
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43 155 50-ml plastic tube in which we placed a sugar cube. The tubes were left open on the
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45 156 ground in the evening, and collected the next morning. Ants collected were transferred
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47 157 to 70° ethanol and the number of ants of different *Myrmica* species were counted in the
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49 158 lab (using Douwes *et al.* 2012 for identification). Ants belonging to other genera where
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51 159 not identified to species, but counted as “other ants”.

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54 160 **Calculation of neighborhood measures**

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3 161 Field maps were digitized using a Geographic Information System (GIS) created
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5 162 with ArcGIS 10.3.1, assigning relative coordinates to each recorded reproductive shoot
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7 163 of *G. pneumonanthe* (Fig. 1B). For each shoot, we defined a buffer zone with a 3-m
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9 164 radius, centered at the focal shoot (see example in Fig. 1B), and calculated the number
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11 165 of reproductive shoots of *G. pneumonanthe* per m² within this buffer zone (hereafter,
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13 166 “neighbor density”) as well as the mean phenology of these shoots (hereafter, “neighbor
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15 167 phenology”), excluding in each case the focal shoot.

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18 168 **Interpolations of ant abundances**

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21 169 We also incorporated the locations of the 254 points where the ant community was
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23 170 sampled into the GIS. We used inverse distance weighted interpolation (Pebesma 2004)
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25 171 based on the values at the sampling points to generate values of the abundance of ant
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27 172 species over the surface of all occupied subplots. A maximum distance of 3 m was used
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29 173 because it represents the ground foraging distance of most investigated *Myrmica* species
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31 174 (Elmes *et al.* 1998). From these interpolated surfaces (see Figs. S1-5 in Supporting
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33 175 Information), we extracted values of abundance of the different ant species for each of
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35 176 the mapped shoots.

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37 177 **Statistical analyses**

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40 178 The effects of shoot phenology, host ant abundance, neighbor density and neighbor
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42 179 phenology on *P. alcon* egg distribution were examined using two Generalized Linear
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44 180 Models (GLMs). Effects on the probability of a shoot having at least one egg were
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46 181 evaluated using a binomial GLM, and effects on the number of eggs in shoots with at
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48 182 least one egg were evaluated using a negative binomial GLM. Both models included
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50 183 also the effects of three interactions. First, we included the interaction between shoot
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52 184 phenology and ant abundance in order to test if the effects of the two resources on egg

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3 distribution patterns are interdependent. Second, we included the interaction between
4 neighbor density and neighbor phenology in order to test if the effect of host plant
5 density depends on phenology of neighboring host plants. Third, we included the
6 interaction between shoot phenology and neighbor phenology to account for the fact
7 that the relationship between egg distribution and phenology of the focal plant might
8 depend on the phenology of neighboring host plants. As a measure of host ant
9 abundance, we used the summed abundances of *M. rubra* and *M. schencki* (hereafter,
10 "ant abundance"). *M. rubra* is considered to be the most common host ant species of *P.*
11 *alcon* in Sweden (Elmes *et al.* 1994), and *M. schencki* has been cited as host in several
12 places in Europe (Vilbas *et al.* 2016). Our data agreed with this previous knowledge, as
13 the combined abundance of *M. rubra* and *M. schencki* had the strongest positive effect
14 on the probability of host plants receiving eggs (Supporting Information Table S1).

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30 All predictors were standardized by subtracting the mean and dividing by the
31 standard deviation before the analyses. We checked for spatial autocorrelation in the
32 residuals of models by plotting spatial correlograms and by calculating global Moran's I
33 with a permutation test (1000 random permutations). Moran's I was calculated based on
34 a connectivity matrix of pairwise Euclidean distances among the shoots up to a distance
35 of 30 m. Residual spatial autocorrelation could lead to biased model estimates and
36 invalid statistical inference (Dormann *et al.* 2007). A significant spatial autocorrelation
37 was found in the residuals of the binomial GLM, but not for the negative binomial GLM
38 (global Moran's I = 0.0150, p < 0.001 and global Moran's I = 0.0023, p = 0.613,
39 respectively, Fig. S6 and S7 in Supporting Information). We therefore applied Moran's
40 eigenvector mapping (MEM), which translates the spatial arrangement of data points
41 into explanatory variables (eigenvectors) that capture spatial effects, to the binomial
42 model examining effects on the probability of a shoot having at least one egg (Dray *et*
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3 210 *al.* 2006; Thayn & Simanis 2013). The model was refitted including two eigenvectors
4 issued from MEM as spatial predictors, and this strongly reduced the residual spatial
5 autocorrelation (global Moran's I = 0.0003, p = 0.03297, Fig. S6 in Supporting
6 Information). Although residual spatial autocorrelation was still significant, the low
7 value of Moran's I and visual inspection of the spatial correlogram (Fig. S6) indicated
8 that almost all of the residual spatial autocorrelation was removed by the spatial
9 predictors. The results of this model were similar to the results of the binomial GLM not
10 including the spatial predictors (Table S2 in Supporting Information). Statistical
11 analyses were carried out in R 3.4.0 (R Core Team 2017).

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20 219 RESULTS
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26 220 Eggs of *P. alcon* were found on 731 (8.3%) of 8848 reproductive shoots of *G.*
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28 *pneumonanthe* recorded in 154 subplots. On shoots with at least one egg, the mean
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30 number of eggs was 5.03 ± 0.20 SE.

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50 223 The effects of shoot phenology and ant abundance on *P. alcon* oviposition were
224 interdependent. The probability of a shoot of *G. pneumonanthe* having at least one egg
225 increased with an earlier phenology (i.e. with a more advanced floral development at the
226 day of recording, Table 1, Fig. 2A). This increase was stronger in shoots where host
227 ants were more abundant (significant effect of the interaction shoot phenology \times ant
228 abundance, Table 1, Fig. 2A). The number of *P. alcon* eggs on individuals with at least
229 one egg increased with an earlier shoot phenology and with a higher host ant
230 abundance, but there was no significant effect of the interaction between phenology and
231 ant abundance (Table 1, Fig. 2B and C).

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50 232 High densities of host plant shoots resulted in a dilution effect, and the strength
233 of this effect depended on the quality of neighboring plants. Both the probability of

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3 234 having at least one egg and the number of eggs on shoots with at least one egg
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5 235 decreased with the overall density of neighboring host plant shoots (Table 1, Fig. 3). In
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7 236 both cases, the decrease was stronger when neighboring host plants were of higher
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9 237 quality, i.e. had an earlier phenology (significant effect of the interaction neighbor
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11 238 density × neighbor phenology, Table 1, Fig. 3).

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14 239 DISCUSSION
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18 240 The results of this study show that resource use in the myrmecophilous butterfly
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20 241 *P. alcon* is shaped by both the spatial overlap of the two key larval resources and by a
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22 242 dilution effect. Specifically, we found that butterflies prefer to oviposit on early-
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24 243 flowering plants that have a high abundance of host ants, that plants surrounded by
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26 244 many conspecific neighbors receive fewer eggs, and that the dilution effect is stronger
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28 245 when neighbors are of a high quality.

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31 246 We found that both the probability of *P. alcon* butterflies laying at least one egg
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33 247 on a host plant as well as the number of eggs increased with an earlier phenology of its
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35 248 host plant *G. pneumonanthe*. This agrees with previous studies showing that insects
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37 249 usually prefer plants with a particular phenology (Elzinga *et al.* 2007), and more
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39 250 specifically, that antagonists preferentially attack early-flowering plants

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41 251 (Parachnowitsch & Caruso 2008; König *et al.* 2015; Valdés & Ehrlén 2017, *in press*).
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43 252 Interestingly, in our study the strength of this preference for an early plant phenology
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45 253 did depend on the abundance of the antagonist's second resource, i.e. the two host ant
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47 254 species *Myrmica rubra* and *M. schencki*. The preference of *P. alcon* for early-flowering
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49 255 host plants was stronger at locations where the host ants were more abundant. For
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51 256 example, the probability of a shoot with the earliest possible phenology receiving at
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53 257 least one egg was 0.07 at sites where host ants were absent, and 0.40 at sites with the

maximum ant abundance observed ($n = 34$ ants). This indicates that the butterflies are able to simultaneously track the distribution of the two resources, and to preferentially oviposit on plants where both the availability of high-quality food for the caterpillars and the probability of adoption by the right species of *Myrmica* are higher. When suitable host ants were absent or very scarce, host plant phenology did not seem to affect egg-laying, and the probability that early-flowering plants should receive eggs was very low. Spatial overlap between the distribution of host plants and host ant nests at larger scales has previously been shown to increase the density and population persistence of the congeneric species *P. arion* (Thomas *et al.* 2009; Casacci *et al.* 2011). Other studies with *Phengaris* butterflies have demonstrated effects of host plant phenology (Thomas & Elmes 2001; Valdés & Ehrlén 2017, *in press*), host ant presence (van Dyck *et al.* 2000; Wynhoff *et al.* 2008; Wynhoff & Langevelde 2017) or both of these factors (Patricelli *et al.* 2011) for oviposition site selection. Our study shows that the spatial overlap between these two resources also at the scale of the host plant individual is associated with butterfly oviposition preference, and that the effects of plant phenology and ant abundance are interactive. A general implication of our findings is that differences in availability of a resource over very small spatial scales can influence the use of other resource by consumers that depend on multiple resources.

Our results show both that there is a dilution effect of local host plant density on butterfly resource use, and that the strength of this effect depends on the quality of neighboring plants. Higher densities of neighboring host plants were associated with both a decreasing probability of a focal plant receiving at least one egg and a lower number of eggs in plants with eggs. Based on our results we are not able to say whether the lower number of eggs was the result of fewer females visiting the plant, or of each visiting female laying fewer eggs. The observed negative relationship between

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2 consumer density and overall resource abundance was stronger when the neighbors
3 represented high-quality resources during the period of butterfly flight, i.e. when
4 surrounding plants flowered early in the season. In other words, at a given conspecific
5 density more eggs were found in *G. pneumonanthe* plants surrounded by non-attractive,
6 low-quality neighbors (i.e. late-flowering plants). In our study, plant phenology thus
7 influences butterfly oviposition not only because the phenology of a focal plant interacts
8 with host ant availability to determine plant suitability for oviposition, but also because
9 the phenology of neighbors modulates the strength of host plant density effects on
10 oviposition. Our results suggest that oviposition decisions in myrmecophilous
11 butterflies are taken at two levels. When flying over an area populated with host plants,
12 females might primarily use visual cues (Van Dyck & Regniers 2010) to evaluate host
13 plant availability (i.e. density) and identify high-quality (i.e. early-flowering) host
14 plants. When butterflies approach host plants, or after alighting on a plant, females may
15 use both visual cues to evaluate plant quality and chemical cues to detect ant presence
16 (Patricelli *et al.* 2015; Wynhoff *et al.* 2015; Wynhoff & Langevelde 2017), thereby
17 evaluating the spatial overlap of the two resources needed by their offspring. If females
18 use plant developmental stage as a cue indicating plant quality, host plants surrounded
19 by low-quality neighbors would be more attractive to butterflies than host plants
20 surrounded by high-quality neighbors. Negative density-dependence in antagonists has
21 been documented also in other systems, where egg clumping on plants with few
22 conspecific neighbors was explained by a disproportionate attraction of insect
23 herbivores to more isolated host plants (Shea *et al.* 2000; Hasenbank & Hartley 2015).
24 For herbivores feeding on several plant species, associational effects linked to the
25 surrounding plant community have been documented more frequently (e.g. Hjältén *et al.*
26 1993; Bergvall *et al.* 2006). Our study shows that associational effects are present also
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2 308 for a specialized herbivore using a single host species, and that the strength of these
3 309 density-dependent effects depends on the quality of conspecific neighboring host plants.
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8 310 Our results are important to understand the factors causing variation in the
9 intensity of interactions between consumers and their resources. Given that consumers
10 often have important effects on fitness in the consumed organisms and that they show
11 preferences for traits of the resource organisms, identifying the factors that influence the
12 intensity of interactions is also important to understand the mechanisms underlying
13 variation in natural selection. In our study system, the butterfly seed predator has strong
14 negative effects on plant fitness and shows a preference for plants with an early
15 flowering phenology, leading to butterfly-mediated selection for later flowering (Valdés
16 & Ehrlén 2017). The results of this study show that the strength of butterfly preferences
17 for early-flowering plants is influenced by both population context, in terms of
18 population density and the trait distribution within the population, and by community
19 context in terms of the abundance of the ant species that function as the second host of
20 butterfly caterpillars. Taken together, these findings illustrate that observed spatial
21 variation in intensities of interactions and consumer-mediated selection on traits of the
22 resource organisms can be the result of processes acting at the levels of individuals,
23 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* 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		

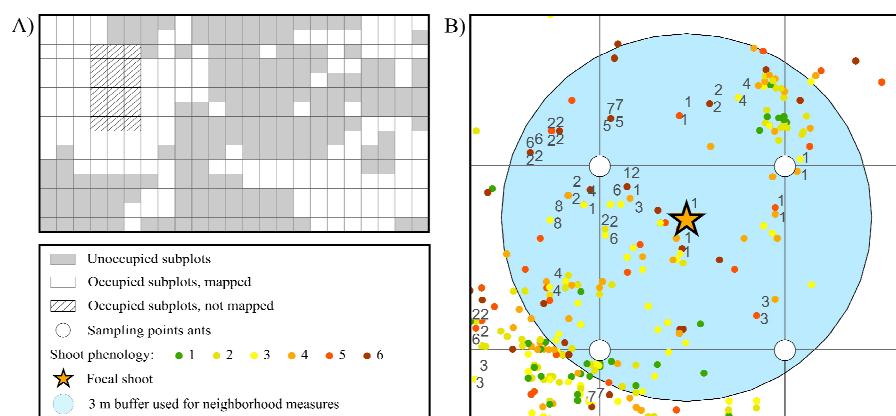
***P < 0.001; **P < 0.01; *P < 0.05

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2 FIGURE LEGENDS
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45 Figure 1: Sampling design. A) Study plot ($69 \times 45 \text{ m}^2$), comprising $345 \text{ } 3 \text{ m}^2$ subplots.
67 B) Detail of several occupied subplots with reproductive shoots of *Gentiana*
8 *pneumonanthe* and sampling points for ants. Shoots are represented by points, and
9 colored according to shoot phenology. Numbers indicate the number of *Phengaris alcon*
10 eggs found on the shoot. An example of a 3-m buffer used for neighbor measures on a
11 focal shoot (represented by a star) is shown.
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1314
15 Figure 2: Effects of shoot phenology and host ant abundance on the distribution of
16 *Phengaris alcon* eggs on its host plant *Gentiana pneumonanthe*. A) Effects on the
17 probability of a shoot having at least one egg, the relationship between the probability
18 of having at least one egg and shoot phenology shown for different ant abundances. B)
19 Effects of shoot phenology on the number of eggs in shoots with at least one egg .
20 Higher values of shoot phenology indicate earlier flowering. C) Effects of ant
21 abundance on the number of eggs in shoots with at least one egg. In A), binomial GLM
22 fit lines are represented with a color gradient for a continuous increment in ant
23 abundance within the range of observed values. In B) and C), negative binomial GLM
24 fit lines and confidence intervals are shown.
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4344 Figure 3: Effects of the interaction between neighbor density and neighbor phenology
45 on the probability of a flowering shoot of *Gentiana pneumonanthe* having at least one
46 egg of the butterfly *Phengaris alcon* (A) and the number of eggs in shoots with at least
47 one egg (B). The relationships with neighbor density are shown for different values of
48 neighbor phenology. Binomial (A) or negative binomial (B) GLM fit lines are
49 represented with a color gradient for a continuous increment in neighbor phenology
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2 within the range of observed values. Higher values of neighbor phenology indicate
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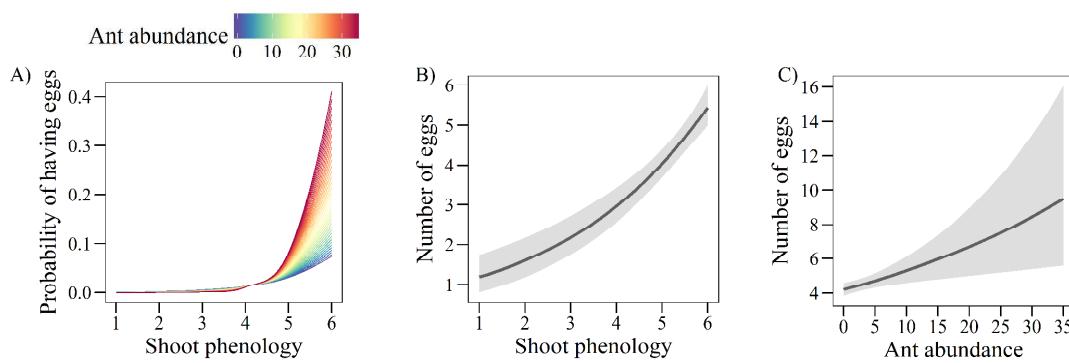
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473 Figure 1



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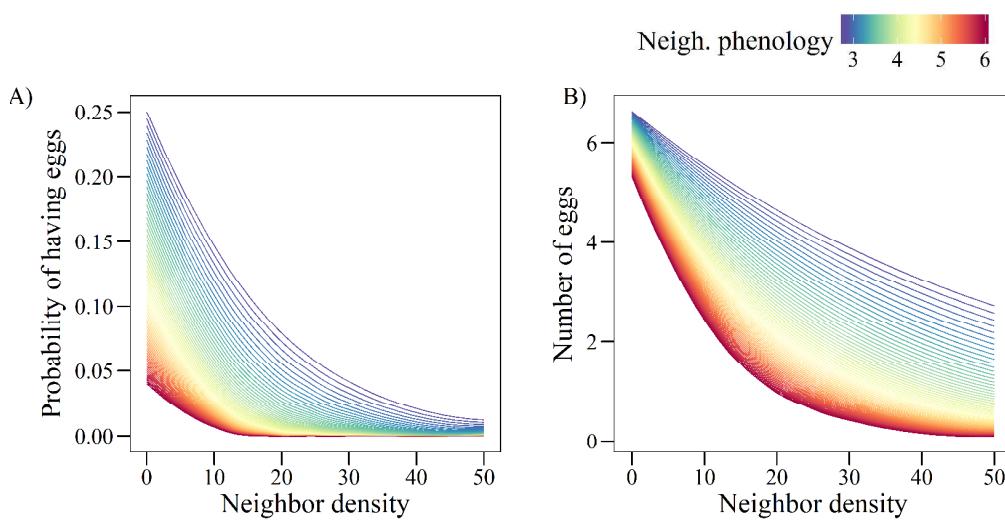
475 Figure 2



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478 Figure 3



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2 Supporting information
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5 479 Table S1: Coefficients from univariate GLMs relating the probability of having eggs (A,
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7 binomial model) and the number of eggs in plants with at least one egg (B, negative
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9 binomial model) to the abundance of different ant species.
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	A) Probability of having eggs (n = 8848)	B) Number of eggs (n = 731)
All <i>Myrmica</i>	-0.522 ***	-0.006
<i>M. rubra</i>	0.174 ***	0.137 ***
<i>M. scabrinodis</i>	-1.364 ***	-0.120 ***
<i>M. ruginodis</i>	-0.215 ***	-0.016
<i>M. schencki</i>	0.358 ***	0.006
Other ants	-0.403 ***	-0.061
<i>M. rubra + M. schencki</i>	0.360 ***	0.115 ***

26 ***P < 0.001; **P < 0.01; *P < 0.05
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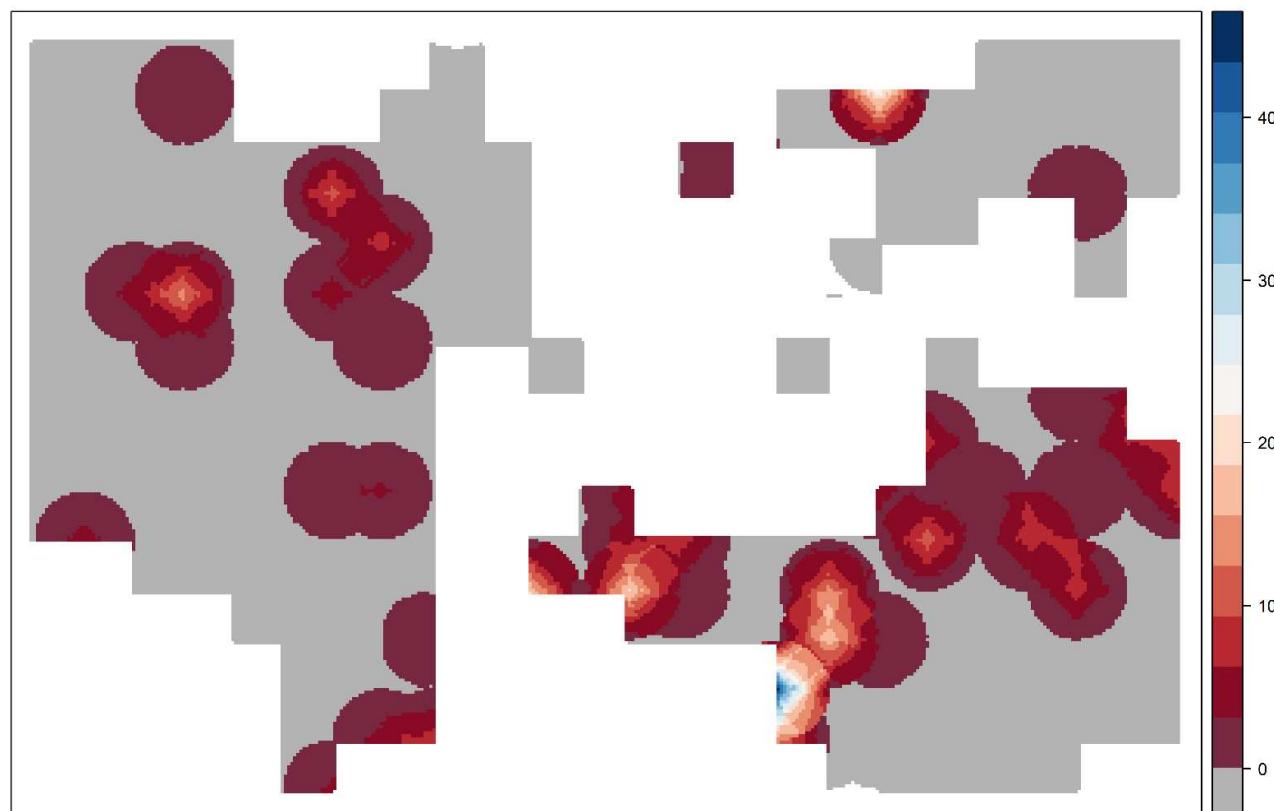
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2 484 Table S2: Results of the binomial GLM ($n = 8848$, $R^2 = 0.42$) relating the probability of
3 485 a shoot of *G. pneumonanthe* having eggs of *P. alcon* to shoot phenology, ant
4 486 abundance, neighbor density and neighbor phenology, and to three different two-way
5 487 interactions of these predictors.
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	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

30 31 ***P < 0.001; **P < 0.01; *P < 0.05
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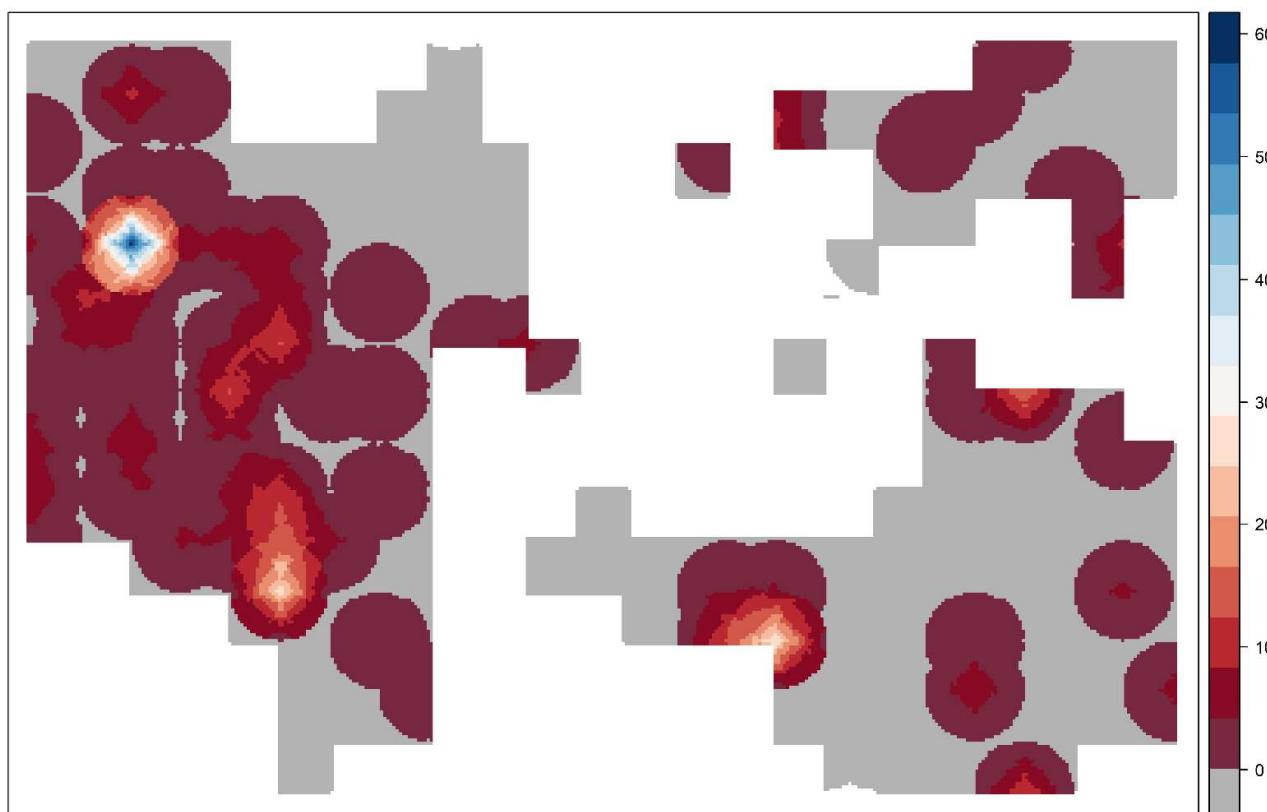
Figure S1: Result of the inverse distance weighted interpolation for abundance of *Myrmica rubra* based on abundance values (sum of individuals collected in 2 sampling sessions) at 254 sampling points. The color scale indicates the interpolated abundance values.



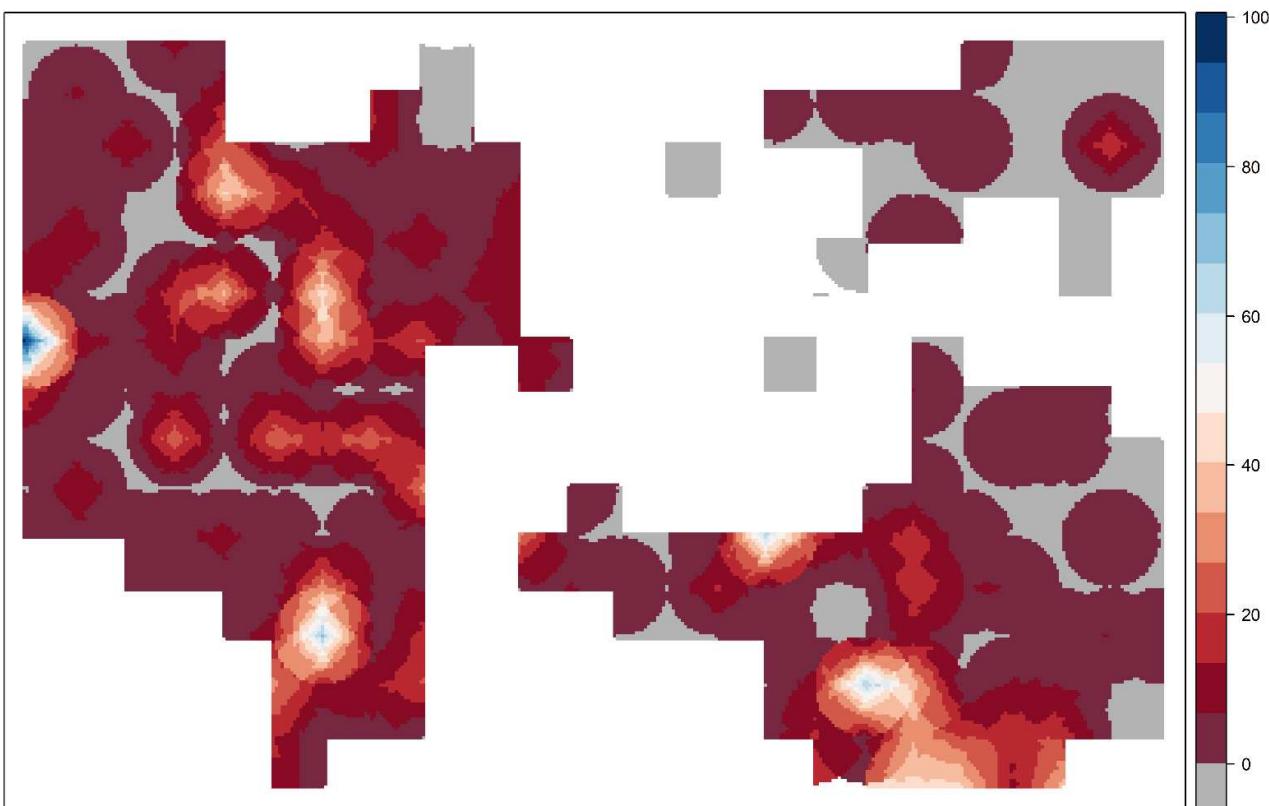
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489 Figure S2: Result of the inverse distance weighted interpolation for abundance of *Myrmica scabrinodis* based on abundance values (sum of
490 individuals collected in 2 sampling sessions) at 254 sampling points. The color scale indicates the interpolated abundance values.
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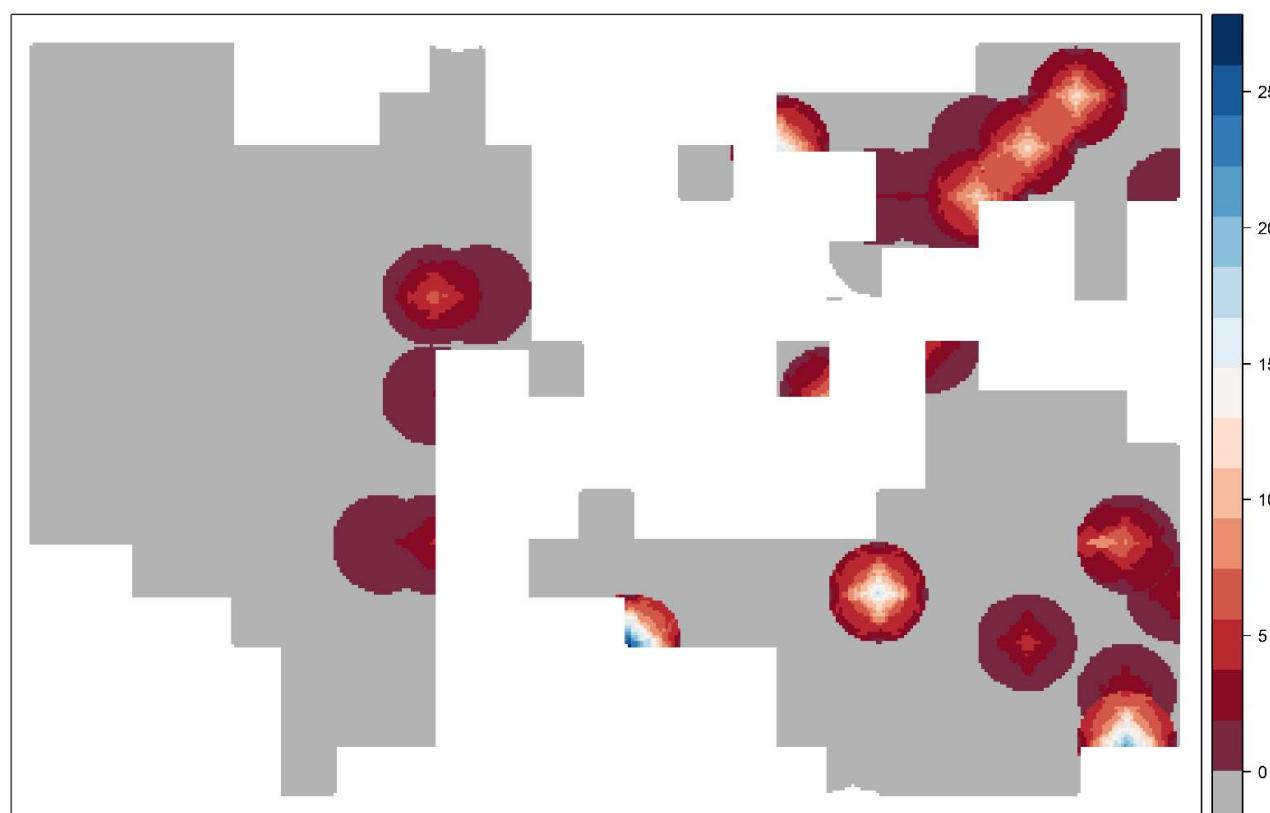
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6 492 Figure S3: Result of the inverse distance weighted interpolation for abundance of *Myrmica ruginodis* based on abundance values (sum of
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8 individuals collected in 2 sampling sessions) at 254 sampling points. The color scale indicates the interpolated abundance values.
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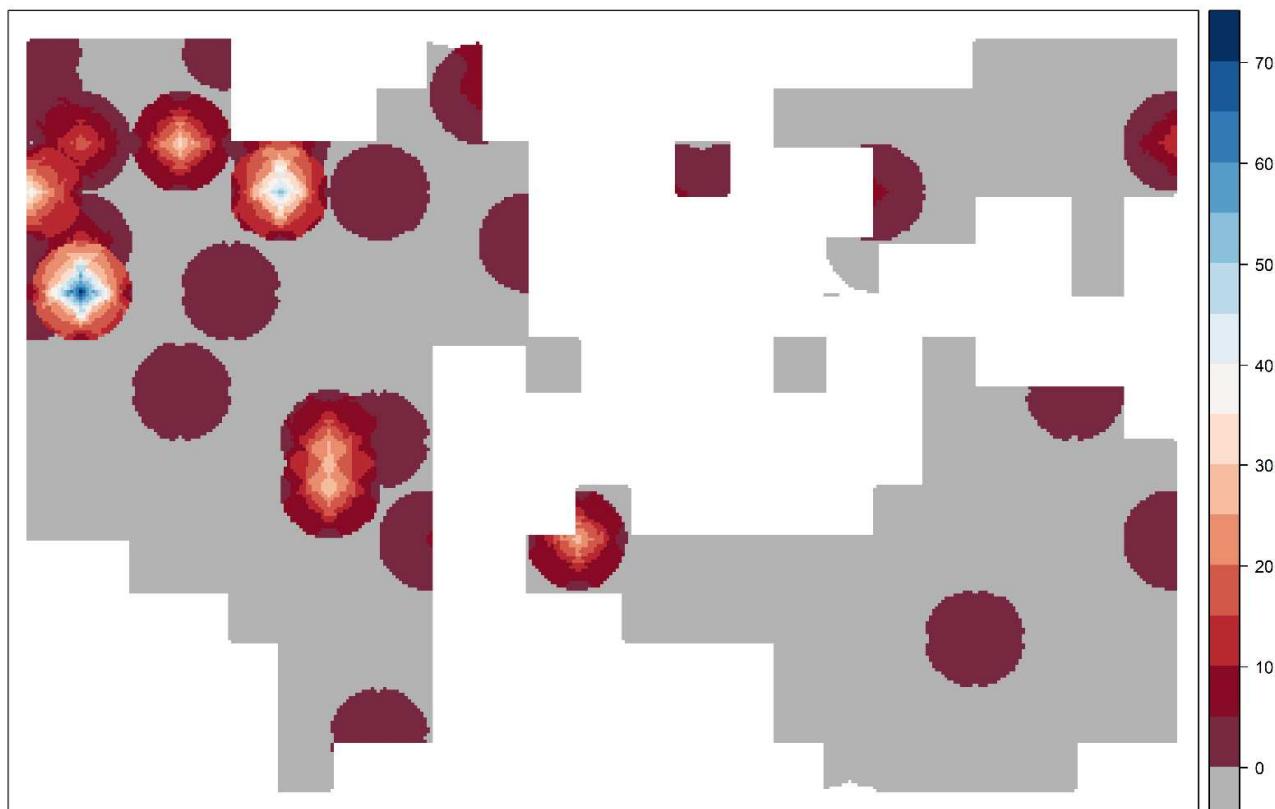
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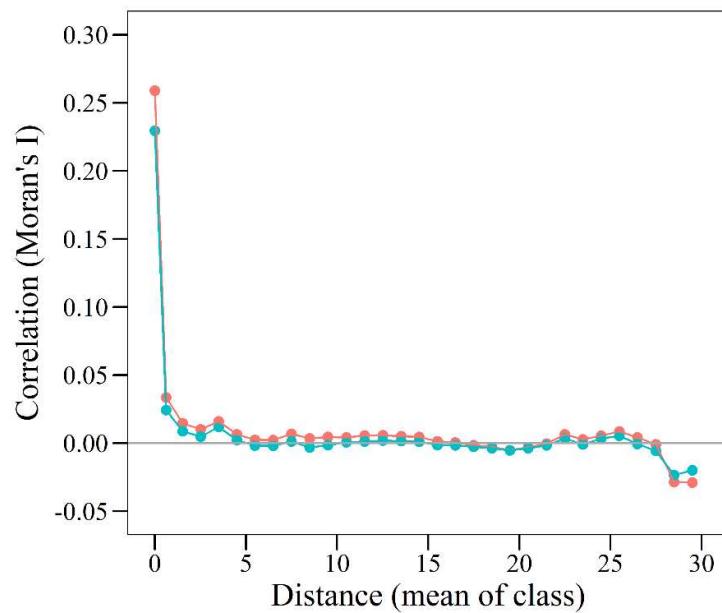
495 Figure S4: Result of the inverse distance weighted interpolation for abundance of *Myrmica schencki* based on abundance values (sum of
496 individuals collected in 2 sampling sessions) at 254 sampling points. The color scale indicates the interpolated abundance values.
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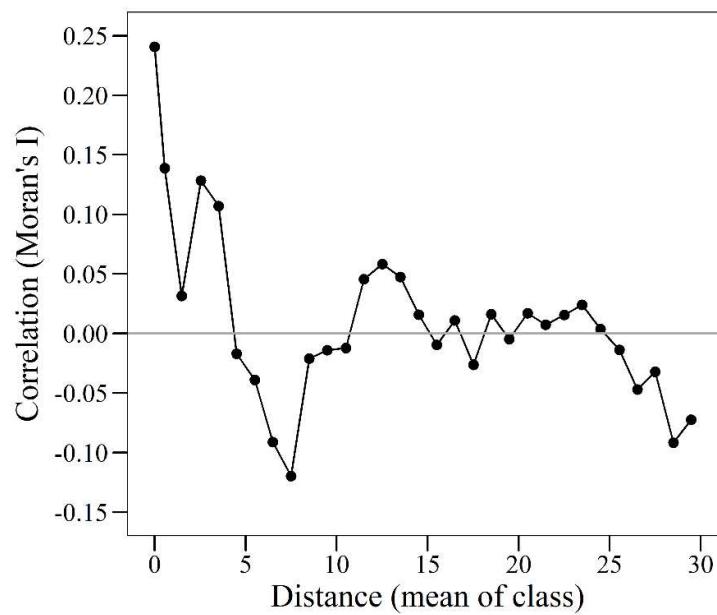
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6 498 Figure S5: Result of the inverse distance weighted interpolation for abundance of non-*Myrmica* ants based on abundance values (sum of
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8 499 individuals collected in 2 sampling sessions) at 254 sampling points. The color scale indicates the interpolated abundance values.
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3 501 Figure S6: Spatial correlogram of the residuals of the binomial GLMs for the
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5 502 probability of a shoot having eggs before (red) and after (blue) including the two
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3 505 Figure S7: Spatial correlogram of the residuals of the negative binomial GLM for the
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5 506 number of eggs in shoots with at least one egg.
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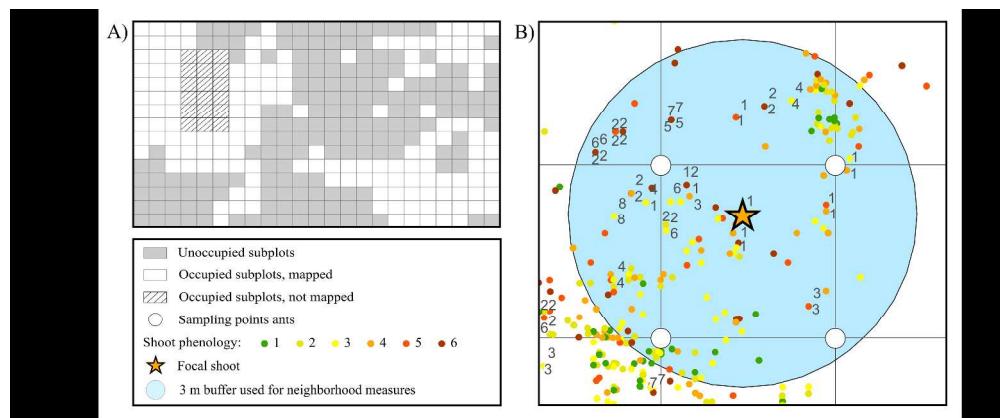


Figure 1: Sampling design. A) Study plot (69 × 45 m²), comprising 345 3 m² subplots. B) Detail of several occupied subplots with reproductive shoots of *Gentiana pneumonanthe* and sampling points for ants. Shoots are represented by points, and colored according to shoot phenology. Numbers indicate the 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.

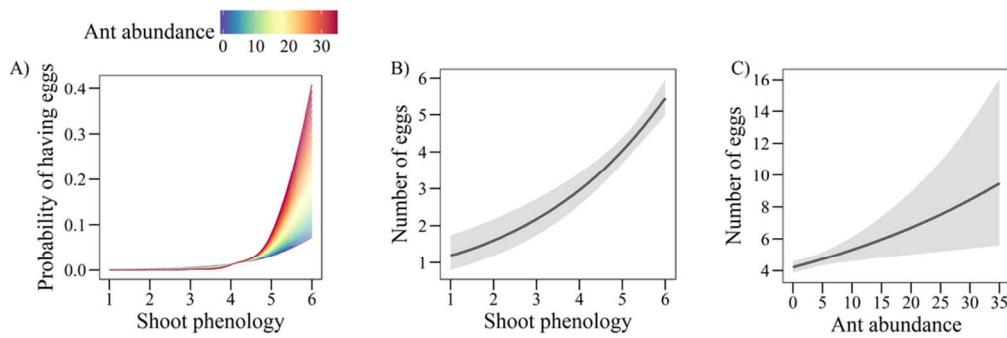


Figure 2: Effects of shoot phenology and host ant abundance on the distribution of *Phengaris alcon* eggs on its host plant *Gentiana pneumonanthe*. A) Effects on the probability of a shoot having at least one egg, the relationship between the probability of having at least one egg and shoot phenology 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.

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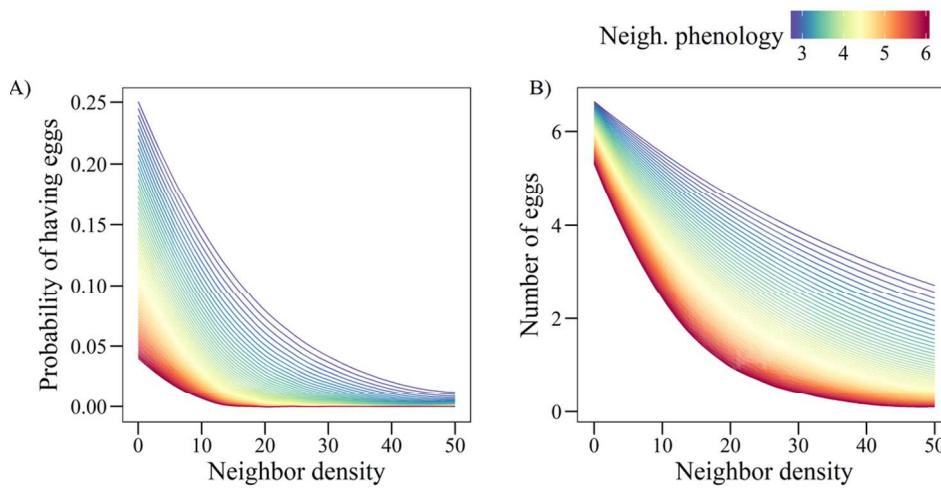


Figure 3: Effects of the interaction between neighbor density and neighbor phenology on the probability of a flowering shoot of *Gentiana pneumonanthe* having at least one egg of the butterfly *Phengaris alcon* (A) and the number of eggs in shoots with at least one egg (B). The relationships with neighbor 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.

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