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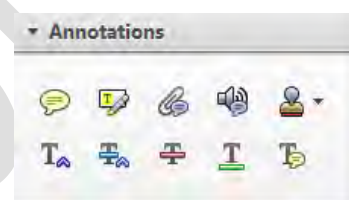
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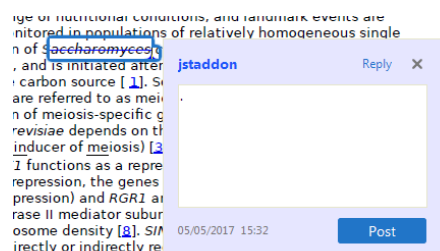
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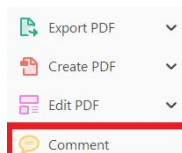
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1. Small size (35–250 amino acids).
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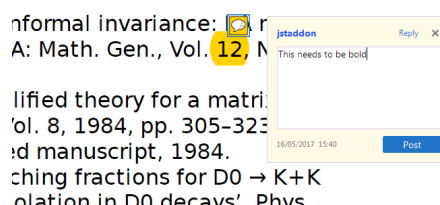   both ends; or ORF containing a tRNA.

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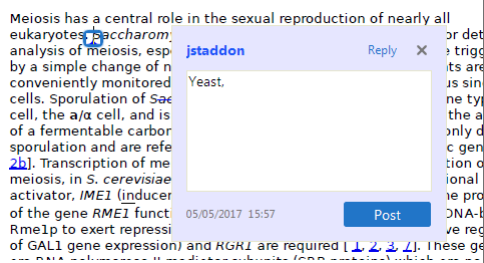This needs to be bold

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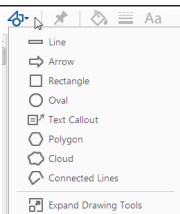Inserts a selected stamp onto an appropriate place in the proof.

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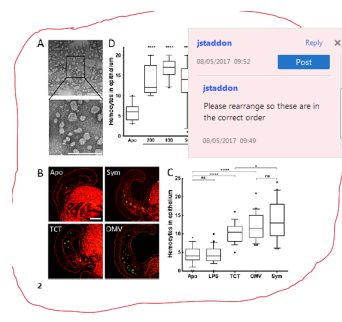- Cloud
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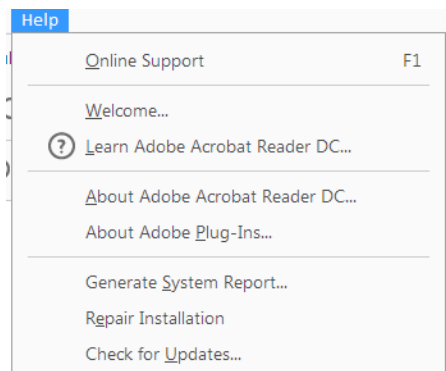
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Resource overlap and dilution effects shape host plant use in a myrmecophilous butterfly

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Abstract

1. The effects of consumers on fitness of resource organisms are a complex function of the spatio-temporal distribution of the resources, consumer functional responses and trait preferences, and availability of other resources.

2. The ubiquitous variation in the intensity of species interactions has important consequences for the ecological and evolutionary dynamics of natural populations. Nevertheless, little is known about the processes causing this variation and their operational scales. Here, we examine how variation in the intensity of a consumer–resource interaction is related to resource timing, resource density and abundance of other resources.

3. Using the butterfly consumer *Phengaris alcon* and its two sequential resources, the host plant *Gentiana pneumonanthe* and the host ants *Myrmica* spp., we investigated how butterfly egg-laying depended on focal host plant phenology, density and phenology of neighbouring host plants and host ant abundance.

4. Butterflies preferred plants that simultaneously maximized the availability of both larval resources in time and space, that is, they chose early-flowering plants that were of higher nutritional quality for larvae where host ants were abundant. Both the probability of oviposition and the number of eggs were lower in plant individuals with a high neighbour density than in more isolated plants, and this dilution effect was stronger when neighbours flowered early.

5. Our results show that plant–herbivore interactions simultaneously depend on the spatio-temporal distribution of a focal resource and on the small-scale spatial variation in the abundance of other herbivore resources. Given that consumers have negative effects on fitness and prefer certain timing of the resource organisms, this implies that processes acting at the levels of individuals, populations and communities simultaneously contribute to variation in consumer-mediated natural selection.

KEYWORDS
butterflies, flowering phenology, myrmecophily, plant–herbivore interactions, resource use, spatial variation

1

1 | INTRODUCTION

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

The quantitative relationship between the abundance of consumers and the abundance of resource organisms, and thus resource exploitation, will depend both on the birth and death processes and on consumer behaviour. Consumer behaviour may specifically cause consumer density and resource exploitation to increase (cf. resource concentration hypothesis, e.g. Hambäck & Englund, 2005; Root, 1973; Stephens & Myers, 2012) or decrease (cf. resource dilution, e.g. Otway, Hector, & Lawton, 2005) with increasing patch size and resource abundance. Observed differences in the relationships between resource exploitation and patch size or patch density among different consumers have been suggested to be the result of differences in how emigration and immigration rates depend on patch size and patch density, and on the scale of consumer selection (Andersson, Löfstedt, & Hambäck, 2013; Hambäck & Englund, 2005). For example, a strong negative relationship between consumer density and patch area observed in visual searchers like butterflies might be the result of that immigration is diameter-dependent while emigration is perimeter-dependent. Not only should the abundance of the resource organism be important for consumer responses, but also its timing and the temporal matching with the activity period of the consumer. For example, in herbivores that depend on a specific developmental stage of their host plant, the density of plants that are in suitable developmental stages at the time when the herbivore is active, rather than the overall density, is expected to influence host use. Although the effects of resource density on plant–insect interactions (Kim & Underwood, 2015; Kula, Castillo, Dudash, & Fenster, 2014; Verschut, Becher, Anderson, & Hambäck, 2016; Yamamura, 2002) are well studied, the role of resource timing and the effects of the availability of other resources have rarely been considered in these studies. Moreover, while the ecological and evolutionary effects of variation in consumer–resource interaction intensities have been documented for many systems (e.g. Chamberlain, Bronstein, & Rudgers, 2014; Kolb, Ehrlén, & Eriksson, 2007; Vanhoenacker, Ågren, & Ehrlén, 2013), the simultaneous effects of factors at different levels: individuals (e.g. timing), populations (e.g. resource density) and communities (e.g. availability of other resources) have rarely been explored. This is particularly true for small spatial scales, such as variation in the intensity of herbivory among individuals within plant populations.

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

In this study, we investigated how the phenology, in terms of the developmental stage of the reproductive structures, of one resource, the focal host plant *Gentiana pneumonanthe*, the density and phenology of neighbouring conspecific plants, and the abundance of host ants influence resource use, in terms of egg-laying, by the consumer butterfly *Phengaris alcon*. We used an extensive field dataset to test two hypotheses: (a) effects of plant phenology and ant abundance on egg distribution patterns are interdependent: butterflies choose plants for oviposition that simultaneously maximize the availability of both resources, that is they have a stronger preference for early-flowering host plants where host ants are abundant, and (b) the probability of a plant receiving at least one egg, as well as the number of eggs in oviposited plants, decreases with increasing conspecific neighbour density (i.e. a dilution effect), and this decrease is stronger when neighbours show the preferred phenology (i.e. flower early).

2 | MATERIALS AND METHODS

2.1 | Study system

The marsh gentian (*Gentiana pneumonanthe* L.) is a rare, long-lived perennial herb, occurring in open habitats, such as wet heathlands and grasslands (Simmonds, 1946). Plants can have one to many, up to 45 cm high, shoots and produce deep blue flowers that are pollinated by bumblebees. The species is self-compatible and flowers in July and August in the study area (SW Sweden). Fruits are capsules containing a high number of minute, wind-dispersed seeds (mean seed number per fruit ± *SD* = 490 ± 243, mean seed weight = 0.041 mg, authors' unpublished data). *Gentiana pneumonanthe* is the host plant of the Alcon Blue butterfly (*Phengaris alcon*), a specialist predispersal seed predator which oviposits on young flower buds in July and August (Appelqvist & Bengtsson, 2007). During an oviposition event, adult female butterflies usually lay more than one egg on the same plant and even on the same bud, and there is no evidence of avoiding plants that already carry eggs (Van Dyck & Regniers, 2010). The caterpillars feed inside the capsule until they reach the fourth instar, when they drop to the ground to be picked up by *Myrmica* ants. Caterpillars mimic the surface chemistry of the ant brood (Nash, Als, Maile, Jones, & Boomsma, 2008) and the acoustic signals of queen ants (Sala, Casacci, Balletto, Bonelli, & Barbero, 2014), and these features cause ants to carry them to their nest, where they spend the rest of their larval period as brood parasites. Females of *Phengaris* detect *Myrmica* presence through plant chemicals produced by ants or by plants in response to root tissue damage caused

by ants (Patricelli et al., 2015; Van Dyck et al., 2000; Wynhoff & van Langevelde, 2017). Contrary to the majority of *Phengaris* species, which prey on ant brood, *P. alcon* is a "cuckoo" species (Als et al., 2004), and caterpillars feed primarily on regurgitants from ant workers, trophic eggs (i.e. nutritious, infertile eggs which are fed to the queens and ant larvae) and prey items brought to the nest by ants. Only ants belonging to *Myrmica* sp. can act as hosts of *P. alcon*. In Sweden, *M. rubra* is considered to be the most common host ant species (Elmes et al., 1994), although *M. ruginodis* has also been reported as a host (Nash & Andersen, 2015).

2.2 | Data collection

The study was carried out in a population of *G. pneumonanthe*, where the butterfly *P. alcon* was present, located in Tånga Hed nature reserve in the county of Västra Götaland, SW Sweden (58°01′40.0″N 12°49′47.0″E). Field work was conducted between 9 July and 3 September 2016. The plant population occupies a fenced meadow that is grazed by cattle at the end of the summer every year. A study plot measuring 69 m × 45 m was established in the meadow. This plot was further divided into a grid comprising 345 3 m × 3 m subplots with corners permanently marked by wooden poles (Figure 1a). *G. pneumonanthe* was present in 172 of these subplots. In 154 of the subplots where *G. pneumonanthe* was present, all reproductive shoots of *G. pneumonanthe* were mapped (Figure 1b), and their phenology and the number of eggs of *P. alcon* were recorded between 29 July and 5 August (18 additional occupied subplots were
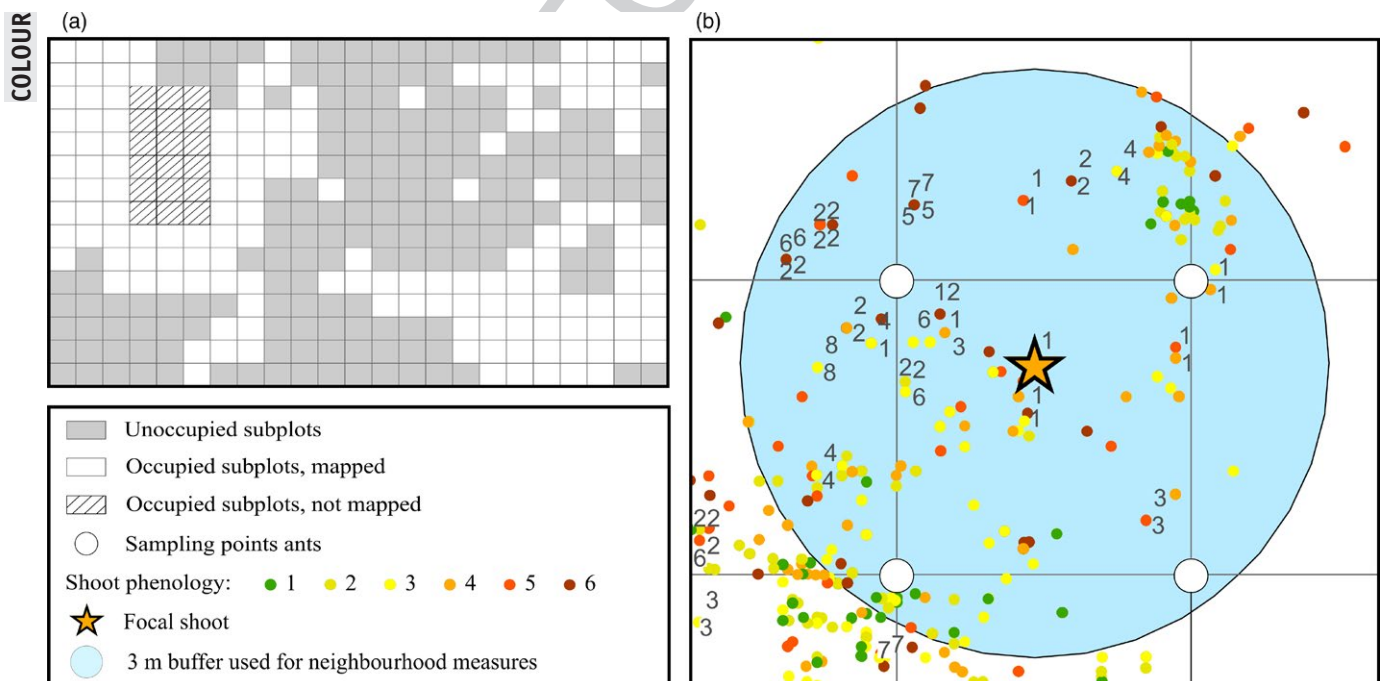

FIGURE 1 Sampling design. (a) Study plot (69 × 45 m²), comprising 345 3 m² subplots. (b) Detail of several occupied subplots with reproductive shoots of *Gentiana pneumonanthe* and sampling points for ants. Shoots are represented by points and coloured according to shoot phenology. Numbers indicate the number of *Phengaris alcon* eggs found on the shoot. An example of a 3-m buffer used for neighbour measures on a focal shoot (represented by a star) is shown

not possible to fully survey due to time constraints). Shoots were mapped by recording their coordinates within subplots. We mapped shoots rather than plant individuals (that may have one or several shoots) because we judged that individual shoots are the relevant unit for the butterfly to assess the timing of the food resource, and because individual shoots act as the unit of attraction for butterfly females. For each shoot, phenology was recorded as the developmental stage of the most advanced bud, according to six ordinal categories: (a) the sepals covering the bud completely, (b) bud becoming visible, (c) bud growing over the sepals, (d) bud turning blue, (e) flower opening and (f) flower showing signs of wilting (Valdés & Ehrlén, 2017). Each stage corresponds to a time interval of flower development, with higher values indicating a more advanced floral development at the day of recording, that is an earlier flowering phenology. According to the observed average duration of the stages, a one-unit increase in this phenology measure roughly corresponds to 1 week earlier development (Valdés & Ehrlén, 2017, 2018a). The number of eggs was counted on the whole shoot.

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

2.3 | Interpolations of ant abundances

We also incorporated the locations of the 254 points where the ant community was sampled into the GIS. We used inverse distance weighted interpolation (Pebesma, 2004) based on the values at the sampling points to generate values of the abundance of ant species over the surface of all occupied subplots. The ground foraging distance of most investigated *Myrmica* species is up to 2 m, although some species can forage further afield (Elmes et al., 1998). For our interpolations, we therefore used a maximum distance of 3 m because we considered it to include most foraging events. From these interpolated surfaces (see Supporting Information Figures S1–S5), we extracted values of abundance of the different ant species for each of the mapped shoots.

2.4 | Calculation of neighbourhood measures

Field maps were digitized using a Geographic Information System (GIS) created with ArcGIS 10.3.1, assigning relative coordinates to each recorded reproductive shoot of *G. pneumonanthe* (Figure 1b). For each, we defined a buffer zone with a 3-m radius, centred at the focal shoot (see example in Figure 1b) and calculated the number of reproductive shoots of *G. pneumonanthe* per m^2 within this buffer zone (hereafter, "neighbour density") as well as the mean phenology of these shoots (hereafter, "neighbour phenology"), excluding in each case the focal shoot.

2.5 | Statistical analyses

The effects of shoot phenology, host ant abundance, neighbour density and neighbour phenology on *P. alcon* egg distribution were examined using two generalized linear models (GLMs). Shoot phenology was treated as a discrete numeric variable taking values of 1, 2, 3, 4, 5 or 6. We chose to treat phenology as a numeric variable rather than an ordinal variable because the relationship between oviposition probability and phenological stage was monotonic and approximately linear (Supporting Information Figure S6). Neighbour phenology could take any values between 1 and 6 and was therefore treated as a continuous numeric variable. In order to minimize the effects of multicollinearity, we checked for correlations between explanatory variables, which were generally low (Supporting Information Table S1). Effects on the probability of a shoot having at least one egg were evaluated using a binomial GLM, and effects on the number of eggs in shoots with at least one egg were evaluated using a negative binomial GLM. Both models included also the effects of three interactions. First, we included the interaction between shoot phenology and ant abundance in order to test whether the effects of the two resources on egg distribution patterns are interdependent. Second, we included the interaction between neighbour density and neighbour phenology in order to test whether the effect of host plant density depends on phenology of neighbouring host plants. Third, we included the interaction between shoot phenology and neighbour phenology to account for the fact that the relationship between egg distribution and phenology of the focal plant might depend on the phenology of neighbouring host plants. As a measure of host ant abundance, we used the abundance of *M. rubra* (hereafter, "ant abundance"). *M. rubra* is considered to be the most common host ant species of *P. alcon* in Sweden (Elmes et al., 1994), although *M. ruginodis* has also been reported as a host in areas near our study site (Nash & Andersen, 2015). As we have no direct information on host ant use from our study site (no nests have been opened), we cannot exclude either of these two species as being used as hosts by *P. alcon*. Our decision to use the abundance of only *M. rubra* in our models was based on that it was the only species that showed positive effects on the probability of host plants receiving eggs and the number of eggs in plants with at least one egg (*M. rugnodis* had in fact a negative effect, Supporting Information Table S2). However, as we have no conclusive evidence that *M. rubra* serves as the only or main host at our site, we also performed alternative analyses using the abundance of *M. ruginodis* and the summed abundances of both *M. rubra* and *M. ruginodis* (Supporting Information Table S3).

All predictors were standardized by subtracting the mean and dividing by the standard deviation before the analyses. We checked for spatial autocorrelation in the residuals of models by plotting spatial correlograms and by calculating global Moran's I with a permutation test (1000 random permutations). Moran's I was calculated based on a connectivity matrix of pairwise Euclidean distances among the shoots up to a distance of 30 m. Residual spatial autocorrelation could lead to biased model estimates and invalid statistical inference (Dormann et al., 2007). A significant spatial autocorrelation was

found in the residuals of the binomial GLM, but not for the negative binomial GLM (global Moran's I = 0.0148, p < 0.001 and global Moran's I = −0.0013, p = 0.479, respectively, Supporting Information Figures S7 and S8). We therefore applied Moran's eigenvector mapping (MEM), which translates the spatial arrangement of data points into explanatory variables (eigenvectors) that capture spatial effects, to the binomial model examining effects on the probability of a shoot having at least one egg (Dray, Legendre, & Peres-Neto, 2006; Thayn & Simanis, 2013). The model was refitted including two eigenvectors issued from MEM as spatial predictors, and this strongly reduced the residual spatial autocorrelation (global Moran's I = 0.0004, p = 0.004, Supporting Information Figure S7). Although residual spatial autocorrelation was still significant, the low value of Moran's I and visual inspection of the spatial correlogram (Supporting Information Figure S7) indicated that almost all of the residual spatial autocorrelation was removed by the spatial predictors. The results of this model were similar to the results of the binomial GLM not including the spatial predictors (Supporting Information Table S4). Statistical analyses were carried out in R 3.4.0 (R Core Team 2017).

3 | RESULTS

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

The effects of shoot phenology and ant abundance on *P. alcon* oviposition were interdependent. The probability of a shoot of *G. pneumonanthe* having at least one egg increased with an earlier phenology (i.e. with a more advanced floral development at the day of recording, Table 1, Figure 2a, Supporting Information Figure S6). This increase was stronger in shoots where *M. rubra* was more abundant (the effect of the interaction shoot phenology × ant abundance being significant in the model without spatial predictors and marginally significant after including the spatial predictors, Supporting Information Table S3, Figure 2a, Table 1). In analyses based on the abundance of *M. ruginodis* or the summed abundance of *M. rubra* and *M. ruginodis*, the probability of a shoot of *G. pneumonanthe* having at least one egg instead decreased with a higher ant abundance (Supporting Information Table S2). The number of *P. alcon* eggs on individuals with at least one egg increased with an earlier shoot phenology and with a higher host ant abundance, and the effect of the interaction between phenology and ant abundance was marginally significant and in the same direction as in the model for the probability of having eggs (Table 1, Figure 2b,c).

High densities of host plant shoots resulted in a dilution effect, and the strength of this effect depended on the quality of neighbouring plants. Both the probability of having at least one egg and the number of eggs on shoots with at least one egg decreased with the overall density of neighbouring host plant shoots (Table 1, Figure 3). In both cases, the decrease was stronger when neighbouring host plants showed the preferred phenology, that is, had an earlier phenology (significant effect of the interaction neighbour density × neighbour phenology, Table 1, Figure 3).

4 | DISCUSSION

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

We found that both the probability of *P. alcon* butterflies laying at least one egg on a host plant and the number of eggs increased with an earlier phenology of its host plant *G. pneumonanthe*. This agrees with previous studies showing that insects usually prefer plants with a particular phenology (Elzinga et al., 2007), and more specifically, that antagonists preferentially attack early-flowering plants (König, Wiklund, & Ehrlén, 2015; Parachnowitsch & Caruso, 2008; Valdés & Ehrlén, 2017, 2018a). The timing of butterfly oviposition relative to plant phenology is likely to vary among years, depending on temporal variation in both plant and butterfly phenology. Higher temperatures associated with climate change are expected to cause significant advances in the phenology of many organisms (Parmesan, 2006), and the synchrony of plant–insect interactions, like the one examined in this study, might be affected if interacting species respond differently to warming. Anyway, our results, together with previous studies (Valdés & Ehrlén, 2017, 2018a) provide convincing evidence of the important role of the timing of the plant resource (i.e. host plant phenology) relative to the oviposition period of *P. alcon*.

Interestingly, in our study the strength of this preference for an early plant phenology did depend on the abundance of a possible second resource for the antagonist, that is the ant species *Myrmica rubra*. The preference of *P. alcon* for early-flowering host plants tended to be stronger at locations where *M. rubra* was more abundant. For example, the probability of a shoot with the earliest possible phenology receiving at least one egg was 0.07 at sites where *M. rubra* was absent, and 0.62 at sites with the maximum *M. rubra* abundance observed (*n* = 34 ants). This suggests 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 a suitable 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. Our use of abundance of *M. rubra* as a measure of host ant abundance was not based on actual host identification but on correlations between abundance and occurrence and number of eggs. Although the other *Myrmica* species investigated had a negative effect on egg occurrence (Table S2), we cannot completely rule out the possibility that these species act as hosts in our study site, and that the correlations with *M. rubra* abundance are due to the effect of some unmeasured environmental variable, rather than to butterflies directly tracking the abundance

TABLE 1 Results of the generalized linear models (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 (measured as abundance of *Myrmica rubra*), neighbour density and neighbour 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)
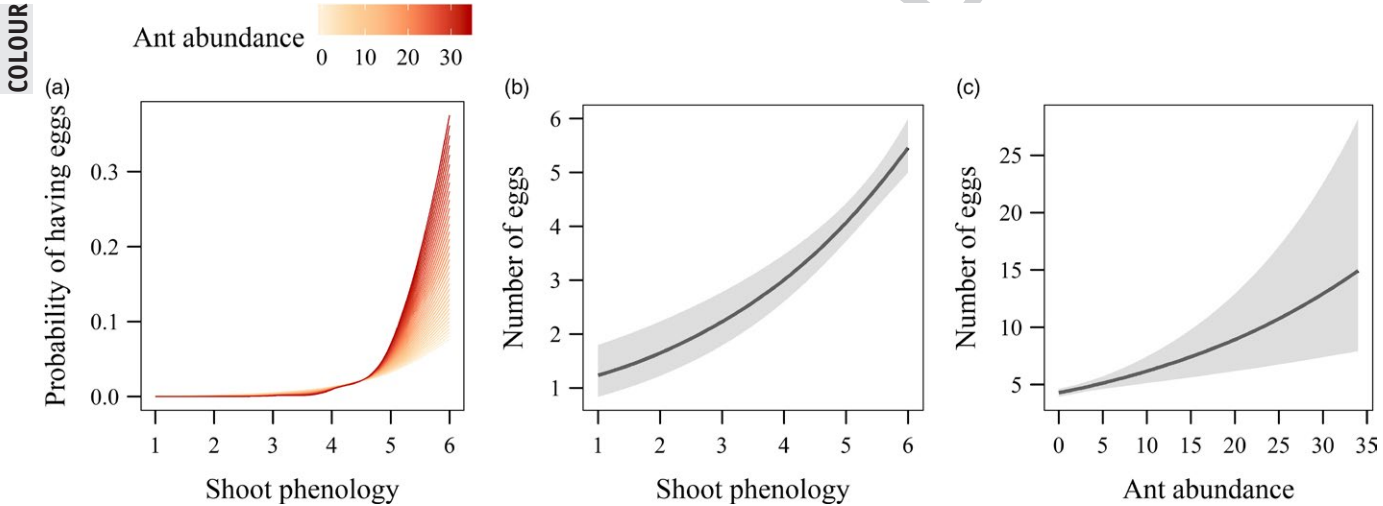
	Probability of having at least one egg (n = 8,848, R^2 = 0.45)			Number of eggs (n = 731, R^2 = 0.23)		
	Estimate	SE	p	Estimate	SE	p
Shoot phenology	1.476	0.079	<0.001	0.251	0.036	<0.001
Ant abundance	−0.028	0.051	0.588	0.117	0.067	<0.001
Neighbour density	−1.673	0.101	<0.001	−0.351	0.067	<0.001
Neighbour 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 × Neighbour phenology	0.100	0.072	0.163	0.002	0.034	0.943
Neighbour density × Neighbour 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 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 generalized linear model (GLM) fit lines are represented with a colour 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

of this ant species. Previous observational studies have suggested that oviposition is host species dependent (Van Dyck et al., 2000). Experimental studies have found *Phengaris* oviposition to be dependent on *Myrmica* ant presence, but found no effect of species identity (Patricelli et al., 2015; Wynhoff & van Langevelde, 2017). Lastly, there are several studies that have found no evidence of ant-dependent oviposition (Fürst & Nash, 2010; Nowicki, Witek, Skorka, & Woyciechowski, 2005; Thomas & Elmes, 2001). Still, in combination with previous evidence of *M. rubra* being the most common host ant species of *P. alcon* in Sweden (Elmes et al., 1994), the results of our analyses suggest that *M. rubra* serves as a host species at our study site.

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* (Casacci et al., 2011; Thomas, Simcox, & Clarke, 2009). Other studies with *Phengaris* butterflies have demonstrated effects of host plant phenology (Thomas & Elmes, 2001; Valdés & Ehrlén, 2017, 2018a), *Myrmica* presence (Van Dyck et al., 2000; Wynhoff & van Langevelde, 2017; Wynhoff et al., 2008) or both of these factors (Casacci et al., 2011) for oviposition site selection. Our study suggests 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. An important general implication of these findings is that differences in availability of a resource over very small spatial scales might influence the use of other resource by consumers that depend on multiple resources. The results also
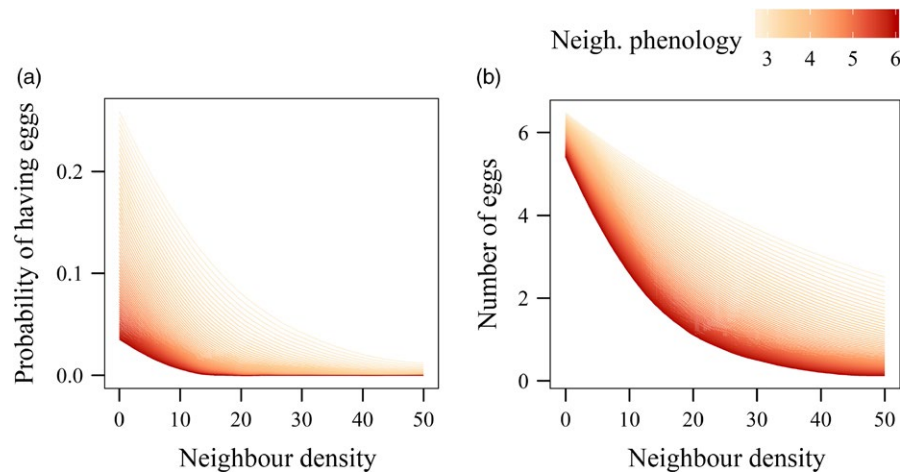
FIGURE 3 Effects of the interaction between neighbour density and neighbour phenology on the probability of a flowering shoot of *Gentiana pneumonanthe* having at least one egg of the butterfly *Phengaris alcon* (a) and the number of eggs in shoots with at least one egg (b). The relationships with neighbour density are shown for different values of neighbour phenology. Binomial (a) or negative binomial (b) generalized linear model (GLM) fit lines are represented with a colour gradient for a continuous increment in neighbour phenology within the range of observed values. Higher values of neighbour phenology indicate earlier flowering

suggest that the effects of factors at the levels of the individual (plant phenology) and the community (availability of the ant resource) on small-scale spatial variation in consumer–resource interactions are interactive.

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 phenology of neighbouring plants. Higher densities of neighbouring 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, that is a lower consumer pressure. The results of previous studies with this species (Van Dyck & Regniers, 2010) suggest that females usually lay more than one egg on the same plant, and that they do not avoid oviposition on plants that already carry eggs. If this is true also in our study, then the eggs observed on an individual plant correspond to the offspring of either a single or several females (but this is something we cannot determine because oviposition was not directly observed in this study). Because we cannot be sure whether the lower number of eggs was the result of fewer females visiting the plant, or of each visiting female laying fewer eggs, it is more appropriate here to talk about "consumer pressure" than about "consumer abundance." In any case, the observed negative relationship between consumer pressure and overall resource abundance was stronger when the surrounding plants flowered early in the season, that is they had buds in early developmental stages during the period of butterfly oviposition. In other words, at a given conspecific density more eggs were found in *G. pneumonanthe* plants surrounded by non-attractive neighbours (i.e. late-flowering plants). In our study, plant phenology thus appears to influence butterfly oviposition not only because the phenology of a focal plant interacts with host ant availability to determine plant suitability for oviposition, but also because the phenology of neighbours modulates the strength of host plant density effects on oviposition. Therefore, not only factors at the levels of

individuals and communities, but also at the level of the plant population, drive variation in resource use.

Our results suggest that oviposition decisions in myrmecophilous butterflies are taken at two levels. When flying over an area populated with host plants, females might primarily use visual cues (Van Dyck & Regniers, 2010) to evaluate host plant availability (i.e. density) and identify host plants with the preferred phenology (i.e. early-flowering). When butterflies approach host plants, or after alighting on a plant, females may use both visual cues to evaluate plant phenology and chemical cues to detect ant presence (Patricelli et al., 2015; Wynhoff & van Langevelde, 2017; Wynhoff et al., 2015), thereby evaluating the spatial overlap of the two resources needed by their offspring. If females use plant developmental stage as a cue indicating the availability of high-quality food for the caterpillars, host plants surrounded by late-flowering neighbours would be more attractive to butterflies than host plants surrounded by early-flowering neighbours. Negative density-dependence in antagonists has been documented also in other systems, where egg clumping on plants with few conspecific neighbours was explained by a disproportionate attraction of insect herbivores to more isolated host plants (Hasenbank & Hartley, 2015; Shea, Smyth, Sheppard, Morton, & Chalimbaud, 2000). For herbivores feeding on several plant species, associational effects linked to the surrounding plant community have been documented more frequently (e.g. Bergvall, Rautio, Kesti, Tuomi, & Leimar, 2006; Hjältén, Danell, Lundberg, & Hjalten, 1993). Our study shows that associational effects are present also for a specialized herbivore using a single host species, and that the strength of these density-dependent effects depends on the phenology of conspecific neighbouring host plants.

Our results are important to understand the factors causing variation in the intensity of interactions between consumers and their resources. Given that consumers often have important effects on fitness in the consumed organisms and that they show

preferences for timing of the resource organisms, identifying the factors that influence the intensity of interactions is also important to understand the mechanisms underlying variation in natural selection. In our study system, the butterfly seed predator has strong negative effects on plant fitness and shows a preference for plants with an early-flowering phenology, leading to butterfly-mediated selection for later flowering (Valdés & Ehrlén, 2017). The results of the current study strongly suggest that the strength of butterfly preferences for early-flowering plants is influenced by both population context, in terms of population density and the trait distribution with the population, and by community context in terms of the abundance of the ant species that function as the second host of butterfly caterpillars. Taken together, these findings illustrate that observed spatial variation in intensities of interactions and consumer-mediated selection on traits of the resource organisms can be the result of processes acting at the levels of individuals, populations and communities.

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AUTHORS' CONTRIBUTIONS

A.V. and J.E. designed the study. A.V. collected and analysed the data with inputs from J.E. A.V. and J.E. wrote the manuscript. Both authors gave final approval for publication.

DATA ACCESSIBILITY

The data associated with this paper are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.p3q2rq1 (Valdés & Ehrlén, 2018b).

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SUPPORTING INFORMATION

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Graphical Abstract

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Plant–herbivore interactions simultaneously depend on the spatio-temporal distribution of a focal resource and on the small-scale spatial **7** variation in the abundance of other resources. This shows that variation in consumer-mediated natural selection can be the outcome of simultaneous and interactive processes acting at the levels of individuals, populations and communities.