

1 Title:

2 **Altered parasitism of a butterfly assemblage associated with a range-**
3 **expanding species**

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23 **Biosketch**

24 H  l  ne Audusseau's research focuses on the ecological and evolutionary responses of species
25 to changes in climate and land use. During her postdoctorat, she became more specifically
26 interested in the impact of environmental changes on biotic interactions and their consequences
27 for species and communities.

28 **Title: Altered parasitism of a butterfly assemblage associated with a**
29 **range-expanding species**

30 **Running title: butterfly assemblage and parasitism**

31 **Abstract**

32 **Aim** Biotic interactions are an important factor structuring ecological communities but data
33 scarcity limits our understanding of the impact of their response to climate and land use changes
34 on communities. We studied the impact of a change in species assemblage on biotic interactions
35 in a community of closely-related butterflies. Specifically, we examined the impact of the
36 recent range expansion of *Araschnia levana* on the resident species, with a particular focus on
37 natural enemies, parasitoids, shared with other butterfly species in the assemblage.

38 **Location** Sweden.

39 **Time period** Two years (2017-2018).

40 **Major taxa studied** Nettle-feeding butterflies (*Aglais urticae*, *Aglais io*, *Araschnia levana*,
41 and *Vanessa atalanta*) and their parasitoids.

42 **Methods** We assessed parasitism in 6777 butterfly larvae sampled in the field from 19 sites
43 distributed along a 500 km latitudinal gradient, and every two weeks throughout species'
44 reproductive seasons. We identified the parasitoid complex of each butterfly species and their
45 overlap, and analysed how parasitism rates were affected by species assemblage, variations in
46 abundance, time, and the arrival of *A. levana*.

47 **Results** Parasitoids caused high mortality, with substantial overlap across the four host species.
48 The composition of the host community influenced parasitism rates and this effect was specific
49 to each species. In particular, the rate of parasitism in resident species was comparatively
50 higher at sites where *A. levana* has been established for longer.

51 **Main conclusions** Parasitoid pressure is a significant source of mortality in the nettle-feeding
52 butterfly community studied. Variations in butterfly species assemblages are associated with
53 substantial variations in rates of parasitism. This is likely to affect the population dynamics of
54 their butterfly host species, and, potentially, the larger number of species with which they
55 interact.

56 **Keywords**

57 *Aglais io*, *Aglais urticae*, apparent competition, *Araschnia levana*, biotic interactions, invasive
58 species, parasitism, parasitoids, Sweden, *Vanessa atalanta*.

59 **Introduction**

60 Biotic interactions are important drivers structuring ecological communities. While
61 occurring locally, the impact of biotic interactions is visible across ecological scales,
62 influencing population dynamics, determining community structures and patterns of species
63 co-occurrence, and shaping distribution ranges and abundances (Araújo & Luoto, 2007;
64 Heikkinen et al., 2007; Meier et al., 2010; Wisz et al., 2013; Belmaker et al., 2015). Biotic
65 interactions can nevertheless be altered by climate and land use changes, thereby disrupting
66 ecological communities (Tylianakis et al., 2008; Blois et al., 2013). The importance of biotic
67 interactions is widely recognised in the literature, including its importance for refining
68 predictions of species' responses to environmental change (Wisz et al., 2013; Dormann et al.,
69 2018), but the scarcity of comprehensive empirical data strongly limits our ability to understand
70 the larger-scale impact of their response to environmental change on populations and
71 communities. Most studies that examined changes in ecological networks along environmental
72 gradients are based on correlative approaches (Pellissier et al., 2017) and, therefore, cannot
73 disentangle the effect of biotic interactions from the effects of environmental change. Thus,
74 measuring and understanding the impact of biotic interactions in a context of change remains
75 a major challenge.

76 This difficulty is partly due to the dynamic nature of biotic interactions and the many ways and
77 different scales that environmental change can affect biotic interactions (Wisz et al., 2013;
78 Kissling & Schleuning, 2015; Pellissier et al., 2017; Dormann et al., 2018). For example,
79 changes in climate and land use can affect the distribution and demography of species, which
80 in turn might alter the nature and strength of biotic interactions and their impact on ecological
81 communities and species distribution (Tylianakis et al., 2008; Early & Keith 2019). Differences
82 in sensitivity of interacting species to environmental changes can 1) alter their respective

83 abundances and/or spatial pattern of co-occurrence, 2) disrupt the temporal synchrony between
84 them, or 3) induce new interactions in the case of the establishment of invasive or alien species.

85 Understanding and identifying the forces that shape biotic interactions in changing
86 environments is particularly important for invertebrates such as insects, a group that constitutes
87 more than half of the biodiversity of Earth and underlies ecosystem services that directly
88 contribute to ecosystem productivity and stability, and to human well-being (see Losey &
89 Vaughan, 2006). While direct interactions such as predator-prey and insect-plant interactions
90 are widely studied and documented, the vast majority of interactions operate in complex
91 networks where species are connected through both direct and indirect interactions. The
92 process of apparent competition is an example of an indirect interaction, where the population
93 dynamics of species at the same trophic level can be linked via the action of shared natural
94 enemies (Holt & Lawton, 1993; 1994). For example, the invasion and establishment of a
95 closely-related insect species can be detrimental to a native species by increasing the resources
96 available for their shared parasitoids. Apparent competition mediated by shared parasitoids was
97 shown for leafhopper communities in California where the introduction of a new host species,
98 combined with the strong preference for the native species, resulted in an overall increase in
99 parasitoid pressure and decline of the native species (Settle & Wilson, 1990). In contrast to
100 direct interactions, indirect interactions are generally more complex and involve several trophic
101 levels, which makes their identification, as well as the evaluation of their effects on species and
102 communities, more difficult. Laboratory experiments conducted on *Drosophila* assemblages in
103 microcosms have shown that changes in biotic interactions (both direct and indirect) along a
104 climatic cline influence population dynamics (Davis et al., 1998). In natural systems, the impact
105 of apparent competition has been shown to vary with the size of the community, the abundance
106 of hosts and their phenology (Bonsall & Hassell, 1997; Van Nouhuys & Hanski, 2000; Morris
107 et al., 2004; Blitzer & Welter, 2011), and can affect multiple species that share common

108 enemies (Morris et al., 2004, Frost et al., 2016). However, our understanding of indirect
109 interactions is mainly derived from a small amount of experimental data gathered under
110 laboratory conditions or at relatively small spatial and temporal scales. The lack of detailed
111 data collected across regions and over multiple generations limits our ability to quantify and
112 predict the impacts of indirect biotic interactions on populations and communities in the context
113 of environmental change.

114 Here we focus on apparent competition mediated by shared parasitoids in a community of
115 closely-related (Nymphalidae: Nymphalinae, Nymphalini) nettle-feeding butterflies (*Aglais*
116 *urticae*, *Aglais io*, *Vanessa atalanta*) along a latitudinal gradient in Sweden. We investigate the
117 impact of the range expansion of *Araschnia levana*, a newly-arrived butterfly also feeding on
118 nettle (*Urtica dioica*). The establishment and expansion of *A. levana* in Sweden is most likely
119 a result of the warmer conditions observed over the last decades and has the potential to modify
120 the interactions that structure the community of resident nettle-feeding butterflies. Recent
121 analyses of species co-occurrence of three butterfly species (*Aglais urticae*, *Aglais io*, and *A.*
122 *levana*, Audusseau et al., 2017) have shown the potential effect of the newly-established
123 species in southern Sweden on the distribution and niche partitioning of the resident species.
124 Audusseau et al. (2017) observed a shift in the distribution of *A. urticae* and *A. io* following
125 the establishment of *A. levana* in Sweden, and suggested that these shifts could be explained
126 by apparent competition, mediated by shared parasitoids. To further investigate this hypothesis
127 and document the impact of such a change in species assemblage, we conducted a field study
128 spanning a 500 km latitudinal gradient in Sweden, along the establishment gradient of *A.*
129 *levana*. We investigated the phenology of parasitism of the nettle-feeding butterflies and its
130 spatio-temporal structuring, and whether the change in parasitism rate was linked to a change
131 in potential for apparent competition that the resident species experienced when co-occurring
132 with the newly-established species.

133 **Material and Methods**

134 **Study system**

135 *Aglais urticae*, *Aglais io*, *Araschnia levana* and *Vanessa atalanta* are closely-related
136 butterfly species from the same tribe (Nymphalini) within Nymphalidae family. The larvae of
137 all four species feed (practically exclusively) on nettle (*Urtica dioica*), but they differ in their
138 egg-laying behaviour, phenology, and distribution.

139 *Aglais urticae*, *A. io*, and *A. levana* are batch-laying species, with batches of 10 to 40 eggs for
140 *A. levana* and of 200-300 eggs for *A. urticae* and *A. io*, while *V. atalanta* lays eggs singly (Ebert
141 1993). *Aglais urticae* and *A. io* batches are laid at the apex of nettle plants. During the first
142 three instars of their development, the larvae are gregarious and conspicuous as they feed near
143 the apex of the nettle stem. At their fourth instar, larvae become solitary and feed over all of
144 the plant and may hide in the foliage. Larvae of *A. levana* are also gregarious in the early instars
145 and become solitary later on. However, batches of this species are less conspicuous to the
146 human eye. The smaller size of both the batches and the larvae causes less damage to the plant,
147 and larvae often feed on the lower surface of the leaf.

148 The four species have broadly overlapping phenologies, with adults flying from March to
149 September. However, due to differences in voltinism (the number of generations a species has
150 every year) and yearly variations in weather conditions, the time periods during which larvae
151 of each species are found in the field vary. Populations of *A. urticae* are bivoltine in south
152 Sweden and becomes progressively univoltine as we move to the northernmost part of the
153 country. Larvae of this species are recorded from early May to the end of August. Butterfly
154 individuals from the first generation correspond to the eggs laid in May. In the south,
155 individuals from the second generation are the offspring of adult butterflies from the first

156 generation and correspond to eggs that start to be laid about six weeks later. In between these
157 two peaks, the abundance of *A. urticae* larvae drops. *Aglais io* is univoltine in Sweden and
158 starts reproducing soon after *A. urticae*, with larvae observed from late May to early August.

159 *Araschnia levana* is an obligate bivoltine species. In contrast to *A. urticae* and *A. io*, which
160 overwinter as adults, individuals of *A. levana* hibernate in the pupal stage. Butterfly larvae from
161 the first generation are found in the field in June; larvae from the second generation are found
162 from end of July to early September. Last, *V. atalanta* is a migratory butterfly in Sweden and
163 its population depends on the migratory influx from the areas where the species is resident. It
164 is univoltine in Sweden with larvae observed in the field from May to early September.

165 These species are distributed over most of Sweden, except for *A. levana* whose distribution is
166 so far limited to the southern half of the country. The first anecdotal observations of *A. levana*
167 were reported in the county of Skåne in Sweden in 1982 and the species is now well-established
168 in the southern part of the country (Eliasson et al., 2005). Further, opportunistic occurrence
169 data extracted from Artportalen (Swedish Species Observations System, www.artportalen.se,
170 30/08/2019) showed that the species has progressively expanded from the county of Skåne to
171 Kronoberg and further north, but has not yet reached the Stockholm area (most northerly latitude
172 of observation in 2017: 58.6981, see Appendix S1 in Supporting Information).

173 **Field sampling**

174 We collected larvae of the four study butterflies, *A. urticae*, *A. io*, *A. levana*, and *V.*
175 *atalanta*, over two years (2017-2018) and fortnightly throughout the species' reproductive
176 season (May-August). Our sampling was distributed across 19 sites along a 500 km latitudinal
177 gradient from south Sweden to the Stockholm area (Fig. S1). The 13 sites located in the

178 southern part of Sweden fall within the distribution range of all four butterfly species, while
179 the six sites in the Stockholm area are north of *A. levana*'s current range.

180 **Larval sampling and monitoring**

181 We focused on larval parasitism. Pupal parasitism is also likely to cause high mortality
182 in the species studied (Pyörnilä, 1977; Shaw et al., 2009), but the solitary and concealed pupae
183 are difficult to collect in sufficient numbers for reliable estimates of pupal mortality. To
184 maximize the diversity of captured parasitoid species, we sampled butterfly larvae at different
185 developmental stages. We followed such a stratification of the sampling effort because the
186 temporal window of attack of butterfly larvae differ among parasitoids species and can be
187 restricted to a few developmental stages. For example, while ichneumonids of the genus
188 *Thyrateles* attack very late larval or prepupal stages, *Cotesia vestalis*, which can be an
189 important opportunistic parasitoid of at least *A. urticae*, parasitizes first instar larvae and
190 emerges mainly from second instar larvae (MRS, personal observation). Therefore, at each
191 sampling occasion and for each butterfly species we aimed to collect seven second instar larvae
192 per batch from a maximum of five batches, 20 fourth instar larvae per batch from a maximum
193 of five batches, and up to 20 fifth instar larvae, where possible from different batches.

194 We kept the collected larvae in transparent plastic boxes (155x105x45mm) with up to five
195 individuals from the same batch in a box. We reared larvae under laboratory conditions
196 (temperature 23°C, light regime 22L:2D) and fed them daily with *Urtica* leaves from location
197 from where the larvae had been collected. This was because some of the Tachinidae parasitoids
198 (*Sturmia bella* and *Pales pavidus*, of those encountered) lay microtype eggs on nettle leaves and
199 the butterfly larvae become parasitized only when they eat the infected leaves.

200 For larvae that were parasitized, we recorded the date and stage from which the parasitoid
201 emerged (larval instar or pupa). We kept parasitoids individually or per batch in plastic vials,
202 under the same laboratory conditions as the butterfly larvae. We preserved freshly-dead adult
203 parasitoids in 95% alcohol, before taxonomic identification. The parasitoid pupae that did not
204 hatch by early September, as well as the pupae from the second generation of *A. levana* (which
205 have an obligate diapause before adult emergence), were kept cool during the winter period,
206 until we broke their diapause around mid-April (see Appendix S2 for details on the diapause
207 conditions).

208 **Analyses**

209 We performed all analyses in R 3.6.1.

210 *Parasitism rates across counties*

211 We investigated variation in overall parasitism rates per butterfly species and county
212 (Skåne, Kronoberg, and Stockholm). We performed this analysis in a Bayesian framework,
213 using generalized linear and nonlinear multivariate multilevel models. We modelled parasitism
214 rate assuming a binomial distribution and a logit link function. We tested for the effect of
215 species, county, year, and the interaction between species and county as linear effects on
216 parasitism rate and included the week of sampling as a non-linear effect (with k up to 4) to
217 control for phenological variations in parasitism rate for each species. We grouped sites by
218 county (Skåne, Kronoberg, and Stockholm, see Fig. 1) to reflect the south-north progression of
219 the establishment of *A. levana*, and increase the power of our analyses along this gradient. We
220 fitted the model through MCMC sampling, using the Hamiltonian Monte Carlo algorithm
221 implemented in Stan (Carpenter et al., 2017) and the R interface provided in the brms package
222 (Bürkner 2017; 2018). We ran four chains for 10000 iterations with the first 4000 discarded as

223 burn-in and used the default non-informative priors. To test for significant differences in
224 parasitism between county and species, we compared the posterior probability distribution of
225 the model parameters.

226 *Butterfly community and parasitism rate*

227 We examined the effect of the butterfly community composition on each species'
228 parasitism rates. Specifically, we tested for the effect of the presence or absence of each species
229 of butterfly, taken as a binary variable (0/1), and the effect of the abundance of larvae, on the
230 parasitism rate of focal species. We also included in each model the non-linear effect of the
231 sampling week (with k up to 4), to capture phenological variations of parasitism of each
232 species. The abundance of larvae corresponds to the total number of larvae from all species
233 collected per site and sampling week and was zero-centred prior to inclusion in the models. We
234 performed these analyses in a Bayesian framework, using generalized linear and nonlinear
235 multivariate multilevel models. Parasitism was modelled assuming a zero inflated binomial
236 distribution with a logit link function and we used the same parameters as previously mentioned
237 for model fitting. Lack of data on parasitism of *A. levana* prevented us from investigating the
238 impact of community composition on parasitism for this species. Note that this analysis
239 examined the effect of the butterfly community composition on each species' parasitism rates,
240 regardless of the parasitoids responsible for the parasitism rate recorded. Since the parasitoids
241 responsible for the highest mortality are partially or entirely shared between the study
242 butterflies (Table 2), these analyses explored how each species co-occurrence is linked to the
243 parasitism of each of the focal species, by the likely action of parasitoids. These analyses do
244 not investigate, however, the specific impact of the arrival of *A. levana* on the parasitism of
245 native species. In particular, because if apparent competition participates to the structuring of
246 this butterfly community, it can only occur via the action of natural enemies shared between

247 the native species and *A. levana*. In Appendix S3, we offer a specific analysis of the potential
248 impact of *A. levana* on parasitism of native species, examining the effect of the butterfly
249 community composition on parasitism rates by the subset of parasitoids shared with *A. levana*.

250 *Parasitism rate and time since establishment of A. levana*

251 We investigated the role of the establishment of *A. levana* on parasitism rate of the
252 native species. The available observations of *A. levana* clearly suggest that the species has first
253 established in the southern part of the country and is progressively moving northward (see
254 Appendix S1). If the establishment of *A. levana* has induced an increase in parasitism rate in
255 the native species through apparent competition (as proposed by Audusseau et al., 2017), we
256 would expect a decrease in parasitism rates with latitude. In addition, as the establishment of
257 *A. levana* and its progression might not strictly follow the latitudinal gradient and could also
258 be influenced by the configuration of landscape features such as presence of corridors or
259 barriers affecting their dispersal, we also tested for the effect on parasitism rate of the time
260 since first observation of *A. levana* within a 10 km buffer zone around each site and
261 hypothesized that there would be a negative correlation between parasitism rate and the time
262 since first observation.

263 For each species, we tested the effects of latitude and time since the first observation of *A.*
264 *levana* in the 10 km the buffer zone around the sites, using generalized linear models and
265 assuming a binomial distribution. We restricted these analyses to sites where *A. levana* is now
266 established (Skåne and Kronoberg). Data on time since colonization were extracted from
267 Artportalen (Swedish Species Observations System, <http://www.artportalen.se/>, 30/08/2019).
268 The latitude and the time since first observation of *A. levana* at a site are closely correlated, as
269 they both reflect the south-north gradient of progression of *A. levana*. Therefore, we

270 transformed the time elapsed since the first observation of *A. levana* into a 4-level ordinal
271 variable, which corresponds to the division of the distribution of this variable into 4 quartiles,
272 to group sites by periods of establishment of the invading species. The dates of the first, second
273 and third quartiles were 16/05/2004, 22/07/2006 and 02/08/2007. Latitude was zero-centred
274 before it was included in the model.

275 **Results**

276 *General patterns of incidence of butterfly species and parasitoid attack*

277 Over the two sampling seasons, we sampled 6777 butterfly larvae across the 19 sites
278 (*A. io* = 2259, *A.urticae* = 2254, *A. levana* = 1583, *V. atalanta* = 681). The three most
279 widespread butterfly species occurred at all sites, except *A. io* which was absent at three sites
280 (Odensjö, Åsvägen, 31), and *A. urticae* which was absent from site 31. As expected, *A. levana*
281 was not observed at the latitude of the Stockholm area but it was found at all sites further south.

282 Of the 6777 collected larvae, 1508 were parasitized and produced parasitoids from three
283 families: Tachinidae (Diptera), Ichneumonidae (Hymenoptera) and Braconidae
284 (Hymenoptera). We identified 11 species: the tachinids *Pelatachina tibialis*, *Sturmia bella*,
285 *Phryxe vulgaris*, *Phryxe nemea*, *Pales pavidus* and *Blondelia nigripes*, the ichneumonids
286 *Phobocampe confusa*, *Thyrateles haereticus* and *Thyrateles camelinus*, and the braconids
287 *Microgaster subcompleta* and *Cotesia vanessae* (Table 1, 2). Despite collecting very early
288 instar larvae, we did not encounter *Cotesia vestalis*. Overall, 76.7% of the parasitized larvae
289 were parasitized by either *P. tibialis*, *P. confusa* or *S. bella*, which represented 34.6, 28.5 and
290 13.6% of the cases of parasitism, respectively. *Pelatachina tibialis* and *P. confusa*, the two
291 most abundant parasitoid species, were widespread all along the latitudinal gradient while *S.*

292 *bella* was absent from the Stockholm area (Table 1, Fig. 2). We also found *P. vulgaris* and *M.*
293 *subcompleta* in most of the sampling sites and across the three counties (Table 1, Fig. 2). We
294 recorded other parasitoid species in low numbers, which, therefore, provide limited information
295 about their latitudinal distribution. Still *T. haereticus* (n=21) was restricted to the two northern
296 counties and *C. vanessae* (n=30) to the two southern counties (Table 1, Fig. 2).

297 The parasitoid complex varied among the butterfly hosts. *Vanessa atalanta* was the host of
298 most parasitoid species including representatives of all three families (Table 2). *Aglais urticae*
299 was also found to be parasitized by a wide range of species from the three families (Table 2).
300 *Aglais io* and *A. levana* were not parasitized by braconids and *A. levana* was almost exclusively
301 parasitized by *S. bella*, except on two occasions by *P. confusa* (Table 2). Note that the three
302 most abundant parasitoid species were shared among the butterfly hosts, except for *P. tibialis*
303 and *P. confusa* that were never observed in *A. levana* and *V. atalanta* larvae, respectively. We
304 also recorded cases where the cause of larval death was unknown. While, to a certain extent,
305 we relate this mortality to parasitoids that failed to achieve their development within the body
306 of their host either due to a late attack of the parasitoid or to the immune response of their host
307 (HA, personal observation), we also recorded cases of mortality due to viral infection, bacteria
308 or fungi. The overall percentage of dead larvae due to unknown causes varied from 4.2% for
309 *A. levana* to 19.8% for *A. io* (Table 2). The high mortality of *A. io* is not surprising as this
310 species is relatively sensitive to laboratory rearing conditions, especially during the early
311 instars (HA, personal observation).

312 *Effects of latitude and phenology on parasitism rates*

313 Parasitism was responsible for high mortality, particularly in *A. urticae* and *A. io* (Fig.
314 3a, Table S4) and showed a gradual decrease along the latitudinal gradient, from Skåne to

315 Stockholm (Fig. 3a). Over the two field seasons, 40.2% of *A. urticae* and 37.0% of *A. io*
316 larvae collected in Skåne were parasitized. These rates decrease to 20.4% and 17.4% in
317 Stockholm County for *A. urticae* and *A. io*, respectively. *Aglais urticae* showed higher
318 parasitism rates than *A. io*, although this effect is driven mainly by the difference observed in
319 the Stockholm area (Fig. 3a, Table S4). Across counties, *A. urticae* and *A. io* were parasitized
320 at significantly higher frequency than *V. atalanta* and *A. levana* (Fig. 3a). Over the two field
321 campaigns, *V. atalanta* showed highest parasitism rate in Skåne, with 39.9% of the larvae
322 collected parasitized, while it was 12.0% and 13.1% in the counties of Kronoberg and
323 Stockholm, respectively. *Araschnia levana* was very weakly parasitized, with parasitism rates
324 of 4.1% in Skåne and 3.9% in Kronoberg.

325 While the overall parasitism rate was significantly lower in 2017 compared to 2018 (estimate
326 = -0.33, 95% CI = [-0.17, -0.49], Table S4), within each season, parasitism was also lower in
327 early batches than in the later ones. The seasonality of parasitism was, however, specific to
328 each butterfly species (Fig 3b, Table S4) and results from differences in their phenology and
329 the phenology of their parasitoids. Parasitism rate in *A. urticae* followed a bimodal distribution
330 that reflects the bivoltine life cycle of the species in Sweden. In contrast, parasitism rate in *A.*
331 *io* and *V. atalanta* followed a unimodal pattern with a peak at the end of July. We observed a
332 similar unimodal pattern of parasitism in *A. levana* but the low parasitism in this species makes
333 it difficult to form reliable estimates of its phenological variations.

334 *Effect of butterfly species assemblage on parasitism rates*

335 The impact of community composition, that is, the number and identity of co-occurring
336 larval species and the total abundance of larvae, on rates of parasitism is specific to each species
337 (Fig. 4, Table S5).

338 Parasitism in *A. urticae* is higher when larvae are abundant (estimate = 0.26, 95% CI = [0.09,
339 0.42], Fig. 4a, Table S5) and is elevated when *A. urticae* co-occurs with *A. io* (estimate = 0.40,
340 95% CI = [0.05, 0.76], Fig. 4a). Parasitism in *A. io* was not sensitive to the abundance of larvae
341 at the time of collection (estimate = -0.03, 95% CI = [-0.17, 0.10], Fig. 4b, Table S5) but varied
342 according to species assemblage and community size (Fig. 4b). In particular, parasitism rate in
343 *A. io* increased when co-occurring with *V. atalanta* (estimate = 1.05, 95% CI = [0.73, 1.38])
344 and *A. levana* (estimate = 0.82, 95% CI = [0.57, 1.07]), and decreased when co-occurring with
345 *A. urticae* (estimate = -0.83, 95% CI = [-1.32, -0.34], Table S5). We also observed that
346 parasitism rate in *A. io* increased with the number of co-occurring species (Fig. 4b). We did not
347 observed an effect of larvae abundance or species assemblage on parasitism in *V. atalanta* (Fig.
348 4c, Table S5).

349 *Parasitism rate and time since establishment of A. levana*

350 The time period since first observation of *A. levana* significantly explained variations
351 in parasitism rate in *A. urticae* and *A. io* (LR Chisq(3) = 35.15, $p < 0.001$ for *A. urticae* and LR
352 Chisq(3) = 15.88, $p = 0.001$ for *A. io*, Fig. 5, Appendix S5), which showed higher parasitism
353 rates in the earliest colonized sites. Parasitism in *A. io* additionally decreased with latitudinal
354 (LR Chisq(1) = 5.22, $p = 0.022$, Appendix S5). Parasitism in *V. atalanta* was not explained by
355 differences in the time period since first observation of *A. levana* but decreased with latitude
356 (LR Chisq(1) = 24.61, $p < 0.001$, Appendix S5).

357 **Discussion**

358 Our results highlight the influence of species assemblages and trophic interactions on
359 the parasitism of nettle-feeding butterflies. We showed that parasitism was responsible for high

360 mortality rates in two of the native species, *A. urticae* and *A. io*. In comparison, parasitism
361 caused lower mortality in *V. atalanta* and *A. levana*. The parasitoid complex was shared among
362 the nettle-feeding butterflies but *A. levana*, the newcomer in Sweden, was almost exclusively
363 parasitized by the tachinid *S. bella*. We observed that parasitism was influenced by community
364 composition and that this effect was specific to each butterfly species. In addition, we found
365 higher rates of parasitism in the native species at sites where *A. levana* has established for a
366 longer time period.

367 The low parasitism rate in *V. atalanta* and *A. levana* might be the result of
368 morphological, physiological, behavioural, and immunological differences, compared to the
369 other study species. *Vanessa atalanta* larvae are solitary, which may complicate the search for
370 host larvae by their parasitoids, in comparison to the other species that lay batches of eggs
371 (Gentry & Dyer, 2002; Hawkins, 2005). However, *V. atalanta* larvae also live concealed in
372 folded leaves, a shelter-building behaviour that has been shown to concentrate chemical and
373 visual signals that facilitate the localization of individual larvae by parasitoids (Dyer & Gentry
374 1999). Alternatively, differences in feeding guilds between butterflies (solitary versus
375 gregarious) may influence preference of host of parasitoids, as the result of the evolution of
376 different strategies of host searching behaviours in parasitoids, and participate to explain the
377 lower attack rate in *V. atalanta* (Sigiura, 2007). Nevertheless, the low parasitism measured in
378 *V. atalanta* is difficult to explain, considering that this species was host for the largest diversity
379 of parasitoids and that it has been documented to be highly parasitized in other parts of its range
380 (see Rice, 2012). Variation in *V. atalanta* parasitism rates across its range might be related to its
381 migratory behaviour, conditions at overwintering sites, and synchrony between the butterfly
382 and its parasitoids. The pattern is different for *A. levana*, which is resident in Sweden and has
383 been found to be weakly parasitized in other parts of its distribution (Wagner et al., 2011).
384 *Araschnia levana* larva show a pronounced dropping behaviour, which in other species has

385 been shown to be effective against parasitoids which lose track of the chemical and sensory
386 cue of their hosts (Gross and Price, 1988; Fitzpatrick et al., 1994). Alternatively, lower
387 parasitism in *A. levana* could be a result of its recent establishment in Sweden. The enemy
388 release hypothesis (Jeffries & Lawton, 1984; Keane & Crawley, 2002) predicts that in a new
389 area, species experience a period when they escape their natural enemies, until interactions
390 with the local parasitic complex are established (Menéndez et al., 2008). In Sweden, *A. levana*
391 was first reported in the 1980s but probably became established more recently, as there are
392 very few reports of the species before 2000 (see Appendix S1). Considering the relatively short
393 time that was available for recruitment of local parasitoids (Cornell & Hawkins 1992), we can
394 not rule out the possibility that lower level of parasitism observed in *A. levana* are partly a
395 consequence of its recent establishment and that populations have escaped from parasitism
396 during its expansion phase. This hypothesis is strengthened by the fact that Söderlind (2009)
397 reported no parasitism in *A. levana* in South Sweden, while our data reveal that the species has
398 now been colonized by local parasitoid populations. Future monitoring of parasitism load in *A.*
399 *levana* populations in Sweden and across the wider distribution range of the species would be
400 necessary to disentangle the relative importance of these two hypotheses.

401 Butterfly community composition was significantly associated with parasitism in *A. urticae*
402 and *A. io* but not in *V. atalanta*. The differences in egg-laying behaviour mentioned above,
403 where parasitoids prefer gregarious species when present, is again one potential explanation,
404 but *V. atalanta* was also mostly parasitized by *M. subcompleta*, a parasitoid associated almost
405 exclusively with this species. *Aglais io* seemed to benefit from the co-occurrence of *A. urticae*,
406 which was associated with reduced parasitism, while parasitism in *A. urticae* increased when
407 it co-occurred with *A. io*. In contrast, parasitism in *A. io* is increased when co-occurring with
408 *A. levana* and *V. atalanta*. Previous work on this study system hypothesized that a change in
409 the composition of this community, namely, the arrival of *A. levana*, would influence the

410 dynamics and spatial distribution of the resident butterflies through apparent competition
411 (Audusseau et al., 2017). The association between host community composition and parasitism
412 of *A. io* and *A. urticae* is consistent with this prediction. Parasitism rate of the native species
413 decreased along the south-north gradient and was lower in sites recently colonized by *A.*
414 *levana*, highlighting the potential role of *A. levana* in explaining the high parasitism rates of
415 the native species in the southern counties. Nonetheless, while we found an increase in
416 parasitism in *A. io* when the species co-occured with *A. levana*, this was not observed in *A.*
417 *urticae* (Fig. 4a & b). The more pronounced shift in distribution of *A. urticae* reported by
418 Audusseau et al. (2017) could have, however, suggested a relatively stronger response of
419 parasitism in *A. urticae* to the co-occurrence of *A. levana*. The additional analysis that we
420 propose in the Appendix S3 suggests, moreover, that parasitism in *A. urticae*, when restricted
421 to parasitism caused by parasitoids shared with *A. levana*, is elevated when the species co-
422 occurs with *A. levana*. Furthermore, parasitism in *A. urticae* increases with the total abundance
423 of larvae, a phenomenon that might partly be associated with the arrival of the novel host.
424 Differences in the phenology of parasitism between hosts also suggest that *A. levana* could
425 provide a refuge for parasitoids at a time when the native hosts (*A. urticae* and *A. io*) are rare.
426 Thus, species co-occurrence at a site over the season, rather than at a sampling event, may
427 influence their level of parasitism. Last, our study focused on larval parasitoids (for reasons
428 previously mentioned), but pupal parasitoids are known to be shared among our study
429 butterflies and to cause high mortality (Pyörnilä, 1977; Shaw et al., 2009). In particular, the
430 restricted host range of the pteromalid *Pteromalus puparum*, which includes the butterflies of
431 our study (Shaw et al., 2009), and the size of its brood, make this species a strong candidate
432 for driving apparent competition in our study community.

433 From our study, we can not rule-out the effect of other differences across counties, such as
434 changes in parasitoid species richness, population dynamics, habitat quality, or variation in

435 phenological synchrony between the butterflies and their parasitoids, which may all contribute
436 to explain the latitudinal decrease in parasitism. For example, the occurrence of other hosts
437 over the landscape may influence the population dynamics of parasitoids and mediate apparent
438 competition (Davis, 1991; Gaston, 2005). Parasitoids are also responding to the conditions of
439 their habitat (Shaw 2006), which may vary between counties, despite our effort to select sites
440 with comparable landscape. The latitudinal decrease in parasitism could also be associated with
441 a latitudinal trend in weather conditions. Temperature affects insect-parasitoid interactions
442 (Thomas & Blandford, 2003). While in some systems parasitoid activity can increase with
443 temperature (Mann et al., 1990), which could lead to a higher activity period and oviposition
444 rate in the parasitoids at lower and warmer latitude, the literature does not provide consistent
445 evidence of such a pattern (Hawkins, 2005). In our system, the differences in microclimatic
446 conditions across sites did not align with the latitudinal pattern observed for parasitism (see
447 Appendix S7), but we observed latitudinal differences in the parasitoid community. For
448 example, *S. bella*, one of the most abundant parasitoid species in our sample, was only found
449 in the two southern counties. It has also recently established in the U.K. and its arrival coincided
450 with the decline of *A. urticae*. However, Gripenberg et al. (2011) were not able to provide clear
451 support for the role of *S. bella* in the decline of *A. urticae*. Manipulative experiments on
452 community composition while controlling for host abundances would shed further light on
453 parasitoid host preferences and on the mechanism of apparent competition, such as how the
454 parasitoid population built up throughout the season.

455 The systematic sampling that we carried out in the field, at these temporal and spatial scales,
456 and on a set of species that are assembled in a community is rare, but crucial to further our
457 understanding of indirect biotic interactions that structure the community and their persistence
458 and stability over time and space. It enabled us to study the manner by which species
459 composition, variation in abundance, species phenology, and the arrival of *A. levana*, influence

460 local biotic interactions and, ultimately, provide evidence consistent with the role of apparent
461 competition mediated by shared parasitoids in nettle-feeding butterflies. In particular, we
462 showed that parasitoid pressure plays a major role, having an important effect on mortality of
463 our study species in Sweden. We also provide further evidence that modifications favourable
464 to the population dynamics of parasitoids, such as the arrival and establishment of *A. levana*,
465 has the potential to modify the pressure parasitoids exert on their native hosts. Hence,
466 modification of the biotic interactions should be further studied to assess the full impact of
467 environmental change on populations and communities. As mentioned elsewhere (Gaston,
468 2010), this is all the more important in common species as their ubiquity and abundance often
469 makes them connect with a large number of species through trophic interactions.

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602 **Data Accessibility**

603 Data presented in this manuscript will be available upon acceptance.

604 **Table 1** Showing the distribution of larvae dead, according to sampling sites and counties, by parasitoid family and species, and due to
605 unknown causes, covering infection by virus, bacteria, or fungi. The sites are ordered latitudinally. Note that 5 larvae were parasitized by
606 two different species, which lead to the discrepancy between the total by family and the grand total.

Larval death by:		Tachinids					Ichneumonids			Braconids		parasitoid not identified	unknown causes	Grand Total
Species	County	<i>Pelatachina tibialis</i>	<i>Sturmia bella</i>	<i>Phryxe vulgaris</i>	<i>Phryxe nemea</i>	<i>Pales pavida</i>	<i>Blondelia nigripes</i>	<i>Phobocampe confusa</i>	<i>Thyrateles haereticus</i>	<i>Thyrateles camelinus</i>	<i>Microgaster subcompleta</i>			
Stockholm	235	29		5				18	6		1		31	90
	284	40		4				10			9		40	106
	569	29		1				20	5	1	3		132	197
	631	10		2				62	1		2		127	211
	390	14		13				24	5		2		65	127
	590	18		1				30	1		7		42	106
Kronoberg	31		5	1									8	19
	Ljungby	23	6					3			2		24	61
	Odensjö	6	19			1					1		6	33
	37	24	18	3			4	26			1	1	57	148
	178	18	3	4				40	3		2		35	109
Skåne	19	14	2	3	2			4			6		2	34
	Åsvägen	5	14					1			9		13	42
	662	73	17	8			1	14			2	3	24	142
	915	16	17	1				5			16	1	27	86
	63	32						18			13		16	84
	335	64	43	9				33			17	4	42	227
	947	23	51					21			7		49	176
6	88	10	4	1			101			14	21	60	310	
Subtotal		526	205	59	3	1	5	430	21	1	114	30	118	799
Total		799					452			144		118	799	2308

607

608 **Table 2** Table showing the numbers of butterfly larvae of each species dead according to parasitoid species or due to unknown causes, which
609 cover infection by virus, bacteria, or fungi. The table also summarizes the contribution of each parasitoid species to the total parasitism found per
610 butterfly species and intermediate summaries show parasitoids contribution by family. The percentages of larvae dead due to unknown causes are
611 related to the total amount of larvae of each sampled species.

Host butterfly / parasitoid species	<i>A. urticae</i> (n)	<i>A. io</i> (n)	<i>V. atalanta</i> (n)	<i>A. levana</i> (n)	Total (n)	<i>A. urticae</i> (%)	<i>A. io</i> (%)	<i>V. atalanta</i> (%)	<i>A. levana</i> (%)
<i>Pelatachina tibialis</i>	312	207	7		526	45.4	34.5	4.3	
<i>Sturmia bella</i>	39	105	10	51	205	5.7	17.5	6.1	82.3
<i>Phryxe vulgaris</i>	32	18	9		59	4.7	3.0	5.5	
<i>Blondelia nigripes</i>		5			5		0.8		
<i>Phryxe nemea</i>	1		2		3	0.1		1.2	
<i>Pales pavida</i>			1		1			0.6	
Total tachinids	383	335	29	51		55.9	55.8	17.7	82.3
<i>Phobocampe confusa</i>	229	197		2	428	33.3	32.8	0.0	3.2
<i>Thyrateles haereticus</i>	8	11	2		21	1.2	1.8	1.2	
<i>Thyrateles camelinus</i>			1		1			0.6	
<i>Campopleginae, Diadegma sp</i>	1		1		2	0.1		0.6	
Total ichneumonids	238	208	4	2		34.6	34.7	2.4	3.2
<i>Microgaster subcompleta</i>	1		113		114	0.1		68.9	
<i>Cotesia vanessae</i>	24		6		30	3.5		3.7	
Total braconids	25	0	119	0		3.6	0.0	72.6	0.0
Unknown parasitoids	40	57	12	9	118	5.8	9.5	7.3	14.5
Unknown causes	205	447	83	64	799	9.1	19.8	12.2	4.2

613 **Figure legends**

614 **Figure 1** Map showing the 19 sites, spread across three counties, visited fortnightly over the
615 two field campaigns (2017-2018).

616 **Figure 2** Quantitative host butterflies-parasitoid species association in the counties of (a)
617 Stockholm, (b) Kronoberg, (c) Skåne. For each web, the bottom boxes represent, for each
618 butterfly species, the proportion of larvae parasitized within the total amount of larvae sampled,
619 the upper boxes correspond to the contribution of each parasitoid species to the overall
620 parasitism. Associations are ordered according to parasitoid family.

621 **Figure 3** (a) Estimation of marginal means of parasitism rates (%) at representative values
622 (week = 4.4, year = 2017) according to butterfly species and counties (mean and 95%
623 confidence interval). (b) Estimated variation in the parasitism rate by species over time (weeks)
624 in 2017 in Skåne. Non-overlapping confidence intervals correspond to significant differences
625 in parasitism rate between groups. Note that we have adjusted for week 4.4 as at this time,
626 differences in parasitism between species reflect the overall differences observed the season.
627 The phenology of parasitism is illustrated in Skåne but follows the same pattern in the other
628 two counties, modulated by a variation in the intercept. The red line on (b) indicates week 4.4,
629 the time of the reproductive season for which the marginal means shown in (a) were extracted
630 for Skåne. We restricted the plot of estimated variation in parasitism rate to the time window
631 for which each species was sampled in the field.

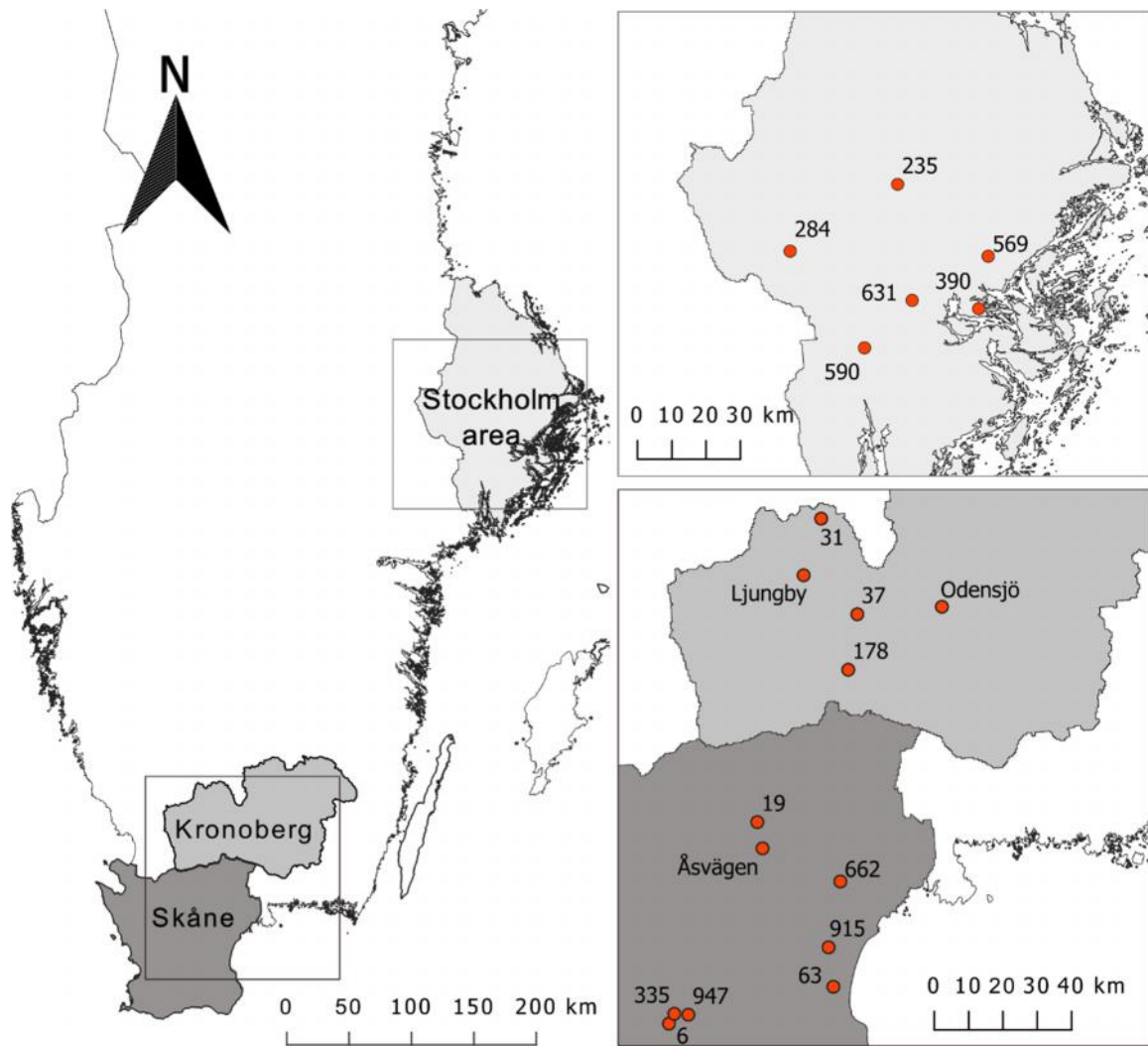
632 **Figure 4** Contrasting effects of community composition, taken as the presence/absence of the
633 other species, including *A. levana*, on parasitism rate of (a) *A. urticae*, (b) *A. io*, and (c) *V.*
634 *atalanta*. Estimation of marginal means of parasitism rates (%) are given at representative

635 values (week = 4.74) and parasitism rates of each of the focal species are ordered on the x-axis
636 according to the number of species which co-occur. The first bar on each plot corresponds to
637 parasitism rate of the focal species found alone (mean \pm CI) at each site and the letter stands
638 for the identity of the focal species with A for *A. urticae*, B for *A. io*, C for *V. atalanta*. The
639 following bars correspond to parasitism rate of the focal species (mean \pm CI) when co-occurring
640 with other nettle-feeding butterflies with +A when the species co-occur with *A. urticae*, +B
641 with *A. io*, +C with *V. atalanta*, and +D with *A. levana*. Non overlapping confidence intervals
642 correspond to significant differences in parasitism rate between groups.

643 **Figure 5** Parasitism rate (mean \pm se) of *A. urticae*, *A. io*, and *V. atalanta*, according to the time
644 period of establishment of *A. levana* at the site. The four time periods correspond to the division
645 of the distribution of the time since first observation of *A. levana* into four quantiles and are
646 ordered chronologically.

647

Figure 1

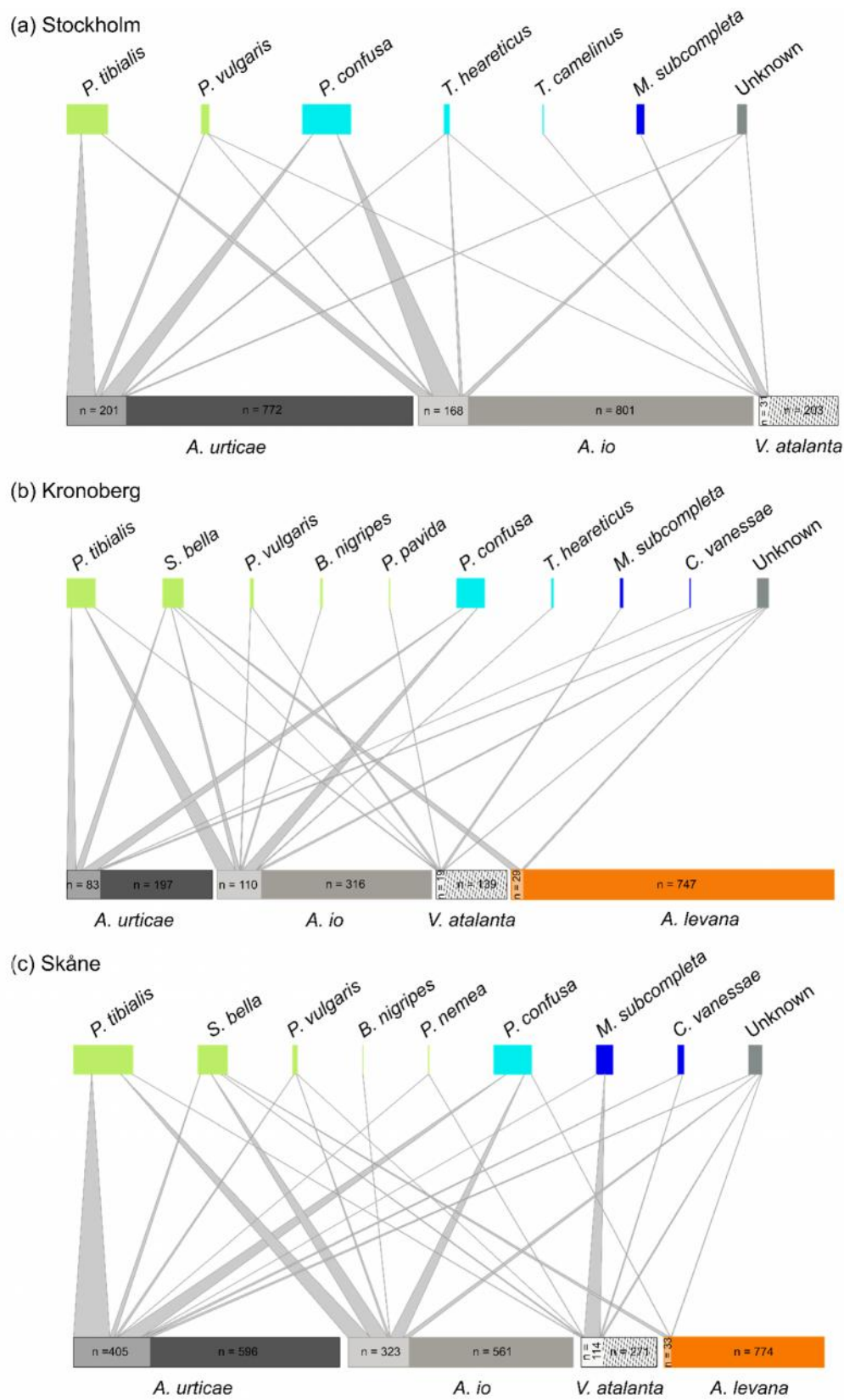


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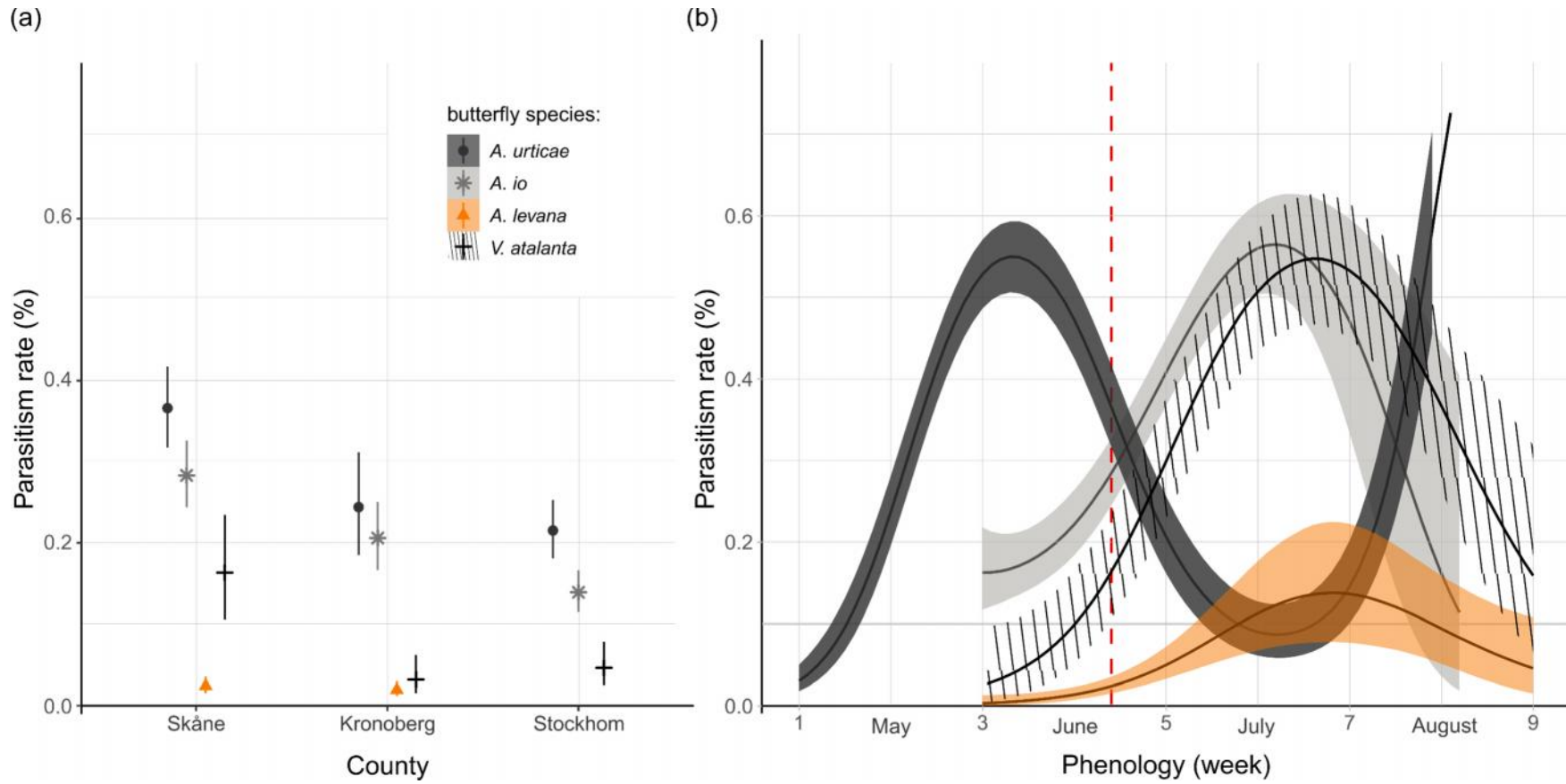
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Figure 2



651

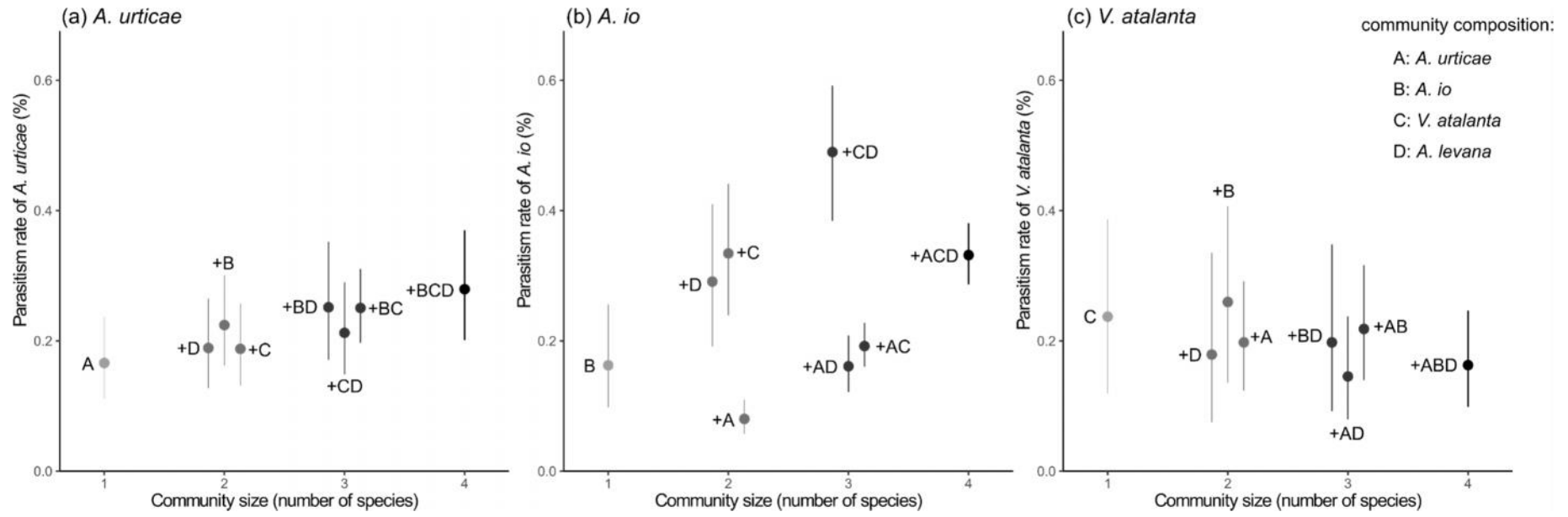
652 **Figure 3**



653

654

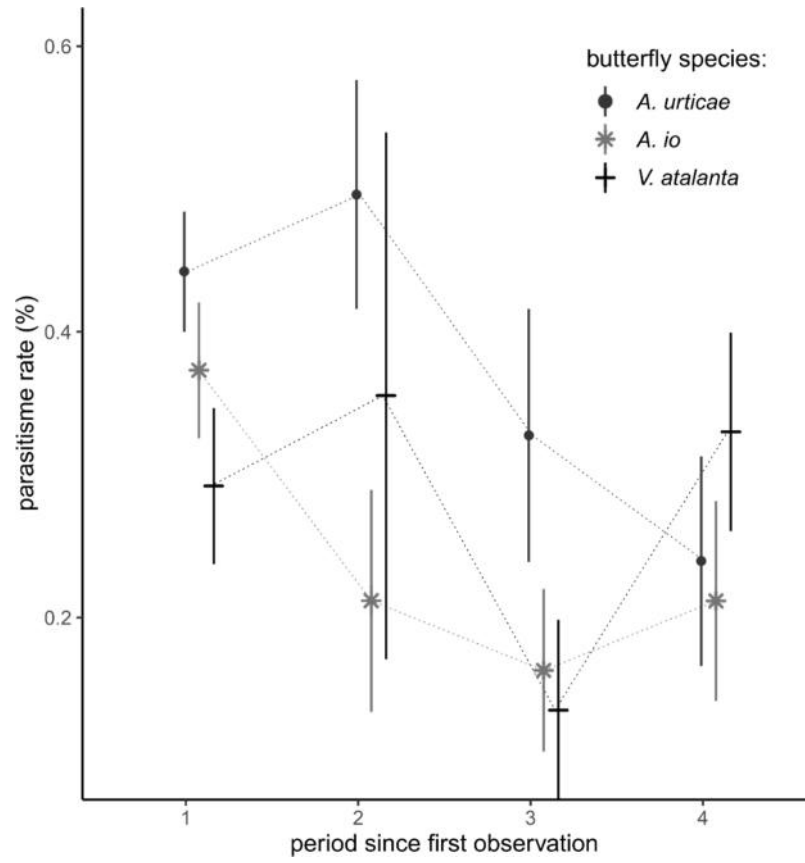
655 **Figure 4**



656

657

658 **Figure 5**



659

660 **Supporting information**

661 **Appendix S1** Animation showing the expansion of *Araschnia levana* over the period 1995-
662 2018. The data used are the opportunistic occurrence data collected by amateurs and available
663 from Artportalen (Swedish Species Observations System, www.artportalen.se). The black dots
664 correspond to species occurrences, red dot correspond to new occurrences as time goes. The
665 red halo around each new observation is expanding until it vanishes after 200 days.

666 **Appendix S2 Details on the winter diapause conditions.**

667 In mid-September, we stored the moist plastic vials containing the pupae of *A. levana* and
668 parasitoids at +8 °C. In November, we transferred them to a climate chamber with a day/night
669 temperature of +4 / 0°C and a light regime of 12L:12D and changed the day/night temperature
670 to -4 / -2 ° C from mid-December to the end of February. Subsequently, we reversed the
671 temperature cycle by following the same temperature scheme. Throughout the hibernation
672 period, we frequently checked the moisture conditions and adjusted them if necessary. We
673 broke diapause of the pupae of *A. levana* and of the parasitoids around mid-April. To do this,
674 we transferred the plastic vials to ambient temperature and light conditions, and sprayed them
675 with water regularly so that the individuals rehydrated.

676 **Appendix S3 Effect of butterfly species assemblage on each of the native species'**
677 **parasitism by the subset of shared parasitoid species with *A. levana*.**

678 **Aim and dataset**

679 Apparent competition among species can only occur when species share a natural
680 enemy, that is, parasitoids in the case of our butterfly community. From our field sampling,
681 while most parasitoid species attack different host butterflies, the only parasitoid that is shared
682 by all four study butterflies is *S. bella* (Table 2), and would, therefore, be the only one species
683 potentially involved in apparent competition between our study butterflies.

684 **As our aim is to provide further evidence consistent with the fact that the**
685 **establishment of *A. levana* may have increased parasitism in the native species, as a result**
686 **of apparent competition, we provide, here, an extra analysis on parasitism by shared**
687 **parasitoids between the native species and *A. levana*.** Restricting the analysis of the effect
688 of species assemblage on parasitism by *S. bella* would, however, drastically reduce the dataset
689 to use. First, because *S. bella* is only found in the two southern counties¹. Second, this could
690 also lead, for consistency, to restrict our analysis to the phenological window of occurrence of
691 the *S. bella* (five sampling occasions per site in 2017).

692 Considering that other parasitoids have been documented as attacking *A. levana* (they
693 are *Apechthis compunctor*, *Thyrateles camelinus*, *Compsilura concinnate*, *Phryxe nemea*,
694 *Phryxe vulgaris*, and *Sturmia bella*, Herting & Simmonds, 1976), **we will examine the effect**
695 **of butterfly assemblage on parasitism by the following subset of parasitoids, *Thyrateles***
696 ***camelinus*, *Phryxe nemea*, *Phryxe vulgaris*, *Sturmia bella*, and *Phobocampe confusa*, on the**

¹ Note on *S. bella*: the species has probably only recently established in Sweden from a different migration route than *A. levana*, as the first occurrence was reported on the East coast of Sweden (Christer Bergström, personal communication, with a first observation in Götland on 2003-07-24, coordinates: 57°31'52.7"N 18°08'52.4"E). Moreover, Söderlind (2009) reported no parasitism in *A. levana*, and therefore, no case of parasitism by *S. bella*.

697 basis that these parasitoids were also collected over our study sites. These analyses are limited
698 to the two southern counties (*Skåne and Kronoberg*), where *A. levana* occurs.

699 **Analyses**

700 These analyses followed the same procedure as described in the main text. We tested
701 for the effect of the presence or absence of each species of butterfly, taken as a binary variable
702 (0/1), and the effect of the abundance of larvae, on the parasitism rate of each of the native
703 species. We also included in each model the non-linear effect of the sampling week (with k up
704 to 4), to capture phenological variations of parasitism of each species. The abundance of larvae
705 corresponds to the total number of larvae from all species collected per site and sampling week
706 and was zero-centred prior to inclusion in the models. We performed these analyses in a
707 Bayesian framework using generalized linear and nonlinear multivariate multilevel models.
708 Parasitism was modelled assuming a zero inflated binomial distribution with a logit link
709 function. The models were fitted through MCMC sampling, using the Hamiltonian Monte
710 Carlo algorithm implemented in Stan (Carpenter et al., 2017) and the R interface provided in
711 the brms package (Bürkner 2017; 2018). We ran four chains for 10000 iterations with the first
712 4000 discarded as burn-in and used the default priors. To test for significant differences in
713 parasitism between county and species, we compared the posterior probability distribution of
714 the model parameters.

715 **Results**

716 We observed that the number and identity of co-occurring larval species and the total
717 abundance of larvae affected parasitism by the subset of parasitoids considered in this analysis,
718 and was specific to each species (Fig. S3, Table S3). However, the patterns of variation of each
719 species' parasitism rates are different from the observed patterns when including all parasitoid
720 species and the three counties.

721 Parasitism in *A. urticae* is higher when the species co-occurs with *A. levana* (estimate
722 = 1.01, 95% CI = [0.31, 1.70], Fig. S3, Table S3). Parasitism in *A. io* no longer showed
723 sensitivity to the co-occurrence of *A. urticae* and *A. levana*, but still increased when the species
724 co-occurs with *V. atalanta* (estimate = 3.46, 95% CI = [2.51, 4.48], Fig. S3, Table S3).
725 Parasitism in *A. io* is also higher when larvae are abundant (estimate = 0.65, 95% CI = [0.35,
726 0.96]). Similarly to the analysis present in the main manuscript, we did not observed an effect
727 of larvae abundance or species assemblage on parasitism in *V. atalanta* (Fig. S3, Table S3).

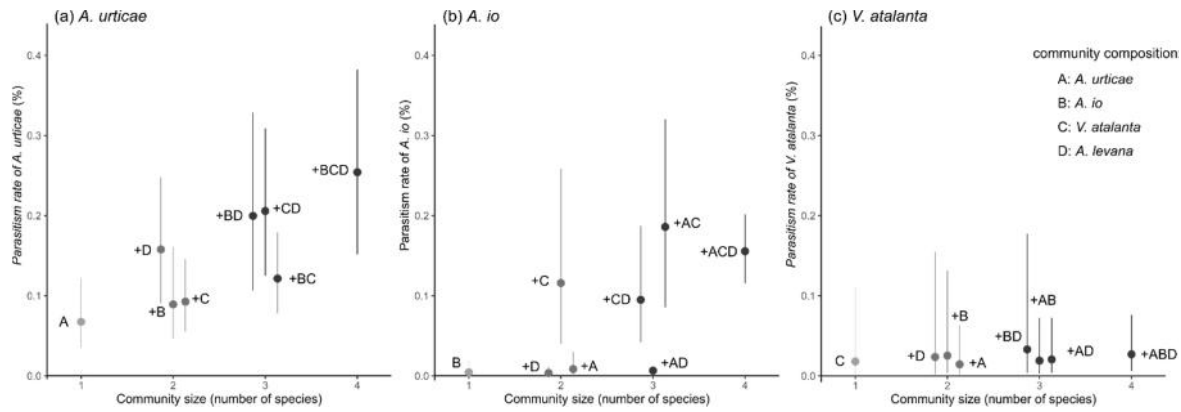
728 **This analysis showed that, when focusing on the specific subset of parasitoids**
729 **known to be shared between the native species and *A. levana*, parasitism in *A. urticae* is**
730 **increased when the species co-occurs with *A. levana*.**

731

732 **References**

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741 Brubaker, M., Guo, J., Li, P., & Riddell, A. (2017). Stan : A Probabilistic Programming
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743



744

745 **Figure S3** Contrasting effects of community composition, taken as the presence/absence of the
746 other species, including *A. levana*, on parasitism rate by of (a) *A. urticae*, (b) *A. io*, and (c) *V.*
747 *atalanta*. Only parasitism by the following parasitoid species is considered here: *Thyrateles*
748 *camelinus*, *Phryxe nemea*, *Phryxe vulgaris*, *Sturmia bella*, and *Phobocampe confusa*.
749 Estimation of marginal means of parasitism rates (%) are given at representative values (week
750 = 4.74) and parasitism rates of each of the focal species are ordered on the x-axis according to
751 the number of species which co-occur. The first bar on each plot corresponds to parasitism rate
752 of the focal species found alone (mean \pm CI) at each site and the letter stands for the identity
753 of the focal species with A for *A. urticae*, B for *A. io*, C for *V. atalanta*. The following bars
754 correspond to parasitism rate of the focal species (mean \pm CI) when co-occurring with other
755 nettle-feeding butterflies with +A when the species co-occur with *A. urticae*, +B with *A. io*, +C
756 with *V. atalanta*, and +D with *A. levana*. Non overlapping confidence intervals correspond to
757 significant differences in parasitism rate between groups.

758 **Table S3** Summary table of the population-level effects of the presence/absence of each species
759 of butterfly, the abundance of larvae, and seasonality (week of sampling), and of the non-linear
760 effect of the seasonality (sds), on parasitism rates of the focal species. Estimates are provided
761 on the logit-scale. Non overlapping confidence intervals correspond to significant differences
762 in parasitism rate between groups. We assessed model fit by checking that the chains have

763 mixed well and by looking at the distribution of the predictive values. Sds corresponds to the
 764 variance parameter (higher values reflecting more wiggly smoother). Note that the confidence
 765 intervals of the smooth terms are not overlapping zero. The smooth term is, therefore, required
 766 over the linear parametric effects of the week (see sweek: species). “zi” corresponds to the zero
 767 inflated estimate. The zero inflated binomial distribution model has two parts, a binomial count
 768 model and the logit model for predicting excess zeros.

Butterfly species	variables	Estimate	95% CI	Eff. Sample	Rhat
<i>A. urticae</i>	Intercept	-1.57	[-1.87, -1.28]	10223	1
	Presence <i>V. atalanta</i>	0.36	[-0.15, 0.87]	10805	1
	Presence <i>A. io</i>	0.32	[-0.14, 0.81]	10890	1
	Presence <i>A. levana</i>	1.01	[0.31, 1.70]	11162	1
	Larvae abundance	0.06	[-0.27, 0.40]	10412	1
	week	1.90	[1.14, 2.66]	10495	1
	sds(sweek)	16.32	[6.81, 37.26]	8118	1
	zi	0.30	[0.19, 0.41]	10712	1
<i>A. io</i>	Intercept	-4.33	[-5.72, -2.99]	8323	1
	Presence <i>V. atalanta</i>	3.46	[2.51, 4.48]	7498	1
	Presence <i>A. urticae</i>	0.63	[-0.24, 1.53]	10036	1
	Presence <i>A. levana</i>	-0.24	[-1.05, 0.62]	10089	1
	Larvae abundance	0.65	[0.35, 0.96]	9070	1
	week	2.24	[-1.53, 7.56]	4964	1
	sds(sweek)	19.79	[3.04, 52.66]	6147	1
	zi	0.41	[0.30, 0.52]	11010	1
<i>V. atalanta</i>	Intercept	-3.35	[-5.00, -1.84]	10920	1
	Presence <i>A. io</i>	0.38	[-1.47, 2.29]	10161	1
	Presence <i>A. urticae</i>	-0.23	[-1.55, 1.13]	10488	1
	Presence <i>A. levana</i>	0.28	[-0.99, 1.50]	10335	1
	Larvae abundance	-0.06	[-0.79, 0.64]	9918	1
	week	0.07	[-2.56, 2.25]	8209	1
	sds(sweek)	7.54	[0.36, 23.04]	8582	1
	zi	0.21	[0.01, 0.56]	10210	1

769 **Appendix S4** Summary table of the population-level effects of butterfly species, counties,
 770 sampling year, and seasonality (week of sampling), and of the non linear effect of the
 771 seasonality for each butterfly (sds), on parasitism rates. Estimates are provided on the logit-
 772 scale. Non overlapping confidence intervals correspond to significant differences in parasitism
 773 rate between groups. We assessed model fit by checking that the chains have mixed well and
 774 by looking at the distribution of the predictive values. Sds corresponds to the variance
 775 parameter (higher values reflecting more wiggly smoother). Note that the confidence intervals
 776 are not overlapping zero. The smooth term is, therefore, required over the linear parametric
 777 effects of the week (see sweek: species).

variables		Estimate	Estimated error	95% CI	Eff. Sample	Rhat
<i>A. urticae</i>	Skåne	-0.71	0.10	[-0.91, -0.51]	9584	1.00
	Kronoberg	-1.29	0.16	[-1.61, -0.99]	10395	1.00
	Stockholm	-1.45	0.10	[-1.66, -1.25]	10871	1.00
<i>A. io</i>	Skåne	-0.91	0.12	[-1.15, -0.69]	9516	1.00
	Kronoberg	-1.34	0.16	[-1.64, -1.03]	9312	1.00
	Stockholm	-1.81	0.13	[-2.07, -1.56]	9708	1.00
<i>V. atalanta</i>	Skåne	-1.76	0.33	[-2.48, -1.18]	8112	1.00
	Kronoberg	-3.54	0.40	[-4.38, -2.80]	8197	1.00
	Stockholm	-3.16	0.37	[-3.93, -2.50]	7552	1.00
<i>A. levana</i>	Skåne	-3.79	0.33	[-4.49, -3.19]	8715	1.00
	Kronoberg	-4.02	0.34	[-4.73, -3.40]	8660	1.00
	Stockholm	-	-	-	-	-
Year 2018		0.33	0.08	[0.17, 0.49]	9607	1.00
sweek: <i>A. Urticae</i>		5.20	0.39	[4.43, 5.98]	10431	1.00
sweek: <i>A. io</i>		-2.89	1.08	[-5.07, -0.79]	10036	1.00
sweek: <i>V. atalanta</i>		-0.02	1.24	[-2.44, 2.48]	7919	1.00
sweek: <i>A. levana</i>		0.38	1.28	[-2.21, 2.99]	8614	1.00
sds(sweek : <i>A. urticae</i>)		25.86	11.62	[12.70, 55.16]	8912	1.00
sds(sweek : <i>A. io</i>)		17.65	8.73	[6.84, 40.37]	9562	1.00
sds(sweek : <i>V. atalanta</i>)		13.93	7.30	[5.63, 32.41]	10610	1.00
sds(sweek : <i>A. levana</i>)		12.68	6.94	[4.43, 30.89]	10220	1.00

778 **Appendix S5** Summary table of the population-level effects of the presence/absence of each
779 species of butterfly, the abundance of larvae, and seasonality (week of sampling), and of the
780 non linear effect of the seasonality (sds), on parasitism rates of the focal species. Estimates are
781 provided on the logit-scale. Non-overlapping confidence intervals correspond to significant
782 differences in parasitism rate between groups. We assessed model fit by checking that the
783 chains have mixed well and by looking at the distribution of the predictive values. Sds
784 corresponds to the variance parameter (higher values reflecting more wiggly smoother). Note
785 that the confidence intervals are not overlapping zero. The smooth term is, therefore, required
786 over the linear parametric effects of the week (see sweek: species). “zi” corresponds to the zero
787 inflated estimate. The zero inflated binomial distribution model has two parts, a binomial count
788 model and the logit model for predicting excess zeros. For example, the probability of *A.*
789 *urticae* not being parasitized is actually higher than 0.23, but part of this probability is already
790 modeled by the binomial distribution itself.

Butterfly species	variables	Estimate	95% CI	Eff. Sample	Rhat
<i>B. urticae</i>	Intercept	-0.66	[-0.87, -0.46]	10109	1
	Presence <i>V. atalanta</i>	0.16	[-0.18, 0.49]	10615	1
	Presence <i>A. io</i>	0.40	[0.05, 0.76]	9297	1
	Presence <i>A. levana</i>	0.17	[-0.30, 0.63]	10970	1
	Larvae abundance	0.26	[0.09, 0.42]	10154	1
	week	3.55	[2.95, 4.18]	9662	1
	sds(sweek)	24.54	[11.86, 51.90]	7052	1
	zi	0.23	[0.16, 0.30]	10614	1
<i>A. io</i>	Intercept	-1.17	[-1.78, -0.56]	11480	1
	Presence <i>V. atalanta</i>	1.05	[0.73, 1.38]	11735	1
	Presence <i>A. urticae</i>	-0.83	[-1.32, -0.34]	11094	1
	Presence <i>A. levana</i>	0.82	[0.57, 1.07]	11062	1
	Larvae abundance	-0.03	[-0.17, 0.10]	11308	1
	week	-0.04	[-0.67, 0.55]	8848	1
	sds(sweek)	6.93	[1.89, 18.95]	7807	1
	zi	0.22	[0.15, 0.30]	11479	1
<i>V. atalanta</i>	Intercept	-0.85	[-1.61, -0.07]	11653	1
	Presence <i>A. io</i>	0.15	[-0.56, 0.89]	11134	1
	Presence <i>A. urticae</i>	-0.27	[-0.96, 0.40]	11398	1
	Presence <i>A. levana</i>	-0.42	[-1.05, 0.19]	11082	1
	Larvae abundance	-0.09	[-0.40, 0.21]	10617	1
	week	1.36	[-0.05, 3.0]	9383	1
	sds(sweek)	10.74	[3.83, 26.80]	8409	1
	zi	0.34	[0.19, 0.47]	10007	1

791

792 **Appendix S6** Summary tables from the generalized linear models testing for each native butterfly species the effect of latitude and time since first
 793 observation of *A. levana*.

Variables	<i>A. urticae</i>				<i>A. io</i>				<i>V. atalanta</i>			
	Estimate	se	z	p-value	Estimate	se	z	p-value	Estimate	se	z	p-value
Intercept	-0.148	0.121	-1.23	0.22	-0.544	0.092	-5.92	<0.001	-1.083	0.195	-5.56	0.14
Latitude	0.097	0.118	0.82	0.41	-0.196	0.087	-2.26	0.024	-0.790	0.177	-4.46	<0.001
Period 2	-0.155	0.182	-0.85	0.40	-0.775	0.212	-3.66	<0.001	-0.271	0.595	-0.45	0.65
Period 3	-0.73	0.335	-2.23	0.03	-0.462	0.253	-1.82	0.068	0.337	0.567	0.59	0.55
Period 4	-1.34	0.255	-5.28	<0.001	-0.114	0.216	-0.53	0.60	0.610	0.281	2.17	0.03

794

795 **Appendix S7** Summary table showing the effect of counties, years and the interaction between
796 counties and years on the average temperature recorded by the temperature loggers placed in
797 the field from May to August. We investigated differences in temperature averages between
798 counties to test if these differences could explain the latitudinal pattern found in parasitism
799 rates. We found that there is not a linear decrease in the average temperature as we go north.
800 Indeed, the average temperature was +0.4°C higher in the Stockholm county than in
801 Kronoberg. The the average temperature in 2018 is higher that in 2017, with on average +2.8°C.
802 This increase was found to be slightly more pronounced in Skåne (estimate = 0.41, t-value =
803 8.7, $p < 0.001$).

Variables	estimate	Std error	t-value	<i>p</i>
Kronoberg	14.97	0.028	541.54	<0.001
Stockholm	0.40	0.036	11.17	<0.001
Skåne	0.30	0.035	8.59	<0.001
Year 2018	2.79	0.038	73.72	<0.001
Stockholm : year 2018	-0.05	0.050	-0.92	0.36
Skåne : year 2018	0.42	0.048	8.68	<0.001

804