

1 Title:

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

4 **Audusseau, H.<sup>1,2\*</sup>, Ryrholm, N.<sup>3</sup>, Stefanescu, C.<sup>4</sup>, Tharel, S.<sup>1</sup>, Jansson, C.<sup>1</sup>, Champeaux,**  
5 **L.<sup>1</sup>, Shaw, M. R.<sup>5</sup>, Raper, C.<sup>6</sup>, Lewis, O. T.<sup>7</sup>, Janz, N.<sup>1</sup>, Schmucki, R.<sup>2</sup>**

6 1. Department of Zoology, Stockholm University, Stockholm, Sweden

7 2. UK Centre for Ecology & Hydrology, Wallingford, United Kingdom

8 3. Department of Electronics, Mathematics and Natural Sciences, University of Gävle, Gävle, Sweden

9 4. Museu de Ciències Naturals de Granollers, Granollers, Barcelona, Spain

10 5. National Museums of Scotland, Chambers Street, Edinburgh, United Kingdom

11 6. Angela Marmont Centre for UK Biodiversity, Natural History Museum, London, United Kingdom

12 7. Department of Zoology, University of Oxford, Oxford, United Kingdom

13 \* Corresponding author; e-mail address: [helene.audusseau@zoologi.su.se](mailto:helene.audusseau@zoologi.su.se)

14 **Acknowledgments**

15 H. Audusseau acknowledges support from the Swedish Research Council (2016-06737). This  
16 work benefited from technical assistance by Maria Celorio-Mancera de la Paz and Houshuai  
17 Wang, from taxonomic assistance on the tachinids by Christer Bergström, and from genetic  
18 assistance (for molecular confirmation of a subset of the parasitoids determined) by Lise  
19 Dupont and Claire Brice. Tom August provided the script for the *A. levana* range expansion  
20 animation. We are also grateful to all reporters of the Swedish Biomonitoring Scheme and

21 specifically to Evald Jonsson, Sven Nilsson, Peter Rolfson, Pål Axel Olsson, Kurt Norell, and  
22 Mats Hansson for valuable advice on the distribution of species at the sites.

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](http://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 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.

## 470 References

- 471 1. Araújo, M. B., & Luoto, M. (2007). The importance of biotic interactions for modelling  
472 species distributions under climate change. *Global Ecology and Biogeography*, 16(6),  
473 743-753.
- 474 2. Audusseau, H., Le Vaillant, M., Janz, N., Nylin, S., Karlsson, B., & Schmucki, R.  
475 (2017). Species range expansion constrains the ecological niches of resident butterflies.  
476 *Journal of Biogeography*, 44(1), 28-38.
- 477 3. Belmaker, J., Zarnetske, P., Tuanmu, M.-N., Zonneveld, S., Record, S., Strecker, A., &  
478 Beaudrot, L. (2015). Empirical evidence for the scale dependence of biotic interactions.  
479 *Global Ecology and Biogeography*, 24, 750–761.
- 480 4. Blitzer, E. J., & Welter, S. C. (2011). Emergence asynchrony between herbivores leads  
481 to apparent competition in the field. *Ecology*, 92(11), 2020-2026.
- 482 5. Blois, J. L., Zarnetske, P. L., Fitzpatrick, M. C., & Finnegan, S. (2013). Climate change  
483 and the past, present, and future of biotic interactions, *Science*, 341, 499-504.
- 484 6. Bonsall, M. B., & Hassell, M. P. (1997). Apparent competition structures ecological  
485 assemblages. *Nature*, 388, 371-373.
- 486 7. Bürkner, P.-C. (2017). brms: An R Package for Bayesian Multilevel Models Using  
487 Stan. *Journal of Statistical Software*, 80(1), 1-28. doi:10.18637/jss.v080.i01.
- 488 8. Bürkner, P.-C. (2018). Advanced Bayesian Multilevel Modeling with the R Package  
489 brms. *The R Journal*, 10(1), 395-411. doi:10.32614/RJ-2018-017.
- 490 9. Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M.,  
491 Brubaker, M., Guo, J., Li, P., & Riddell, A. (2017). Stan : A Probabilistic Programming  
492 Language. *Journal of Statistical Software*, 76.
- 493 10. Cornell, H. C., & Hawkins, B. A. (1993). Accumulation of native parasitoid species on  
494 introduced herbivores: a comparison of hosts as natives and hosts as invaders. *The*  
495 *American Naturalist*, 141(6), 847-865.
- 496 11. Davis, B. N. K. (1991). Insects on nettles. in N. H. 1, editor. The Richmond Publishing  
497 Co. Ltd., Slough.
- 498 12. Davis, A. J., Jenkinson, L. S., Lawton, J. H., Shorrocks, B., & Wood, S. (1998). Making  
499 mistakes when predicting shifts in species range in response to global warming. *Nature*,  
500 391, 783-786.
- 501 13. Dormann, C. F., Bobrowski, M., Dehling, D. M., Harris, D. J., Hartig, F., Lischke, H.,  
502 Moretti, M. D., Pagel, J., Pinkert, S., Schleuning, M., Schmidt, S. I., Sheppard, C. S.,  
503 Steinbauer, M. J., Zeuss, D., & Kraan, C. (2018). Biotic interactions in species  
504 distribution modelling: 10 questions to guide interpretation and avoid false conclusions.  
505 *Global Ecology and Biogeography*, 27(9), 1004-1016.



- 506 14. Dyer, L. A., & Gentry, G. (1999). Predicting Natural-Enemy Responses to Herbivores  
507 in Natural and Managed Systems. *Ecological Applications*, 9(2), 402-408.
- 508 15. Early, R. & Keith, S.A. (2019). Geographically variable biotic interactions and  
509 implications for species ranges. *Global Ecology and Biogeography*, 28, 42–53.
- 510 16. Ebert, G. (1993). Die Schmetterlinge Baden-Württembergs, Band 1, Verlag Eugen  
511 Ulmer.
- 512 17. Eliasson, C. U., Ryrholm, N., Holmer, M., Jilg, K., & Gärdenfors, U. (2005).  
513 Nationalnyckeln till Sveriges flora och fauna. Fjärilar. Dagfjärilar. HesperIIDae-  
514 Nymphalidae. Artdatabanken, SLU, Uppsala, Sweden.
- 515 18. Fitzpatrick, S. M., Troubridge, J. T., & Maurice, C. (1994). Parasitoids of blackheaded  
516 fireworm (*Rhopobota naevana* Hbn.) larvae on cranberries, and larval escape  
517 behaviour. *Journal of the Entomological Society of British Columbia*, 91, 73–74.
- 518 19. Frost, C. M., Peralta, G., Rand, T. A., Didham, R. K., Varsani, A., & Tylianakis, J. M.  
519 (2016). Apparent competition drives community-wide parasitism rates and changes in  
520 host abundance across ecosystem boundaries. *Nature communications*, 7, 1-12.
- 521 20. Gaston, K. J., Smith, R. M., Thompson, K., & Warren, P. H. (2005). Urban domestic  
522 gardens (II): experimental tests of methods for increasing biodiversity. *Biodiversity and  
523 Conservation*, 14:395-413.
- 524 21. Gaston, K. J. (2010). Valuing Common Species. *Science*, 327:154-155.
- 525 22. Gentry, G., & Dyer, L. A. (2002). On the conditional nature of neotropical caterpillar  
526 defences against their natural enemies. *Ecology*, 83(11), 3108-3119.
- 527 23. Gripenberg, S., Hamer, N., Brereton, T., Roy, D. B., & Lewis, O. T. (2011). A novel  
528 parasitoid and a declining butterfly: cause or coincidence? *Ecological Entomology*,  
529 36(3), 271-281.
- 530 24. Gross, P., & Price, P. W. (1988). Plant influences on parasitism of two leafminers: a  
531 test of enemy-free space. *Ecology*, 69(5), 1506-1516.
- 532 25. Hawkins, B. A. (2005) Pattern and process in host-parasitoid interactions. Cambridge  
533 University Press.
- 534 26. Heikinen, R. K., Luoto, M., Virkkala, R., Pearson, R. G., & Körber, J.-H. (2007). Biotic  
535 interactions improve prediction of boreal bird distributions at macro-scales. *Global  
536 Ecology and Biogeography*, 16, 754–763.
- 537 27. Holt, R. D., & Lawton, J. H. (1993). Apparent competition and enemy-free space in  
538 insect host-parasitoid communities. *American Naturalist*, 142, 623–45.
- 539 28. Holt, R. D., & Lawton, J. H. (1994). The ecological consequences of shared natural  
540 enemies. *Annual Review of Ecology and Systematics*, 25(1), 495–520.
- 541 29. Jeffries, M. J., & Lawton, J. H. (1984). Enemy free space and the structure of ecological  
542 communities. *Biological journal of the Linnean Society*, 23(4), 269-286.



- 543 30. Keane, R.M., & Crawley, M.J. (2002). Exotic plant invasions and the enemy release  
544 hypothesis. *Trends in Ecology & Evolution*, 17, 164–170.
- 545 31. Kissling, W. D., & Schleuning, M. (2015). Multispecies interactions across trophic  
546 levels at macroscales: retrospective and future directions. *Ecography*, 38(4), 346–357.
- 547 32. Losey, J.E. & Vaughan, M. (2006) The Economic Value of Ecological Services  
548 Provided by Insects. *BioScience*, 56 , 311.
- 549 33. Mann, J. A., Axtell, R. C., & Stinner, R. E. (1990). Temperature-dependent  
550 development and parasitism rates of four species of Pteromalidae (Hymenoptera)  
551 parasitoids of house fly (*Musca domestica*) pupae. *Medical and Veterinary  
552 Entomology*, 4(3), 245–253. doi:10.1111/j.1365-2915.1990.tb00436.x.
- 553 34. Meier, E. S., Kienast, F., Pearman, P. B., Svenning, J.-C., Thuiller, W., Araújo, M. B.,  
554 Guisan, A., & Zimmermann, N. E. (2010). Biotic and abiotic variables show little  
555 redundancy in explaining tree species distributions. *Ecography*, 33, 1038-1048.
- 556 35. Menéndez, R., González-Megías, A., Lewis, O. T., Shaw, M. R., & Thomas, C. D.  
557 (2008). Escape from natural enemies during climate-driven range expansion: a case  
558 study. *Ecological Entomology*, 33, 413-421.
- 559 36. Morris, R. J., Lewis, O. T., & Godfray, H. C. J. (2004). Experimental evidence for  
560 apparent competition in a tropical forest food web. *Nature*, 428, 310-313.
- 561 37. Pellissier, L., Albouy, C., Bascompte, J., Farwig, N., Graham, C., Loreau, M.,  
562 Maglianesi, M. A., Melián, C. J., Pitteloud, C., Roslin, T., Rohr, R., Saavedra, S.,  
563 Thuiller, W., Woodward, G., Zimmermann, N. E., & Gravel, D. (2017). Comparing  
564 species interaction networks along environmental gradients. *Biological reviews*, 93(2),  
565 785-800.
- 566 38. Pyörmilä, M., (1977). Parasitism in *Aglais urticae* (L.) (Lepidoptera, Nymphalidae). iV.  
567 pupal parasitoids. *Annales entomologici fennici*, 43, 21–27.
- 568 39. Rice, A. (2012). Spatial and temporal variability in host-parasitoid interactions of  
569 Lepidoptera feeding on stinging nettle (*Urtica dioica*). (PhD Thesis). University of  
570 Lancaster, Lancaster.
- 571 40. Settle, W. H., & Wilson, L. T. (1990). Invasion by the variegated leafhopper and biotic  
572 interactions: parasitism, competition, and apparent competition. *Ecology*, 71(4), 1461-  
573 1470.
- 574 41. Shaw, M. R. (2006). Habitat considerations for parasitic wasps. *Journal of Insect  
575 Conservation*, 10(2), 117-127.
- 576 42. Shaw, M. R., Stefanescu, C., & Van Nouhuys, S. (2009) Parasitoids of European  
577 Butterflies. In: *Ecology of Butterflies in Europe* (pp. 130-156). Cambridge University  
578 Press, Cambridge.
- 579 43. Sugiura, S. (2007). Structure of a herbivore-parasitoid community: Are parasitoids  
580 shared by different herbivore guilds? *Basic and Applied Ecology*, 8(6), 544-551.

- 581 44. Söderlind, C. (2009). *Parasitering på en expanderande art : har kartfjärilen undkommit*  
582 *sina naturliga fiender?*. SLU, Dept. of Ecology, Uppsala. Uppsala: SLU, Dept. of  
583 Ecology.
- 584 45. Thomas, M. B., & Blanford, S. (2003). Thermal biology in insect-parasite interactions.  
585 *Trends in Ecology & Evolution*, 18(7), 344–350. doi:10.1016/s0169-5347(03)00069-7.
- 586 46. Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. (2008) Global change  
587 and species interactions in terrestrial ecosystems. *Ecology letters*, 11(12), 1351-1363.
- 588 47. Tylianakis, J. M., & Morris, R. J. (2017). Ecological networks across environmental  
589 gradients. *Annual Review of Ecology, Evolution, and Systematics*, 48, 25-48.
- 590 48. Van Nouhuys, S., & Hanski, I. (2000). Apparent competition between parasitoids  
591 mediated by a shared hyperparasitoid. *Ecology Letters*, 3(2), pp.82-84.
- 592 49. Wagner, K. D., Krauss, J., & Steffan-Dewenter, I. (2011). Changes in the life history  
593 traits of the European Map butterfly, *Araschnia levana* (Lepidoptera: Nymphalidae)  
594 with increase in altitude. *European Journal of Entomology*, 108(3).
- 595 50. Wisz, M. S., Pottier, J., Kissling, W. D., Pellissier, L., Lenoir, J., Damgaard, C. F.,  
596 Dormann, C. F., Forchhammer, M. C., Grytnes, J.-A., Guisan, A., Heikkinen, R. K.,  
597 Høye, T. T., Kühn, I., Luoto, M., Maiorano, L., Nilsson, M.-C., Normand, S., Öckinger,  
598 E., Schmidt, N. M., Termansen, M., Timmermann, A., Wardle, D. A., Aastrup, P., &  
599 Svenning, J.-C. (2013). The role of biotic interactions in shaping distributions and  
600 realised assemblages of species: implications for species distribution modelling.  
601 *Biological reviews*, 88(1), 15-30.

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

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.

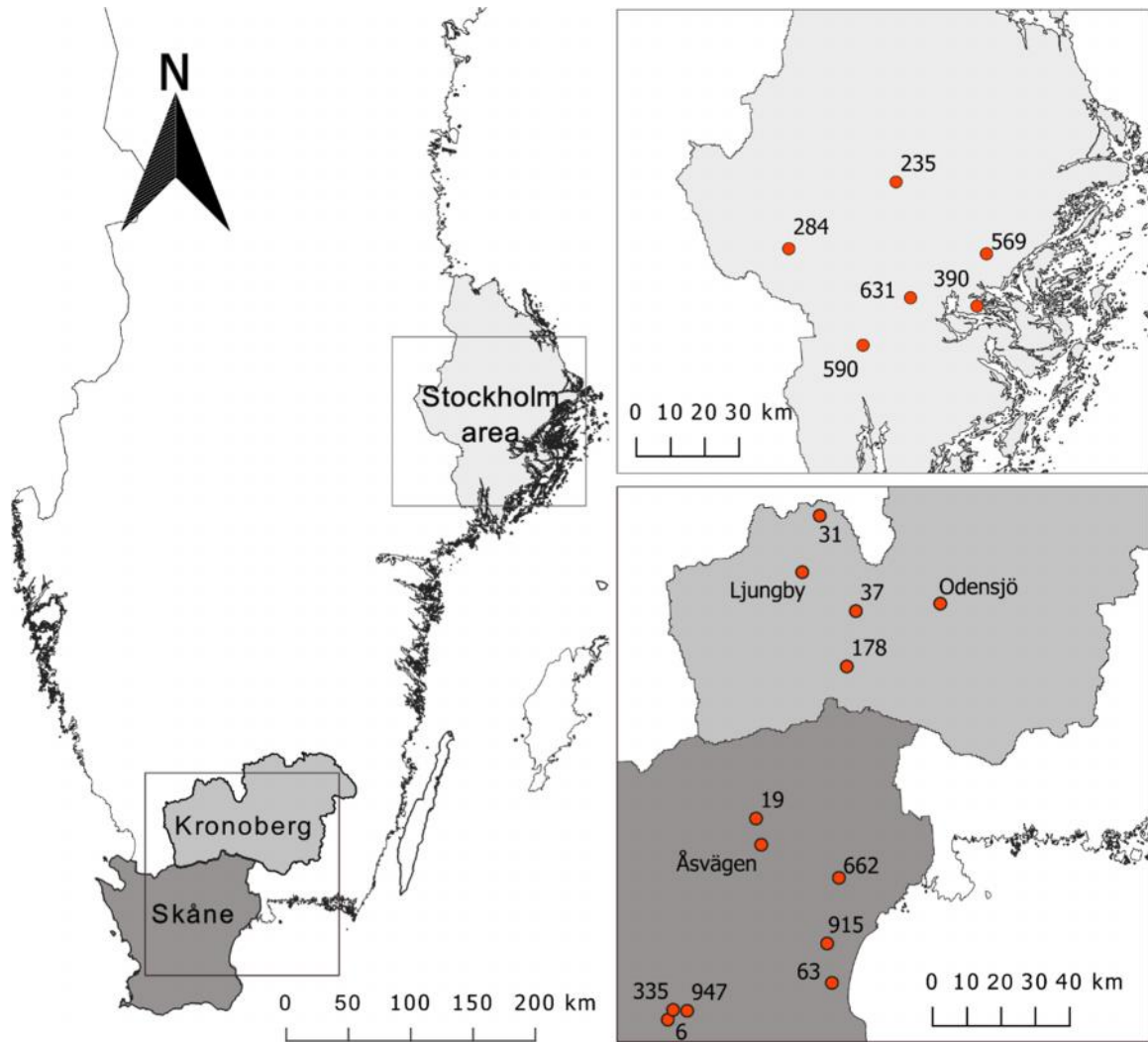
632 **Figure 4** Contrasting effects of community composition, taken as the presence/absence of the  
633 other species, including *A. levana*, on parasitism rate of (a) *A. urticae*, (b) *A. io*, and (c) *V.*  
634 *atalanta*. Estimation of marginal means of parasitism rates (%) are given at representative

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

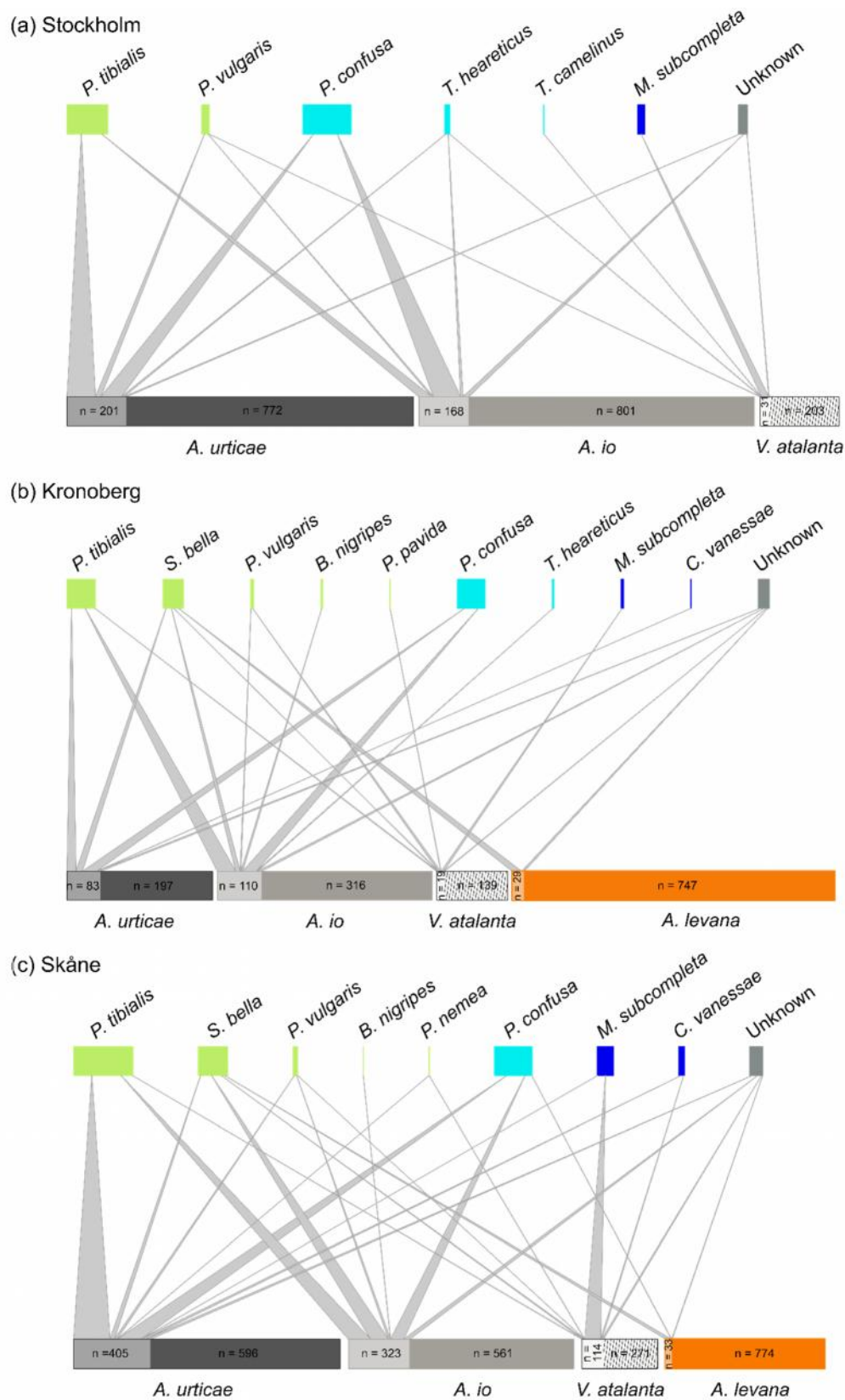


648

649

650

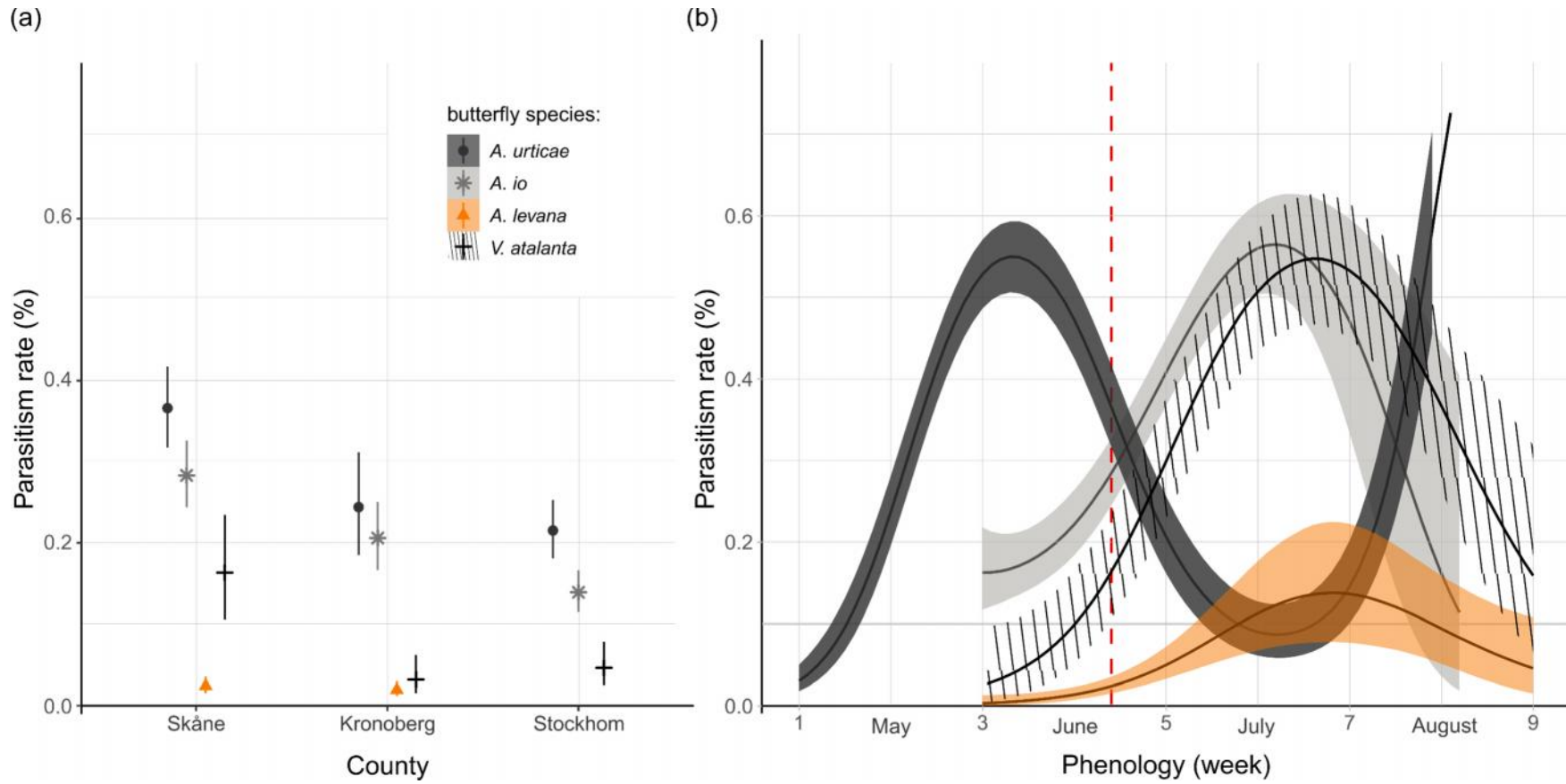
**Figure 2**



651



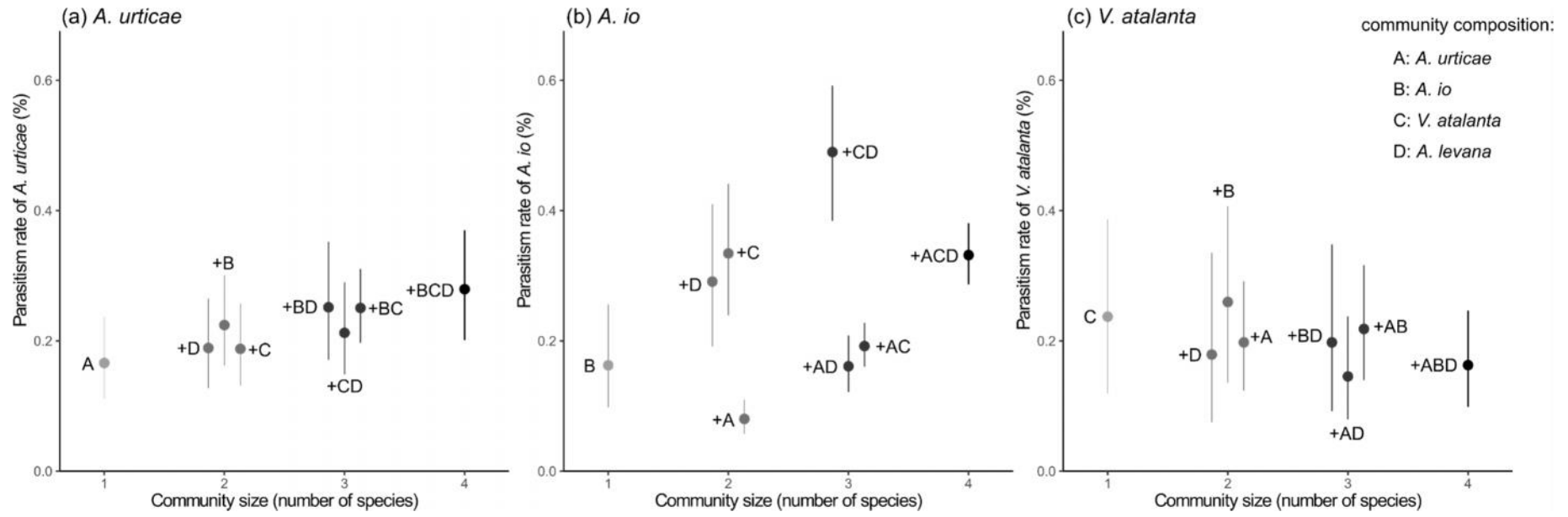
652 **Figure 3**



653

654

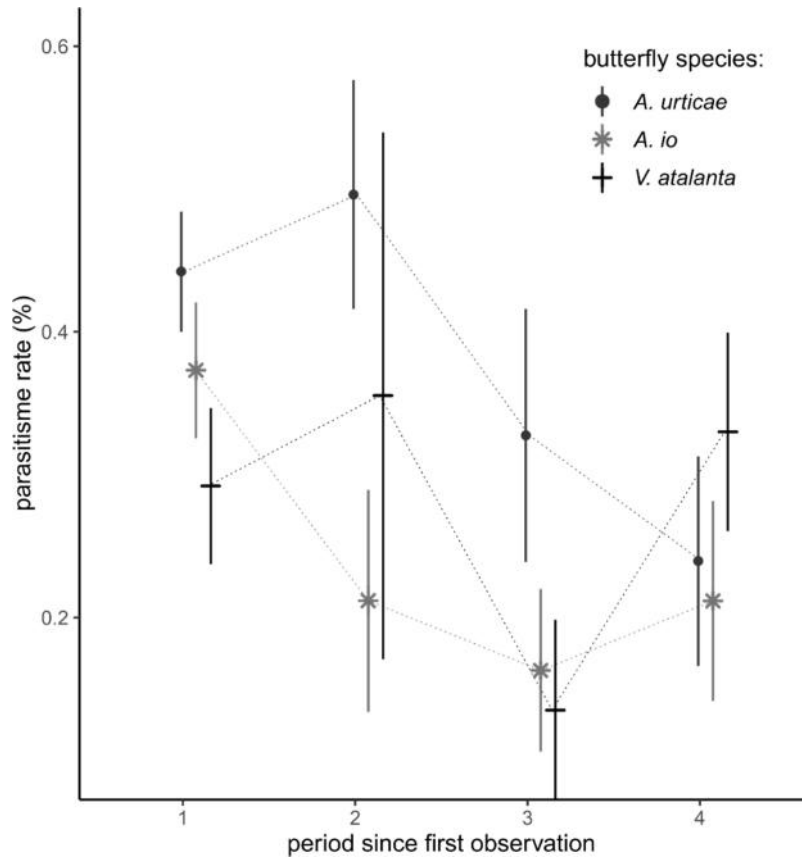
655 **Figure 4**



656

657

658 **Figure 5**



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](http://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 counties<sup>1</sup>. 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**

---

<sup>1</sup> 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*.**

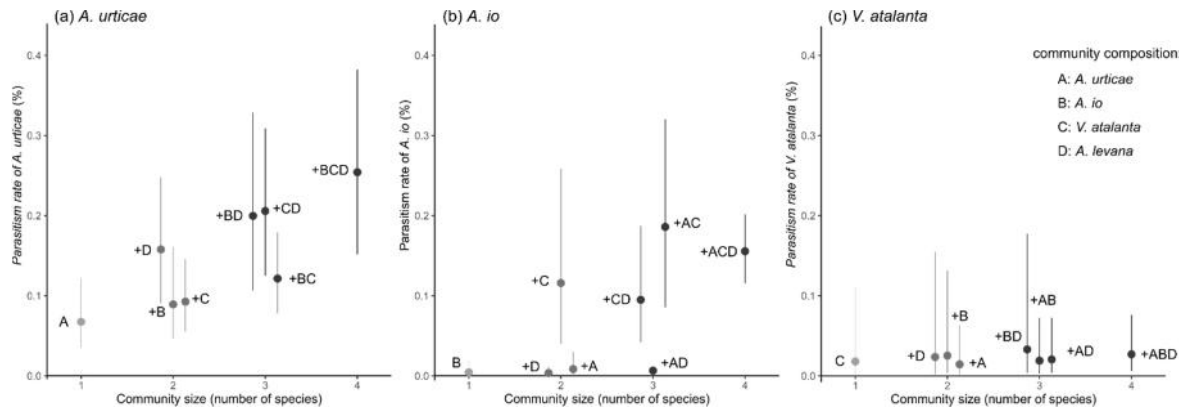
731

## 732 **References**

- 733 1. Herting, B., & Simmonds, F. J. (1976) A Catalogue of Parasites and Predators of  
734 Terrestrial Arthropods. Section A. Host or Prey/Enemy. Volume VII. Lepidoptera, Part  
735 2 (Macrolepidoptera). Royal Commonwealth Agriculture Bureaux, Farnham, 221 pp.
- 736 2. Bürkner, P.-C. (2017). brms: An R Package for Bayesian Multilevel Models Using  
737 Stan. *Journal of Statistical Software*, 80(1), 1-28. doi:10.18637/jss.v080.i01.
- 738 3. Bürkner, P.-C. (2018). Advanced Bayesian Multilevel Modeling with the R Package  
739 brms. *The R Journal*, 10(1), 395-411. doi:10.32614/RJ-2018-017.
- 740 4. Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M.,  
741 Brubaker, M., Guo, J., Li, P., & Riddell, A. (2017). Stan : A Probabilistic Programming  
742 Language. *Journal of Statistical Software*, 76.

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	<b>&lt;0.001</b>	-1.083	0.195	-5.56	0.14
Latitude	0.097	0.118	0.82	0.41	-0.196	0.087	-2.26	<b>0.024</b>	-0.790	0.177	-4.46	<b>&lt;0.001</b>
Period 2	-0.155	0.182	-0.85	0.40	-0.775	0.212	-3.66	<b>&lt;0.001</b>	-0.271	0.595	-0.45	0.65
Period 3	-0.73	0.335	-2.23	<b>0.03</b>	-0.462	0.253	-1.82	0.068	0.337	0.567	0.59	0.55
Period 4	-1.34	0.255	-5.28	<b>&lt;0.001</b>	-0.114	0.216	-0.53	0.60	0.610	0.281	2.17	<b>0.03</b>

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