

1 **Original Article**

2 **Title:** Species range expansion constrains the ecological niches of
3 resident butterflies.

4 **Running header:** Range expansion and changes in species interactions.

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21 **ABSTRACT**

22 **Aim** Changes in community composition resulting from environmental changes modify biotic
23 interactions and affect the distribution and density of local populations. Such changes are currently
24 occurring in nettle-feeding butterflies in Sweden where *Araschnia levana* has recently expanded
25 its range northward and is now likely to interact with the resident species (*Aglais urticae* and *Aglais*
26 *io*). Butterfly occurrence data collected over years and across regions enabled us to investigate
27 how a recent range expansion of *A. levana* may have affected the environmental niche of resident
28 species.

29 **Location** We focused on two regions of Sweden (Skåne and Norrström) where *A. levana* has and
30 has not established, and two time-periods (2001-2006, 2009-2012) during its establishment in
31 Skåne.

32 **Methods** We performed two distinct analyses in each region using the PCA-env and the framework
33 described in Broennimann *et al.* (2012). First, we described the main sources of variation in the
34 environment. Second, in each time-period and region, we characterized the realized niches of our
35 focal species across topographic and land use gradients. Third, we quantified overlaps and
36 differences in realized niches between and within species over time.

37 **Results** In Skåne, *A. levana* has stabilized its distribution over time while the distribution of the
38 native species has shifted. These shifts depicted a consistent pattern of avoiding overlap between
39 the native species and the environmental space occupied by *A. levana*, and it was stronger for *A.*
40 *urticae* than for *A. io*. In both regions, we also found evidence of niche partitioning between native
41 species.

42 **Main conclusions** Interspecific interactions are likely to affect local species distributions. It
43 appears that the ongoing establishment of *A. levana* has modified local biotic interactions, and
44 induced shifts in resident species' distributions. Among the mechanisms that can explain such
45 patterns of niche partitioning, parasitoid-driven apparent competition may play an important role
46 in this community.

47 **KEYWORDS** biotic interactions, citizen science, community composition, environmental niche
48 model, nettle-feeding butterflies, ordination technique, parasitoid-driven indirect competition,
49 realized niche.

50 **INTRODUCTION**

51 Changes in community composition resulting from environmental changes modify biotic
52 interactions that are likely to affect the distribution and the density of local populations. To better
53 predict the widely recorded species' geographical and environmental shifts (Parmesan, 2006) it is
54 crucial to first define and understand species' environmental niches and how they are shaped by
55 local biotic interactions (Davis *et al.*, 1998; Tylianakis *et al.*, 2008; Gilman *et al.*, 2010).
56 Investigations of species co-occurrence across the landscape can provide useful insights for better
57 understanding the effects of species interactions on their distributions, and how community
58 composition is maintained or changed locally in a context of global change.

59 Northern regions offer a highly suitable model system to investigate how changes in species
60 interactions can induce shifts in realized niches. At high latitudes, the impacts of climate change
61 are most pronounced (IPCC, 2014), making it more likely to detect a signature of species'

62 responses to recent warming. Moreover, as species' northern ranges vary greatly and their
63 poleward shifts are not synchronized (Pöyry *et al.*, 2009), changes in community composition are
64 expected to alter interspecific interactions (González-Megías *et al.*, 2008; Devictor *et al.*, 2012)
65 and potentially lead to new interactions.

66 A good way to examine niche shifts and niche partitioning is to measure and test the overlap and
67 the difference in the environmental space occupied (i.e. realized niche) over time and across
68 species (Warren *et al.*, 2008; Broennimann *et al.*, 2012). Recent developments in statistical
69 methods and computational techniques have enabled better estimations of species-environment
70 relationships and thereby contributed to identify the processes and factors shaping species' realized
71 niches. In particular, Environmental Niche Models (ENMs) have been used to model and predict
72 species distributions according to changes in climatic and environmental variables, considered to
73 be the main drivers of species distribution at large and small spatial-scales (Berry *et al.*, 2002;
74 Thuiller *et al.*, 2005). However, ENMs that are based on the relationship between species
75 distribution and abiotic factors have often shown some discrepancy between the potential and the
76 realized niches. This strongly suggests that other processes such as biotic interactions have
77 substantial effect on species distribution and should be accounted for (Leathwick, 1998; Pellissier
78 *et al.*, 2012; Tingley *et al.*, 2014). Better consideration of biotic interactions in distribution models
79 assessing geographic ranges has greatly refined our predictions at both small and large scales
80 (Heikkinen *et al.*, 2007; Araújo & Luoto, 2007). Yet, even though ENMs and ordination techniques
81 have been successfully used to further our understanding of the role of biotic interactions by
82 comparing the realized niches of species (Schweiger *et al.*, 2012; Mason *et al.*, 2014), they have
83 rarely been used to understand how changes in local biotic interactions may induce shifts in species

84 realized niches (Wiszn *et al.*, 2013). Furthermore, the reliability and accuracy of statistical models
85 in predicting the importance of biotic interactions are often limited by the availability of extensive
86 occurrence data, which are also often biased towards particular groups of species.

87 In the last decades, the amount of data collected, organized, and made available through public
88 databases has increased substantially. The use of such databases comes nonetheless with important
89 challenges as they cumulate data collected with no standardized sampling design and by observers
90 with different levels of expertise. Therefore, data contained in such databases have the drawback
91 of being prone to show biases in the region and habitat covered, lacking independence between
92 replicates, and having no explicit measures of sampling effort. However, considering the rapid
93 expansion of programs collating data through volunteer contribution of citizen observers, the real
94 potential of these large datasets is growing and many of them remain largely unexploited. This has
95 led to increased efforts being made to develop robust approaches to estimate and compare the
96 realized niche from occurrence and spatial environmental data, independently of the spatial
97 resolution and sampling biases that are often inherent to species occurrence data. In this context,
98 Broennimann *et al.* (2012) developed and tested an analysis framework to quantify niche overlap
99 and test for niche equivalency and similarity (*cf.* Warren *et al.*, 2008), using Principal Component
100 Analysis to define the environmental space (PCA-env). In contrast to ENM methods, the PCA-env
101 has been shown to be more reliable for defining the environmental space when tested on both
102 simulated and real case data (Broennimann *et al.*, 2012).

103 Here, we investigate the realized niche of three nettle-feeding butterflies (*Aglaia urticae*, *Aglaia*
104 *io*, and *Araschnia levana*) and examine how they vary in space and time as an illustration of the
105 potential role of interspecific interactions in shaping species distributions in the context of ongoing

106 climate change. We use occurrence data available through the internet reporting system
107 Artportalen (www.artportalen.se), a public database of species records based on citizens'
108 contribution in Sweden, to explore niche partitioning of nettle-feeding butterflies at the local scale.
109 In Sweden, *A. urticae* and *A. io* are common native species, easy to identify, and well represented
110 in the database with a large number of records available across the country (over 15 000 records
111 per species for the period 2001-2012). On the other hand, *A. levana*, for which the first anecdotal
112 observation reported in Sweden is from 1982 (Eliasson *et al.*, 2005), is known to be expanding its
113 range northward and is now well established in the southern part of Sweden (Betzholtz *et al.*,
114 2013). All three species are specialists with larvae feeding on stinging nettle, *Urtica dioica*, and
115 showing overlapping phenology (see Fig. S1 in Appendix S1 in Supporting Information). While
116 no obvious direct competition has been documented, the three species are known to share common
117 parasitoids (Hinz & Horstmann, 2007; Shaw *et al.*, 2009), which increase the potential for apparent
118 competition among the species (van Veen *et al.*, 2006; Tylianakis, 2009).

119 Hence, the ongoing establishment of *A. levana* in southern Sweden makes this system a unique
120 opportunity to investigate the impact of such change on the distribution of native butterfly species
121 over a relatively short time period. If interspecific interactions are important determinants of
122 spatial distribution across the landscape, their signature should be detectable in the occupancy
123 pattern of the available environmental space. To model the realized niches of three sympatric
124 species and quantify the degree of niche overlap between them, we used the PCA-env method
125 applied within Broennimann's analysis framework (Broennimann *et al.*, 2012). We gathered high-
126 resolution data on land use and topography, and an index of nitrogen and phosphorus flows in the
127 soil, which reflects agricultural practices. We perform these analyses over two time-periods during

128 the establishment of *A. levana* and two geographically distinct regions (where *A. levana* has and
129 has not yet established), with the aim of assessing the potential effect of the establishment of *A.*
130 *levana* in the southern part of the country during the second period, while controlling for climatic
131 variability over time.

132 Specifically, as a recent colonizer of Sweden, *A. levana* is still in its initial phase of establishment
133 and, therefore, its distribution is expected to not be at equilibrium. Moreover, if changes in local
134 biotic interactions are important in this community, we expect the establishment of *A. levana* to
135 affect the distribution of the native species. We put forward three alternative mechanisms that, in
136 our study system, may explain the observed changes in distribution and density of the local
137 populations. We also discuss the opportunities and limitations of using occurrence records from
138 citizen-science databases and the reliability of the interpretation of the output results from the
139 method used.

140 **MATERIALS AND METHODS**

141 We studied the environmental space occupied by *A. urticae*, *A. io*, and *A. levana* in two regions,
142 corresponding to the county of Skåne in Southern Sweden and the Norrström drainage basin in
143 Central Sweden (including four counties: Södermanland, Stockholm, Uppsala, Västmanland, Fig.
144 1a), and two time-periods (first period 2001-2006 and second period 2009-2012). The regions are
145 separated by approximately 400 kilometers in a straight line. By aggregating the records over
146 specific time-periods, we aimed to have better estimates of species distributions, assuming these
147 patterns to remain relatively stable over short time-periods (i.e. to avoid yearly variation). Data
148 extraction was based on a regular grid covering both regions with a resolution of 1 km.

149 Species distribution is determined by the interplay of multiple variables operating at different
150 spatial scales (Pearson & Dawson, 2003). While at large scales, species distribution is limited by
151 physiological constraints mainly determined by climatic conditions, at small scales we expect their
152 distribution to be shaped by local variables such as land use and topography (Pearson & Dawson,
153 2003), as well as by direct and indirect biotic interactions (e.g. predation, competition, resources).
154 Considering the extent of our study areas, i.e. two regions of Sweden, we expected local-scale
155 variables, namely topography and land use, to be the most relevant factors for investigating niche
156 differences between species and potential niche shifts.

157 **Occurrence Data**

158 We extracted occurrence data for *A. urticae*, *A. io* and *A. levana* from the Swedish Species
159 Information Centre at SLU (www.artportalen.se, accessed on the 18/09/2015, average precision
160 reported for the data \pm se of 168m \pm 2m), a public database of species records in Sweden. The
161 Artportalen database gathers opportunistic occurrence data (presence only) collected at 90% by
162 amateurs with no specific required training in species identification (Gärdenfors *et al.*, 2014) and
163 who do not follow any specific protocol. For each species, we identify all grid cells for which the
164 species was recorded in each of the two time-periods and the two study regions.

165 For each period, we only considered species' presence across the selected grid cells, without
166 accounting for variation in the number of observations per cell as our main interest was to
167 determine species' occurrence patterns across the total available environment. In this way, we
168 reduced the potential bias associated with uneven sampling effort across sites (i.e. over-sampling
169 of more frequently visited sites). As a result of an overall growing interest for citizen science, both
170 the number of observations and the corresponding number of grid cells visited increased between

171 the first and the second period (Table S1 in Appendix S1). While the number of records is likely
172 to affect the extent of the environmental space sampled (surveyed), we are confident that the
173 sampling (reporting) effort for our study species was sufficiently high to limit this potential bias.
174 For the period 2009-2012, *A. urticae* and *A. io* are the first and fourth most reported butterfly
175 species in Artportalen, respectively, and they were in the top fifteen most reported species
176 according to the Swedish Butterfly Monitoring Scheme (records along transects, Petterson *et al.*,
177 2013). As a recently established species in Sweden, *A. levana* may still be in its initial phase of
178 establishment. Hence, its current distribution might not be at equilibrium yet or only reflect a
179 subset of its potential environmental niche. In our final dataset, occurrence of *A. urticae* was
180 recorded in 2935 grid cells, *A. io* in 2457, and *A. levana* in 599. Note that *A. levana* was only
181 recorded in Skåne.

182 **Topographic Data**

183 Aspect and slope were calculated based on a digital elevation map at an original 50m resolution
184 obtained from the Swedish University of Agricultural Science (<https://maps.slu.se/get/>). From the
185 original elevation map, we extracted the mean aspect and mean slope with the `r.slope.aspect`
186 function available in the GRASS GIS plugin for Quantum GIS 1.8 software (2012) and
187 recalculated both metrics for the 1km resolution grid, using PostgreSQL 9.4 and its spatial
188 extension PostGIS 2.1 (2014).

189 **Land use Data**

190 Land use data were collected from Naturvårdsverket at an original 25m resolution
191 (<https://www.naturvardsverket.se/>). The land use classification followed the Corine Land Cover.

192 We extracted the percentage of the different types of land use (forest, open land, arable land, non-
193 intensive agriculture, water body, and urban land) at 1km resolution grid cells. We also used
194 estimates of soil nutrient flow (in nitrogen and phosphorus) – which we used as a proxy for the
195 amount of nutrients available for plant root absorption – accessible from the SMED (Svenska Miljö
196 Emission Data, <http://www.smed.se/>) at an original resolution of the sub-catchment (municipality).
197 These estimates were modeled by means of simulation tools as well as measured data and
198 correspond to nitrogen and phosphorus loads to the water from diffuse sources across the whole
199 sub-catchment (Brandt *et al.*, 2009). Nutrient loads to the water from the sub-catchment result
200 from a combination of the run-off and leaching on the basis of assumptions on type-specific
201 concentrations for each type of land use. From these estimates, we calculated nutrient flow through
202 the 1km grid cells.

203 **Realized Niche Shifts and Overlaps**

204 We first extracted two axes that captured the maximum variation in land use and topography
205 available to the species, using the PCA-env ordination method described in Broennimann *et al.*
206 (2012). Second, we characterized, for each time-period and region, the realized niches of our study
207 species in the environmental space defined by the topographic and land use gradients extracted
208 above. Third, we quantified overlaps and differences for each species over time and between
209 species in each period in how they distributed themselves in this environment, using 100% of the
210 environmental space. All analyses were computed with the ecospat package (Broennimann *et al.*,
211 2015) in R 3.1.3 (R Core Team, 2015). To reduce the risk of generating false absences in un-
212 sampled areas due to the non-systematic sampling process that characterized our dataset, we

213 excluded from our analyses all grid cells where none of the focal species has been recorded, for
214 each time-period.

215 Following the framework proposed by Broennimann *et al.* (2012), we computed a weighted
216 Principal Components Analysis (PCA) on the environmental variables, after applying a kernel
217 density function to the number of sites of each specific environmental condition. The Gaussian
218 kernel density function is used to create a probability density function of each of the environmental
219 conditions available and of the occurrence of each species for each cell of the environmental space
220 (Broennimann *et al.*, 2012). We performed two distinct analyses in each region to prevent
221 environmental differences inherent to these regions (mostly in agricultural activity) to mask the
222 components of most interest for detecting niche partitioning occurring within region. A kernel
223 density function was also fitted on species occurrence records prior to projecting species
224 occupancy in the environmental space. Thereby, each cell of the environmental space is weighted
225 according to the availability of this specific environmental condition and species occurrence
226 records are weighed in a way that all species involved in the comparison are given similar total
227 weights.

228 We further tested for niche equivalency and niche similarity (*cf.* Warren *et al.*, 2008). For that, we
229 performed paired comparisons of the realized niches of each species over time and between species
230 within each period. The first test evaluates if the environmental conditions that define the niches
231 of two entities are identical. Specifically, niche equivalency is tested by comparing the overlap
232 between the two realized niches with the expected distribution of overlap obtained by randomly
233 reallocating the grid cells occupied by the two entities. The second test assesses the similarity in
234 the relative distribution over the environmental conditions defining the niches of two entities.

235 Niche similarity is tested by comparing the overlap between the two realized niches to the expected
236 distribution of overlap obtained by reallocating the density of occurrence of one entity across its
237 range of occupancy, while the occurrence of the other remains constant. In other words, this test
238 estimates the likelihood that niche centroids are significantly different from each other. For both
239 tests, expected distributions were based on 500 iterations of the randomization procedure.

240 **RESULTS**

241 **Description of the available environment and realized niches**

242 The environmental space sampled in each region was described by the first two axes of the
243 principal component analyses, capturing 43.0% and 41.6% of the environmental variation in
244 Norrström and Skåne respectively (Fig 1b & c, and Appendix S2). In both regions, the first PCA-
245 axis was strongly associated to a gradient defined by grid cells having a higher amount of arable
246 land at one end and more forest at the other. Note that in both cases the estimates of soil nitrogen
247 and phosphorus flow explained a large part of the variance captured by the first PCA-axis and were
248 associated with higher amount of arable land. In both regions, the variance along the second axis
249 reflected change in the mean aspect (varying from 0 degree North to 301 degrees at maximum).

250 Overall, the ecological niches occupied by *A. io* and *A. urticae* in each region between time-periods
251 were highly comparable (Figs 2 & 3).

252 Interspecific interactions

253 In spite of the overall similarities, we detected in each region and time-period significant
254 differences among the species' realized niches. In most cases, the null hypothesis of niche
255 equivalency and similarity was rejected (species interactions, $p < 0.05$, Table 1), even though the
256 three species displayed important overlap in their environmental space (Table 1, Figs 4).

257 In the two-dimensional environmental space in Skåne, *A. levana* overlapped with the two native
258 species in both time-periods but the species' realized niches were neither equivalent nor similar
259 ($p < 0.05$, Table 1). Moreover, we observed a large decrease in the overlap of *A. levana* with the
260 native species over time. In the first period it was 0.80 with *A. urticae* and *A. io*, while in the second
261 period it was 0.68 with both native species. In the first period we did not observe a clear
262 differentiation between *A. levana* and the resident species' niches (Fig. 4c & d top), but in the
263 second period this partitioning appears clearly (Fig. 4c & d bottom). In the second period, *A. levana*
264 preferentially occupied habitats with larger amount of forest per 1 km grid cell and the two native
265 species were in comparison more present in mixed and agricultural habitats (Fig. 4c & d bottom).

266 The two native species (*A. urticae* and *A. io*) strongly overlapped in both periods and regions
267 (overlap between 0.89 and 0.91, Table 1). This is not surprising considering that *A. io* and *A. urticae*
268 are often observed in sympatry with ecological niches that are known to be difficult to differentiate.
269 While in the first period, *A. urticae* and *A. io* displayed equivalent niches in Skåne (paired-species
270 comparisons of niche equivalency, $p = 0.327$, Table 1), the null hypothesis of niche equivalency was
271 rejected in the first period in Norrström and in both regions in the second period ($p < 0.05$, Table
272 1). Thus, although the realized niches of *A. urticae* and *A. io* significantly overlapped, they
273 displayed non-random differences in their distributions. For all the paired-species comparisons

274 between *A. urticae* and *A. io*, we rejected the null hypothesis of niche similarity (tests of niche
275 similarity, $p < 0.05$, Table 1); which suggests that these species occupied the available environment
276 differently in both time-periods and regions (shifts in their centroid). In Skåne in the first period,
277 *A. urticae* occupied proportionally more areas with larger amount of forest per 1 km grid cells than
278 *A. io*, whereas *A. io* was more abundant in mixed habitats (Fig. 4b top). In the second period, the
279 prevalence of *A. urticae* slightly shifted in comparison to *A. io* from forested areas toward habitats
280 with increasing amount of agricultural and urban lands (Fig. 4b bottom). In Norrström and for both
281 periods, *A. urticae* and *A. io* prevailed in environments with higher amount of forest (Fig. 2).

282 **Niche shifts over time**

283 The distribution of the three species shifted significantly over time in both regions, their
284 distribution in the environmental space being neither equivalent nor similar between the two time-
285 periods (tests, $p < 0.05$, Table 1). The largest shift was observed for *A. levana* in Skåne, for which
286 the overlap in the realized niche between periods was of 0.75. For the two native species these
287 shifts were comparatively smaller, the overlap in the realized niche of each species between periods
288 varied between 0.82 and 0.87 (Fig. 5), but noticeable considering the short time scale of the study.
289 All shifts detected in the environmental space also corresponded to geographical shifts, as only
290 one layer of land use was available to cover both time-periods. For the recently established *A.*
291 *levana*, the observed shift in realized niche corresponded to a niche contraction as *A. levana* in the
292 first period seemed to have already colonized most of the available environmental conditions in
293 which the species occurred in the second period (Fig. 3c). In the second period, *A. levana*
294 preferentially occupied areas with larger amount of forest (Fig. 5c bottom). For the two native

295 species, the largest changes between the two periods were observed in Skåne (Fig. 5a & b).
296 Moreover, the extent of the environmental shift observed in Skåne was species-specific, being
297 larger for *A. urticae* (niche overlap=0.82, sd=0.052; Fig. 5a bottom) than for *A. io* (niche
298 overlap=0.83, sd=0.041; Fig. 5b bottom). The shift was also more clearly directed for *A. urticae*
299 than for *A. io* (Fig. 5a & b bottom). By shifting its distribution away from areas with larger amount
300 of forest, *A. urticae* reduced its overlap with *A. levana*, which over time has densified its
301 distribution in these environments across Skåne (niche overlap=0.68, sd=0.121; Fig. 4c bottom).
302 We observed the same pattern between *A. io* and *A. levana*, but to a lower extent (niche
303 overlap=0.68, sd=0.111; Fig. 4c bottom).

304 **DISCUSSION**

305 The distributions of our focal species were described and compared along the two first axes of the
306 environmental PCA. In both regions, the first axis was shaped along a gradient from arable land
307 to more forested land and the second axis correlated with topographic parameters (Fig. 1a & b).
308 Based on our knowledge of the ecological niche of our focal species, we are confident in the
309 description of the species' environmental niche revealed by our models. The method developed by
310 Broennimann *et al.* (2012) gave results consistent with the overall characteristics of the realized
311 niches of the three butterfly species, which are known to occupy open habitats and woodlands,
312 wood hedges, and hedgerows (Asher *et al.*, 2001; Haahtela *et al.*, 2011).
313 Yet, the method also identified differences in realized niches among species in each region and
314 within species over time. We used the measure of overlap and the results from the niche

315 equivalency and similarity tests between realized niches to infer the role of interspecific
316 interactions in shaping species distributions. The large overlap in the realized niches of the two
317 native species in both regions and time periods suggests that no clear negative interaction is
318 involved in the partitioning of the niche between *A. urticae* and *A.io*. Nevertheless, the fact that
319 the realized niches of species were neither equivalent, nor similar, suggests some level of non-
320 random niche partitioning in the environmental space. Thus, while our results emphasized that the
321 two native species occupy the available environment differently, we could not identify a specific
322 environmental factor of niche differentiation. For example, we have observed in the field that *A.*
323 *urticae* tends to occupy more sun-facing slopes than *A. io*, but although we detected some effect
324 of aspect on species' distribution, the relatively coarse resolution of our data (1km grid cell)
325 prevents us to firmly support our field observations. Moreover, apart from the spatial component,
326 niche partitioning can also arise from, and in combination with, resource and/or temporal
327 partitioning (MacArthur & Levins, 1967). Regarding resource partitioning, both *A. urticae* and *A.*
328 *io* larvae feed on the leaves of stinging nettles, whose availability is not limited over the season.
329 Stinging nettle has even been shown to expand due to human land use and nitrogen pollution
330 (Taylor, 2009). Together with the lack of strong competition over resources, potential asynchrony
331 (temporal partitioning) in species phenology could also reduce the strength of a spatial signal in
332 the differentiation in species' realized niches.

333 The recently established *A. levana* overlaps with the realized niches of the native species and the
334 overlap decreased over time. In part, this decrease is likely a consequence of the described shifts
335 in realized niche of the three species over time. The largest shift was found for *A. levana* (in Skåne).
336 From the environmental conditions colonized by *A. levana* in the first period, we observed a

337 significant contraction in its realized niche in the second period toward habitats with a higher
338 amount of forest. This pattern suggests that the distribution of *A. levana* was not at equilibrium in
339 the first period and that it has progressively stabilized within habitats with a positive population
340 dynamic. We also found significant shifts in realized niches of the two native species over time, in
341 both regions. However, these shifts were most pronounced in Skåne where *A. urticae*, and to a
342 lower extent *A. io*, shifted their distributions away from forested areas towards habitats with higher
343 amount of agricultural and urban lands.

344 There are several processes that could explain these changes over time. The more pronounced shift
345 in the distribution of the native species in Skåne than in Norrström could partly reflect higher
346 regional climatic fluctuations over time. However, as the amplitudes of climatic variations over
347 time were comparable across the regions (Appendix S3), this factor does not appear to be a major
348 driver in our study system. The observed shifts in niche centroid over time could also be related to
349 the increase in the number of reported observations through time. Yet, this explanation also appears
350 rather unlikely, as the increases in the number of observation records were consistent across species
351 and regions, while all species did not show a consistent shift in their centroids. Thus, even if such
352 shifts may have been strengthened by the higher number of observation records over time, they
353 most likely represent genuine responses to other driving forces affecting the ecological niche of
354 native species.

355 Hence, in this community, changes in interspecific interactions appear to be a sensible explanation
356 for the described changes over time in species occupancy of the environmental space. One
357 contributing factor is probably the stabilization of the distribution of *A. levana*, as this resulted in
358 decreased overlap with the native species (Fig. 4c & d). This response may have been mediated

359 through the action of parasitoids (Dunn *et al.*, 2012). Indeed, studies have shown that the
360 community composition in herbivorous insects can largely be shaped by parasites (van Veen *et*
361 *al.*, 2006; Tylianakis, 2009). All three species are heavily parasitized (personal observation) and
362 share many parasitoids (Hinz & Horstmann, 2007; Shaw *et al.*, 2009). Hence, the population
363 dynamics of these parasitoids might have been positively affected by the increase in potential hosts
364 (*A. levana*) between the two time-periods, as observed in tropical forest communities by Morris *et*
365 *al.* (2004). Moreover, the differences in phenology between *A. urticae*, *A. io*, and *A. levana* (Fig.
366 S1 in Appendix S1) may form a continuous breeding ground to stimulate parasitoid population
367 dynamics, and they may result in a prolonged temporal niche for parasitoids (Blitzer & Welter,
368 2011). In a scenario of parasitoid-driven apparent competition, the phenologically late species is
369 expected to be the more vulnerable as its life cycle will coincide with an increase in parasitoid
370 population size (Blitzer & Welter, 2011). In this study, the native species showed differences in
371 the magnitude of their shifts. The shift in the realized niche of *A. urticae* between periods was
372 stronger than for *A. io*, in terms of niche overlap. Niche partitioning was also stronger between *A.*
373 *levana* and *A. urticae* than with *A. io*. In the context of parasitoid buildup, this may seem
374 counterintuitive, as *A. urticae* is the earliest of the two native species. But because *A. urticae* is
375 bivoltine in Skåne, and produces a second brood later in the season (Fig. S1 in Appendix S1),
376 parasitoid populations may continue to build up over the season and result in the highest parasitoid
377 load for the second brood of *A. urticae*. Although we have no direct data to support the hypothesis
378 of parasitoid-driven niche differentiation, the circumstantial evidence is suggestive, and is further
379 reinforced by the observation that *A. levana* appears to share more parasitoids with *A. urticae* than
380 with *A. io*, based on the limited information available (Shaw *et al.*, 2009).

381 Differences in life history might be another possible explanation for the different shifts in
382 distribution among the three species. Based on experimental studies, Merckx *et al.* (2015)
383 suggested that because of its bivoltine life cycle, the plastic response of *A. urticae* to anthropogenic
384 environmental changes might be faster in comparison to the univoltine *A. io*. If this is true, *A.*
385 *urticae* would be expected to respond faster to the arrival of *A. levana* than *A. io*. This is consistent
386 with the described larger shift in distribution of *A. urticae* than *A. io* over time in Skåne. Likewise,
387 the bivoltine life cycle of *A. levana* may also participate to explain the large shift described in its
388 distribution over time.

389 It is also possible that differences in the way these species are able to adjust to the quality of their
390 host plants and the microclimate they offer may cause individuals of each species to choose
391 different nettle patches when coexisting in a region. The shift in niche centroid of *A. urticae*
392 reported here (toward agricultural land) is consistent with other studies conducted on *A. urticae*
393 and *A. io*, showing that *A. urticae* can to a larger extent be favored by the higher nutrient quality
394 of plants growing in agricultural land than *A. io* (Serruys & Van Dyck, 2014; Audusseau *et al.*,
395 2015; Merckx *et al.*, 2015). Changes in microclimate have been shown to differentially affect the
396 decline of butterfly species' following climate change (Wallisdevries & van Swaay, 2006) and to
397 modify butterflies' habitat associations (Davies *et al.*, 2006). We call for field experiments to
398 understand, at a finer spatial-scale, the differences among species in their optimal microclimatic
399 niche.

400 The method used was successful in handling the potential bias related to the non-standardized
401 sampling design associated to occurrence data extracted from the public database. Indeed, while
402 most observations were recorded in urban areas, the highest densities of occurrence of the two

403 native species based on the grid cell analysis were found in forest habitats (Figs 2 & 3). In addition,
404 the lower number of species records in the first period did not seem to have affected our capacity
405 to extract the main components of the realized niches as their shapes and centroids were consistent
406 through time. Hence, we consider that using occurrence records from citizen-science databases
407 offer great opportunities for investigating the realized niches of species and differences between
408 them, as long as the biological relevance of the modelling results is carefully considered. The
409 results of the method we used to characterize the realized niches of the focal butterfly species was
410 consistent with our knowledge of the species, and we recommend using occurrence data associated
411 with species and regions of high sampling effort in order to get more robust predictions. Such
412 regions often correspond to more densely populated areas as the reporting effort in citizen-based
413 monitoring programs is strongly related to the number of participants.

414 In conclusion, we found indications of niche partitioning among the three species and consider
415 that the observed shifts in species environmental niche were partly driven by the recent changes in
416 interspecific interactions. The establishment during range expansion of *A. levana* may have
417 modified biotic interactions, resulting in associated shifts in species distributions. Based on our
418 knowledge of the system, we suspect that the observed niche differentiation might be partly driven
419 by apparent competition mediated by shared parasitoids. Other factors such as interspecific
420 differences in life history could also have contributed to the observed pattern and lead to species-
421 specific change in habitat preference. The difference in the extent of the shift observed between *A.*
422 *urticae* and *A. io* during the establishment of *A. levana* can be related to their differences in
423 phenology, voltinism, and the higher number of shared parasitoids between *A. urticae* and *A.*
424 *levana*. Further investigations of the niche partitioning of these three nettle-feeding butterflies

425 where they all are native species would allow us to make predictions about the equilibrium this
426 community may reach. More importantly, this framework is a promising tool for investigating the
427 potential role of biotic interactions on species distributions, and for better predicting the outcome
428 of their modifications on community composition and species-environment relationships.

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553 distributions and realised assemblages of species: implications for species distribution

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555 **SUPPORTING INFORMATION**

556 **Appendix S1** Data description, phenology of the study species and consideration of biases.

557 **Appendix S2** Table showing scores for each variable on the first three axes of the PCA-env and
558 the contribution of each axis expressed in percentage of the total variance (inertia).

559 **Appendix S3** Average mean monthly temperature (Jan: 1, Feb: 2, etc.) in Skåne in comparison to
560 Norrström and in the first and second periods (mean±se).

561 **BIOSKETCH** H el ene Audusseau has been granted her PhD at Stockholm University. Her research
562 is concerned by the ecological and evolutionary responses of nettle-feeding butterflies to changes
563 in climate and land use.

564 **Editor:** Daniel Chapman.

565 **AUTHORS' CONTRIBUTIONS**

566 AH, ML, RS, NJ, SN participated in the design of the study. AH, ML, RS performed the analyses.

567 AH, ML, BK collected the data. AH wrote the first draft of the manuscript, which was substantially
568 improved through the contribution of RS, ML, NJ. All authors contributed to the final version of
569 the manuscript.

570 **TABLE**

571 **Table 1** Table showing niche overlap (D) within species over time (time shift) and between species in each period (species interactions)
 572 in Skåne and Norrström, respectively, with the associated *P*-values obtained from the tests of niche equivalency and similarity (no.
 573 iterations=500).

Region	Period	Species	Test of niche equivalency		Test of niche similarity		
			Overlap D	<i>p</i>	Sp 1 -> Sp 2	Sp 2 -> Sp 1	
		Sp 1 - Sp 2			<i>p</i>	<i>p</i>	
Skåne	Time shift	P1 - P2	<i>A. urticae</i>	0.82	0.004	0.002	0.002
		P1 - P2	<i>A. io</i>	0.83	0.004	0.002	0.002
		P1 - P2	<i>A. levana</i>	0.75	0.004	0.002	0.002
	Species interactions	P1 - P1	<i>A. urticae</i> - <i>A. io</i>	0.89	0.327	0.002	0.002
		P1 - P1	<i>A. urticae</i> - <i>A. levana</i>	0.80	0.004	0.002	0.002
		P1 - P1	<i>A. io</i> - <i>A. levana</i>	0.80	0.004	0.002	0.002
		P2 - P2	<i>A. urticae</i> - <i>A. io</i>	0.89	0.032	0.002	0.002
		P2 - P2	<i>A. urticae</i> - <i>A. levana</i>	0.68	0.004	0.002	0.016
		P2 - P2	<i>A. io</i> - <i>A. levana</i>	0.68	0.004	0.002	0.004
Norrström	Time shift	P1 - P2	<i>A. urticae</i>	0.87	0.004	0.002	0.002
		P1 - P2	<i>A. io</i>	0.85	0.004	0.002	0.002
	Species interactions	P1 - P1	<i>A. urticae</i> - <i>A. io</i>	0.91	0.032	0.002	0.002
		P2 - P2	<i>A. urticae</i> - <i>A. io</i>	0.89	0.004	0.002	0.002

575 **FIGURE LEGENDS**

576 Figure 1 (a) Map of the two study-regions (in grey), corresponding to the county of Skåne in
577 Southern Sweden and the Norrström drainage basin in Central Sweden. (b), (c) Correlation circles
578 showing the contribution of the different variables to the two main axes of the PCA, which describe
579 the environmental space in Norrström and Skåne, respectively. S: Sweden, N: Norway, DK:
580 Denmark.

581 **Figure 2** Density of species occurrence across the two-dimensional environmental space
582 describing the Norrström region. In columns are the densities of occurrence of (a) *Aglais urticae*
583 and (b) *Aglais io* for each period (in rows). The black gradient corresponds to the increase in the
584 density of occurrence of the species. The solid line corresponds to the limit of the environmental
585 space available. The dashed line corresponds to the 50% most frequently available environmental
586 conditions.

587 **Figure 3** Density of species occurrence across the two-dimensional environmental space
588 describing the Skåne region. In columns are the densities of occurrence of (a) *Aglais urticae*, (b)
589 *Aglais io* and (c) *Araschnia levana* for each period (in rows). The black gradient corresponds to
590 the increase in the density of occurrence of the species. The solid line corresponds to the limit of
591 the environmental space available. The dashed line corresponds to the 50% most frequently
592 available environmental conditions.

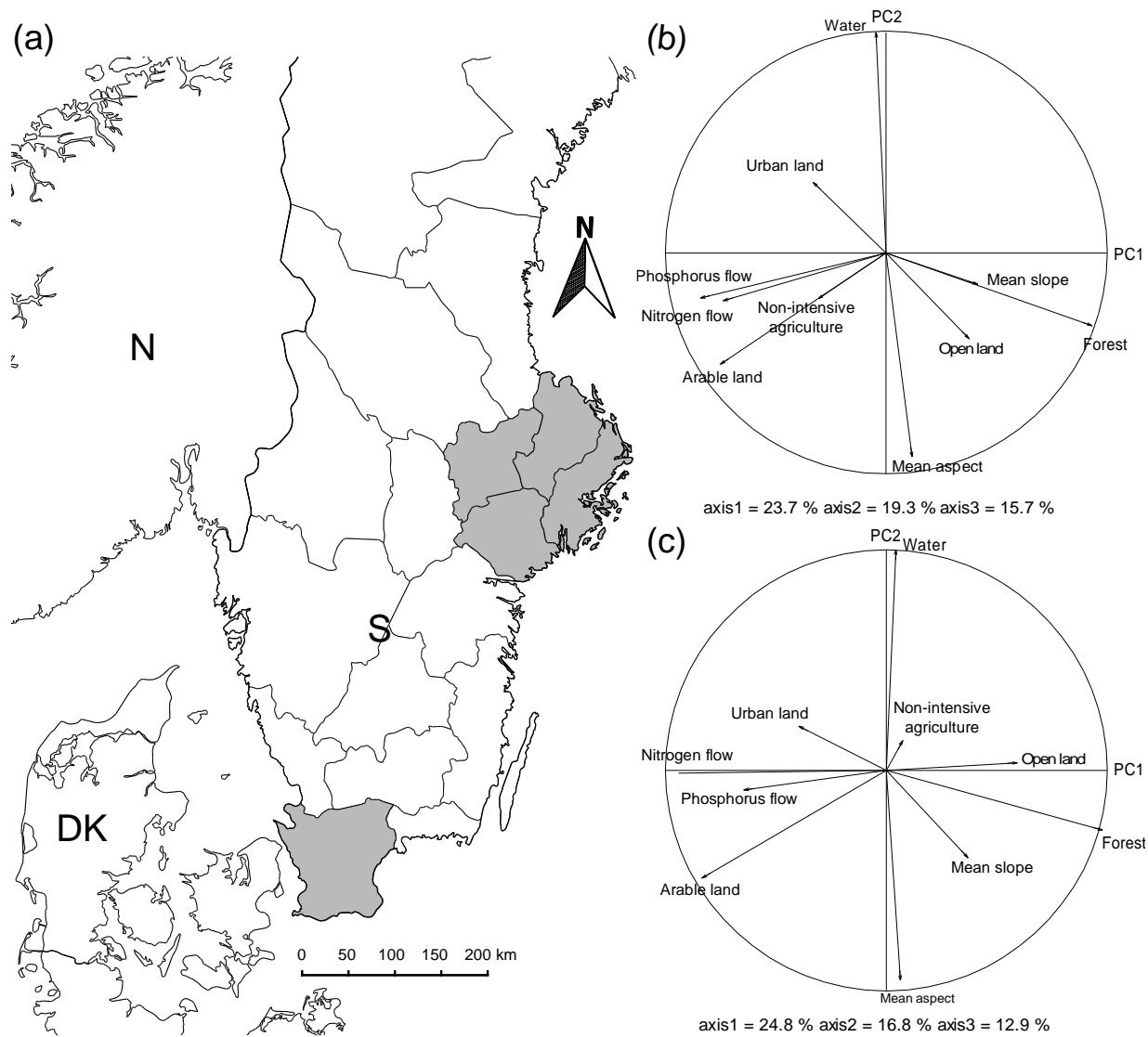
593 **Figure 4** Plots of the differences in density of occurrence, for each region and time-period, between
594 species. In columns are represented the differences in the density of occurrence in Norrström of

595 (a) *Aglais urticae* and *Aglais io* and in Skåne of (b) *A. urticae* and *A. io*, (c) *A. urticae* and *A. levana*
596 and (d) *A. io* and *A. levana*, for each period (in rows). Red cells indicate the prevalence of the first
597 species over the second species. Dark blue cells indicate the prevalence of the second species over
598 the first species. Grid cells with a color value of zero correspond to environmental conditions for
599 which the densities of occurrence of both species were similar. The boxplot and the standard
600 deviation (sd) associated with each graph show the variability of the differences of densities
601 observed across the available environment. The larger the box and the higher the sd are, the more
602 contrasting the species are in their distribution.

603 **Figure 5** Plots of the differences in density of occurrence of each species over time, and for each
604 region. In columns are represented the differences in the density of occurrence of (a) *Aglais urticae*,
605 (b) *Aglais io* and (c) *A. levana* over time and for the regions Norrström and Skåne (in rows). Red
606 cells indicate the prevalence of the species in the second period. Dark blue cells indicate the
607 prevalence of the species in the first period. Grid cells with a color value of zero correspond to
608 environmental conditions for which the density of occurrence of the species did not vary over time.
609 The boxplot and the standard deviation (sd) associated with each graph show the variability of the
610 differences in densities observed across the available environment. The larger the box and the
611 higher the sd are, the more contrasting the species distributions are.

612 **FIGURES**

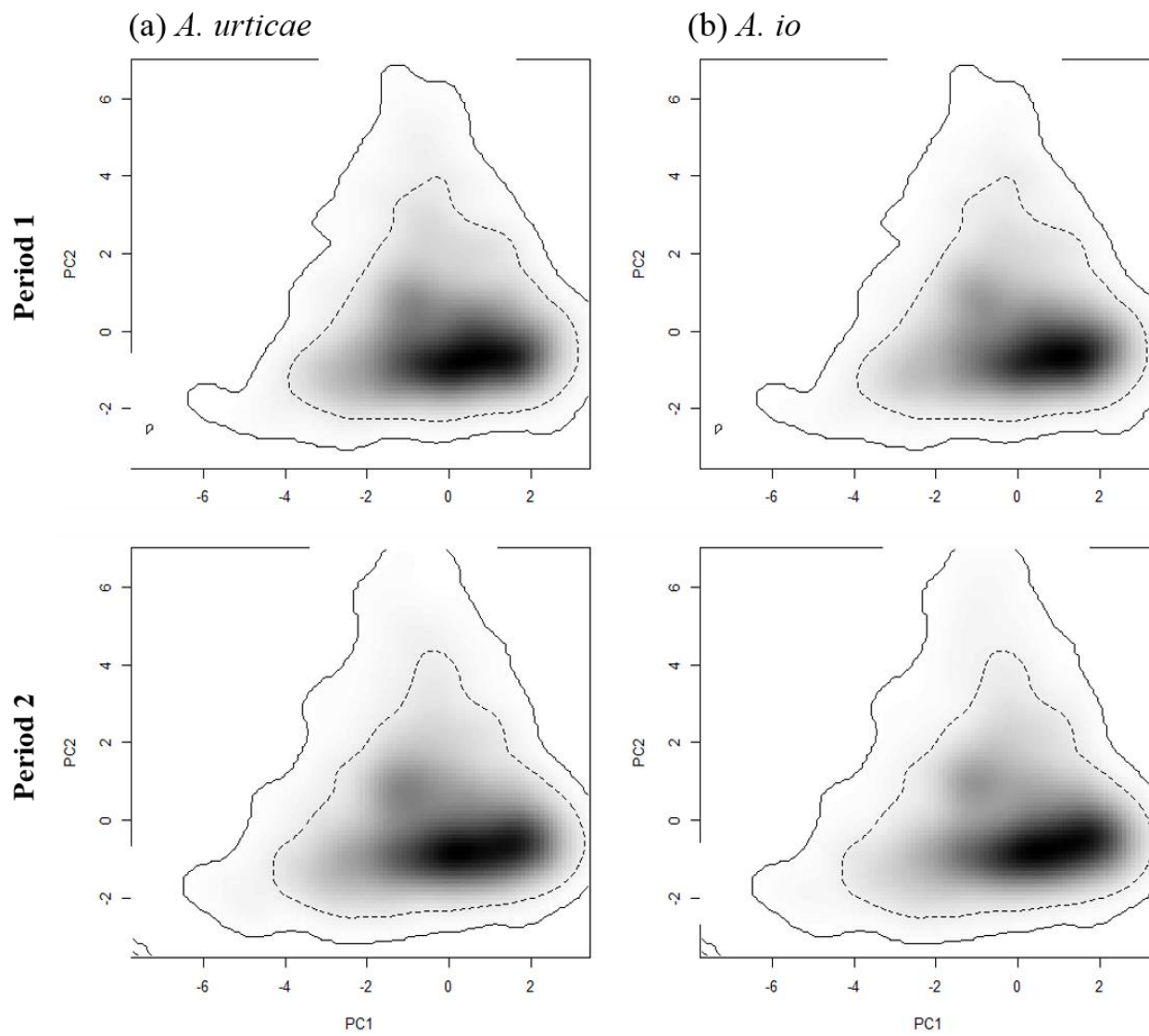
613 **Figure 1**



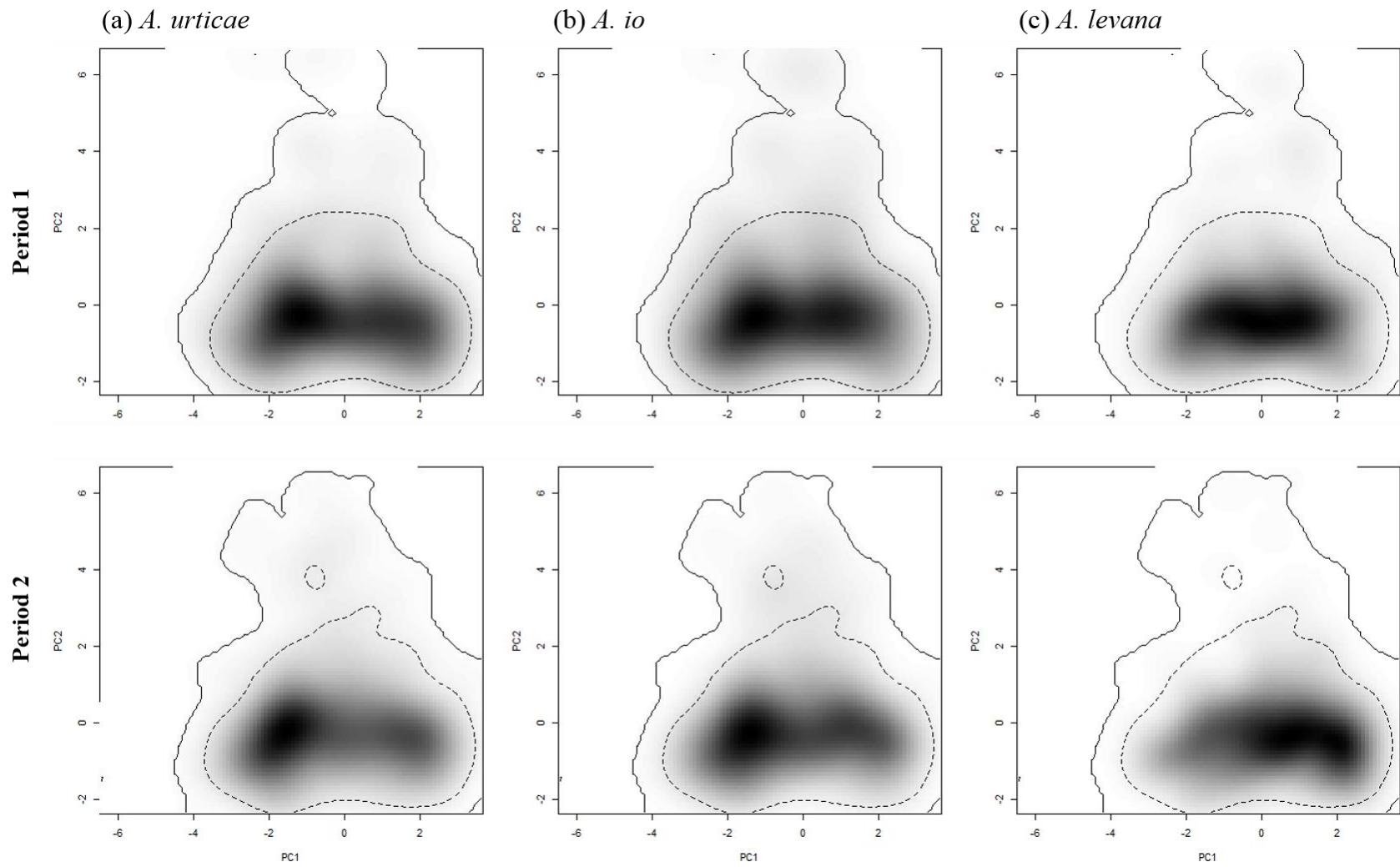
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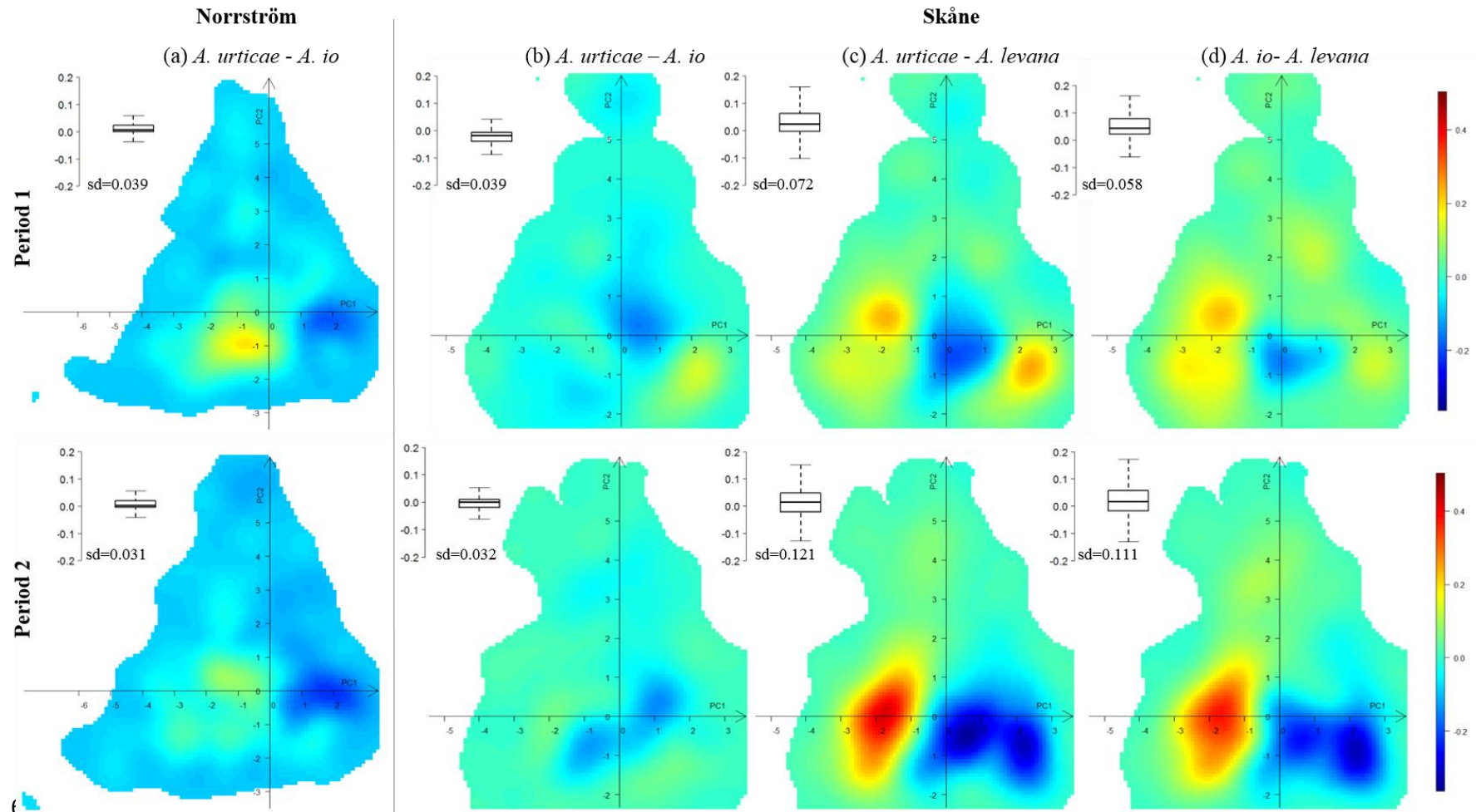
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616 **Figure 2**

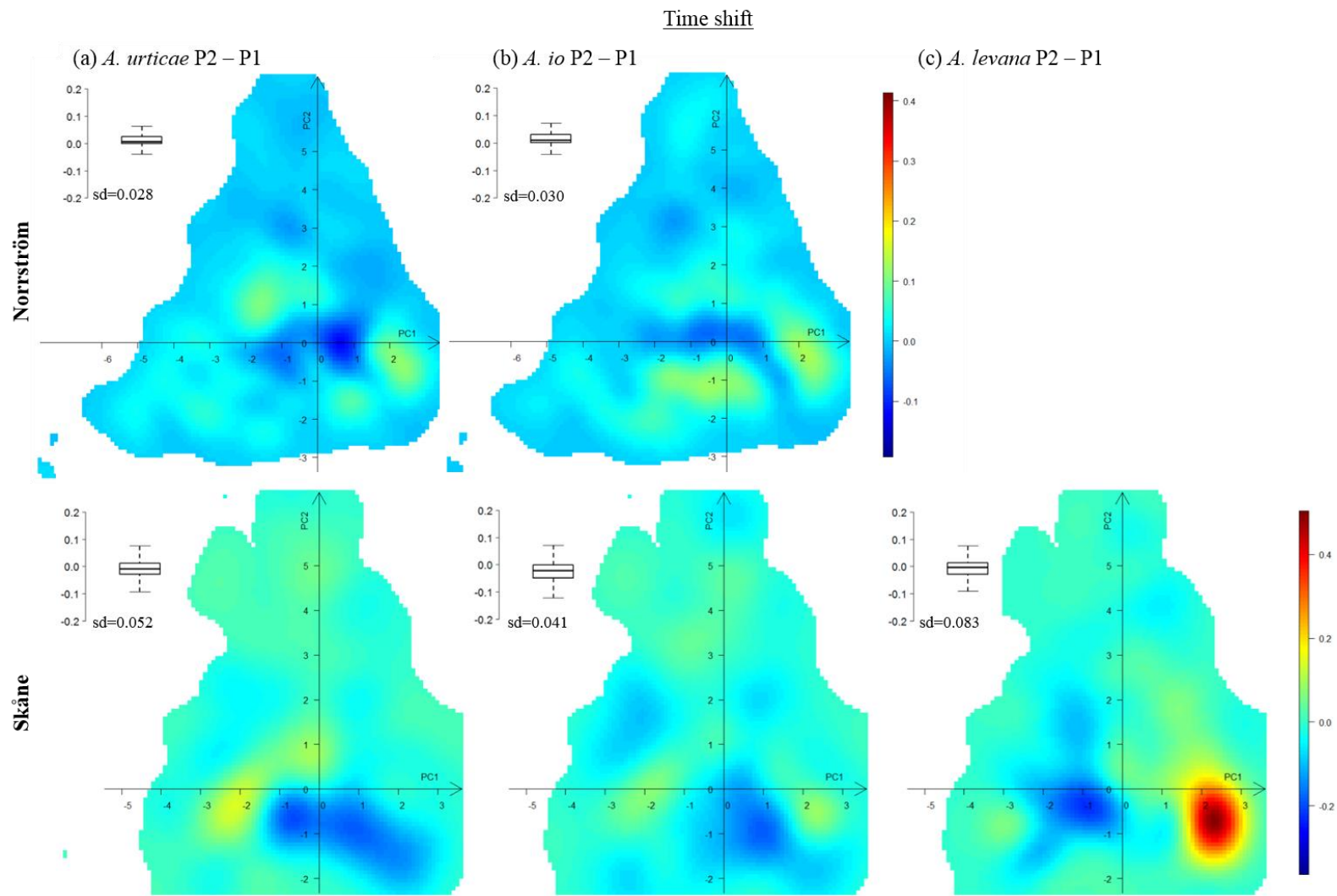


617

618 **Figure 3**

620 **Figure 4**Species interactions

622 Figure 5



623

