Original Article

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

Running header: Range expansion and changes in species interactions.

Authors:

Hélène Audusseau, Department of Zoology, Stockholm University, Stockholm, Sweden.

Maryline Le Vaillant, Department of Zoology, Stockholm University, Stockholm, Sweden.

Niklas Janz, Department of Zoology, Stockholm University, Stockholm, Sweden.

Sören Nylin, Department of Zoology, Stockholm University, Stockholm, Sweden.

Bengt Karlsson, Department of Zoology, Stockholm University, Stockholm, Sweden.

Reto Schmucki, Muséum National D'Histoire Naturelle, 55 rue Buffon, CP 51 75005 PARIS, Centre d'Ecologie et des Sciences de la Conservation, Sorbonne Universités, MNHN-CNRS-UPMC, Paris, France & Centre de Synthèse et d'Analyse sur la Biodiversité, Aix-en-Provence, France.

Correspondence:

Hélène Audusseau, Department of Zoology, Svante Arrhenuis väg 18B, Stockholm University, 106 91 Stockholm, Sweden.

Phone: +468 164058

E-mail: helene.audusseau@zoologi.su.se

Word count: abstract 295 words; main body of the text 6959 words.

ABSTRACT

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

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

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

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

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

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

INTRODUCTION

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

Northern regions offer a highly suitable model system to investigate how changes in species interactions can induce shifts in realized niches. At high latitudes, the impacts of climate change 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

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

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

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

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

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

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

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

MATERIALS AND METHODS

We studied the environmental space occupied by *A. urticae, A. io*, and *A. levana* in two regions, corresponding to the county of Skåne in Southern Sweden and the Norrström drainage basin in Central Sweden (including four counties: Södermanland, Stockholm, Uppsala, Västmanland, Fig. 1a), and two time-periods (first period 2001-2006 and second period 2009-2012). The regions are separated by approximately 400 kilometers in a straight line. By aggregating the records over specific time-periods, we aimed to have better estimates of species distributions, assuming these patterns to remain relatively stable over short time-periods (i.e. to avoid yearly variation). Data 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 ± se of 168m ± 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

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

Topographic Data

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

Land use Data

Land use data were collected from Naturvårdsverket at an original 25m resolution (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

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

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

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

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

Niche shifts over time

The distribution of the three species shifted significantly over time in both regions, their distribution in the environmental space being neither equivalent nor similar between the two time-periods (tests, $p<0.05$, Table 1). The largest shift was observed for *A. levana* in Skåne, for which the overlap in the realized niche between periods was of 0.75. For the two native species these shifts were comparatively smaller, the overlap in the realized niche of each species between periods varied between 0.82 and 0.87 (Fig. 5), but noticeable considering the short time scale of the study.

All shifts detected in the environmental space also corresponded to geographical shifts, as only one layer of land use was available to cover both time-periods. For the recently established *A. levana,* the observed shift in realized niche corresponded to a niche contraction as *A. levana* in the first period seemed to have already colonized most of the available environmental conditions in which the species occurred in the second period (Fig. 3c). In the second period, *A. levana* preferentially occupied areas with larger amount of forest (Fig. 5c bottom). For the two native

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

DISCUSSION

The distributions of our focal species were described and compared along the two first axes of the environmental PCA. In both regions, the first axis was shaped along a gradient from arable land to more forested land and the second axis correlated with topographic parameters (Fig.1a & b). Based on our knowledge of the ecological niche of our focal species, we are confident in the description of the species' environmental niche revealed by our models. The method developed by Broennimann *et al.* (2012) gave results consistent with the overall characteristics of the realized niches of the three butterfly species, which are known to occupy open habitats and woodlands, wood hedges, and hedgerows (Asher *et al.*, 2001; Haahtela *et al.*, 2011).

Yet, the method also identified differences in realized niches among species in each region and within species over time. We used the measure of overlap and the results from the niche

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

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

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

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

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

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

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

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

The method used was successful in handling the potential bias related to the non-standardized sampling design associated to occurrence data extracted from the public database. Indeed, while 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

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

ACKNOWLEDGMENTS

We thank the Strategic Research Program Ekoklim at Stockholm University for funding of this project. HA is acknowledging support from Helge Ax:son Johnsons stiftelse, RS from the FRB and EDF SA (FRB-CESAB project LOLA-BMS), and SN from the Swedish Research Council (2011-5636). We also wish to thank Vlad Dincã and Claudie Daniel for the photos presented in the Supporting Information, and Lars B. Pettersson for an insightful comment on the manuscript. We are also thankful for the comments from C. Stefanescu and two anonymous referees.

REFERENCES

Araújo, M.B. & Luoto, M. (2007) The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography*, **16**, 743–753.

Asher, J., Warren, M., Fox, R., Harding, P., Jeffcoate, G. & Jeffcoate, S. (2001) *The millennium atlas of butterflies in Britain and Ireland*. Oxford University Press, Oxford.

Audusseau, H., Kolb, G. & Janz, N. (2015) Fertilization interacts with life history: variation in performance and stoichiometry in nettle-feeding butterfies. *Plos One*, **10**(5).

Berry, P., Dawson, T., Harrison, P. & Pearson, R. (2002) Modelling potential impacts of climate change on the bioclimatic envelope of species in Britain and Ireland. *Global Ecology and Biogeography*, **11**, 453–462.

Betzholtz, P.E., Pettersson, L.B., Ryrholm, N. & Franzén, M. (2013) With that diet, you will go far: trait-based analysis reveals a link between rapid range expansion and a nitrogen-favoured diet. *Proceedings of the Royal Society of London B: Biological Sciences*, **280**.

Blitzer, E. & Welter, S. (2011) Emergence asynchrony between herbivores leads to apparent competition in the field. *Ecology*.

Brandt, M., Ejhed, H. & Rapp, L. (2009) Nutrient loads to the Swedish marine environment in 2006. *Swedish Environmental Protection Agency Report*, **5815**, 93.

Broennimann, O., Fitzpatrick, M.C., Pearman, P.B., Petitpierre, B., Pellissier, L., Yoccoz, N.G., Thuiller, W., Fortin, M.J., Randin, C., Zimmermann, N.E., Graham, C.H. & Guisan, A. (2012) Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography*, **21**, 481–497.

Broennimann, O., Petitpierre, B., Randin, C., Engler, R., Cola, V.D., Breiner, F., D'Amen, M., Pellissier, L., Pottier, J., Pio, D., Mateo, R.G., Hordijk, W., Dubuis, A., Scherrer, D., Salamin, N. & Guisan, A. (2015) ecospat: Spatial Ecology Miscellaneous Methods. R package version 1.1. URL http://CRAN.R-project.org/package=ecospat

Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B. & Wood, S. (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature*, **391**, 783–786.

Davies, Z.G., Wilson, R.J., Coles, S. & Thomas, C.D. (2006) Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. *Journal of Animal Ecology*, **75**, 247-256.

Devictor, V., van Swaay, C., Brereton, T. *et al.* (2012) Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change*, **2**, 121–124.

Dunn, A.M., Torchin, M.E., Hatcher, M.J., Kotanen, P.M., Blumenthal, D.M., Byers, J.E., Coon, C.A., Frankel, V.M., Holt, R.D., Hufbauer, R.A., Kanarek, A.R., Schierenbeck, K.A., Wolfe, L.M. & Perkins, S.E. (2012) Indirect effects of parasites in invasions. *Functional Ecology*, **26**, 1262–1274.

Eliasson, C. U., Ryrholm, N., Holmer, M., Jilg, K. & Gärdenfors, U. (2005) *Nationalnyckeln till Sveriges flora och fauna. Fjärilar. Dagfjärilar. Hesperiidae–Nymphalidae.* Artdatabanken, SLU, Uppsala, Sweden.

Gärdenfors, U., Jönsson, M., Obst, M., Wremp, A.M., Kindvall, O. & Nilsson, J. (2014) *Swedish LifeWatch – A Biodiversity Infrastructure Integrating and Reusing Data from Citizen Science, Monitoring and Research*.

Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W. & Holt, R.D. (2010) A framework for community interactions under climate change. *Trends in Ecology & Evolution*, **25**, 325–331.

González-Megías, A., Menéndez, R., Roy, D., Brereton, T. & Thomas, C.D. (2008) Changes in the composition of British butterfly assemblages over two decades. *Global Change Biology*, **14**(7), 1464–1474.

Haahtela, T., Saarinen, K., Ojalainen, P., Aarnio, H. (2011). *Butterflies of Britain and Europe: A Photographic Guide*. A. & C. Black Publishers Ltd.

Heikkinen, R.K., Luoto, M., Virkkala, R., Pearson, R.G. & Körber, J.H. (2007) Biotic interactions improve prediction of boreal bird distributions at macro-scales. *Global Ecology and Biogeography*, **16**, 754–763.

Hinz, R. & Horstmann, K. (2007) Uber Wirtsbeziehungen europaischer Ichneumon-Arten (Insecta, Hymenoptera, Ichneumonidae, Ichneumoninae). *Spixiana*, **30**, 39.

IPCC (2014) *Climate Change 2013*. The physical science basis: Working group I contribution to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press.

Leathwick, J.R. (1998) Are New Zealand's Nothofagus species in equilibrium with their environment? *Journal of Vegetation Science*, **9**, 719–732.

MacArthur, R. & Levins, R. (1967) The limiting similarity, convergence, and divergence of coexisting species. *American naturalist*, pp. 377–385.

Mason, T.H., Stephens, P.A., Apollonio, M. & Willis, S.G. (2014) Predicting potential

500 responses to future climate in an alpine ungulate: interspecific interactions exceed climate
501 exceed. *Global change biology*, **20**, 3872–3882.

502 Merckx, T., Serruys, M. & Van Dyck, H. (2015) Anthropogenic host plant expansion leads a
503 nettle-feeding butterfly out of the forest: consequences for larval survival and
504 developmental plasticity in adult morphology. *Evolutionary Applications*.

505 Morris, R.J., Lewis, O.T. & Godfray, H.C.J. (2004) Experimental evidence for apparent
506 competition in a tropical forest food web. *Nature*, **428**, 310–313.

507 Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *The*
508 *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.

509 Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the
510 distribution of species: are bioclimate envelope models useful? *Global ecology and*
511 *biogeography*, **12**, 361–371.

512 Pellissier, L., Pradervand, J.N., Pottier, J., Dubuis, A., Maiorano, L. & Guisan, A. (2012)
513 Climate-based empirical models show biased predictions of butterfly communities along
514 environmental gradients. *Ecography*, **35**, 684–692.

515 Pettersson, L., Mellbrand, K. & Ottvall, R. (2013) *Swedish Butterfly Monitoring Scheme,*
516 *annual report for 2012*.

517 PostgreSQL (2014) *PostgreSQL, version 9.3.5*. PostgreSQL Global Development Group. URL
518 http://www.enterprisedb.com/

519 Pöyry, J., Luoto, M., Heikkinen, R.K., Kuussaari, M. & Saarinen, K. (2009) Species traits
520 explain recent range shifts of Finnish butterflies. *Global Change Biology*, **15**, 732–743.

521 Quantum GIS (2012) *Quantum GIS 1.8 Software.* QGIS Development Team. URL
522 http://qgis.org/

523 R Core Team (2015) *R: A Language and Environment for Statistical Computing*. R Foundation
524 for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/

525 Schweiger, O., Heikkinen, R.K., Harpke, A., Hickler, T., Klotz, S., Kudrna, O., Kühn, I., Pöyry,
526 J. & Settele, J. (2012) Increasing range mismatching of interacting species under global

change is related to their ecological characteristics. *Global Ecology and Biogeography*, **21**, 88–99.

Serruys, M. & Van Dyck, H. (2014) Development, survival, and phenotypic plasticity in anthropogenic landscapes: trade-offs between offspring quantity and quality in the nettle-feeding peacock butterfly. *Oecologia*, **176**, 379–387.

Shaw, M.R., Stefanescu, C. & Van Nouhuys, S. (2009) *Parasitoids of European Butterflies*. Cambridge University Press, Cambridge.

Taylor, K. (2009) Biological Flora of the British Isles: *Urtica dioica* L. *Journal of Ecology*, **97**, 1436–1458.

Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T. & Prentice, I.C. (2005) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 8245–8250.

Tingley, R., Vallinoto, M., Sequeira, F. & Kearney, M.R. (2014) Realized niche shift during a global biological invasion. *Proceedings of the National Academy of Sciences*, **111**, 10233–10238.

Tylianakis, J.M. (2009) Warming up food webs. *Science*, **323**, 1300–1301.

Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology letters*, **11**, 1351–1363.

van Veen, F.F.J., Morris, R.J. & Godfray, H.C.J. (2006) Apparent competition, quantitative food webs, and the structure of phytophagous insect communities. *Annual Review of Entomology*, **51**, 187–208.

Wallisdevries, M.F. & van Swaay, C.A.M. (2006) Global warming and excess nitrogen may induce butterfly decline by microclimatic cooling. *Global Change Biology,* **12**, 1620-1626.

Warren, D.L., Glor, R.E. & Turelli, M. (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution*, **62**, 2868–2883.

Wisz, M.S., Pottier, J., Kissling, W.D. *et al.* (2013) The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution

554 modelling. *Biological Reviews*, **88**, 15–30.

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** Hélène 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.

TABLE

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

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

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

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

FIGURES

Figure 1

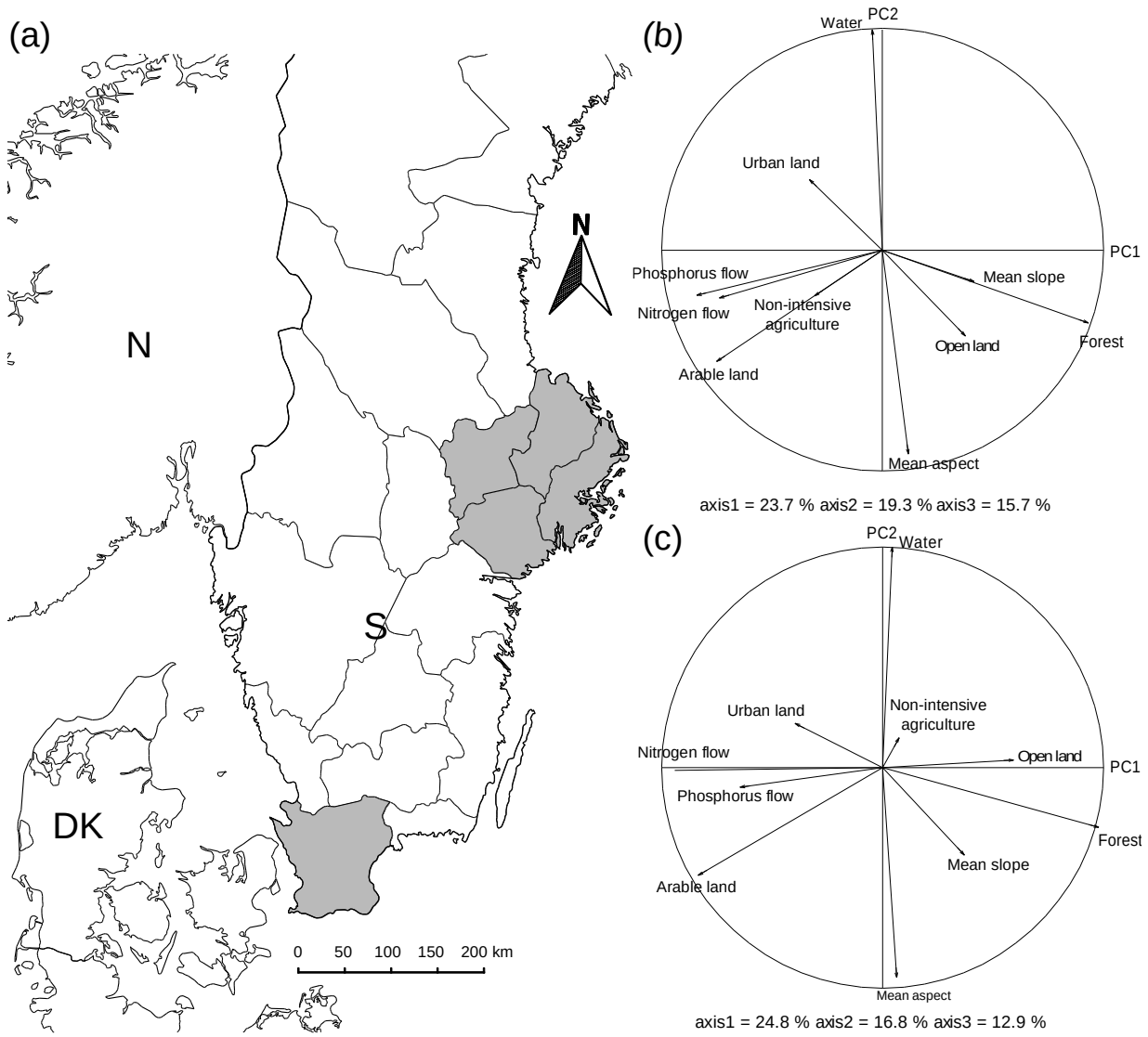


Figure 2

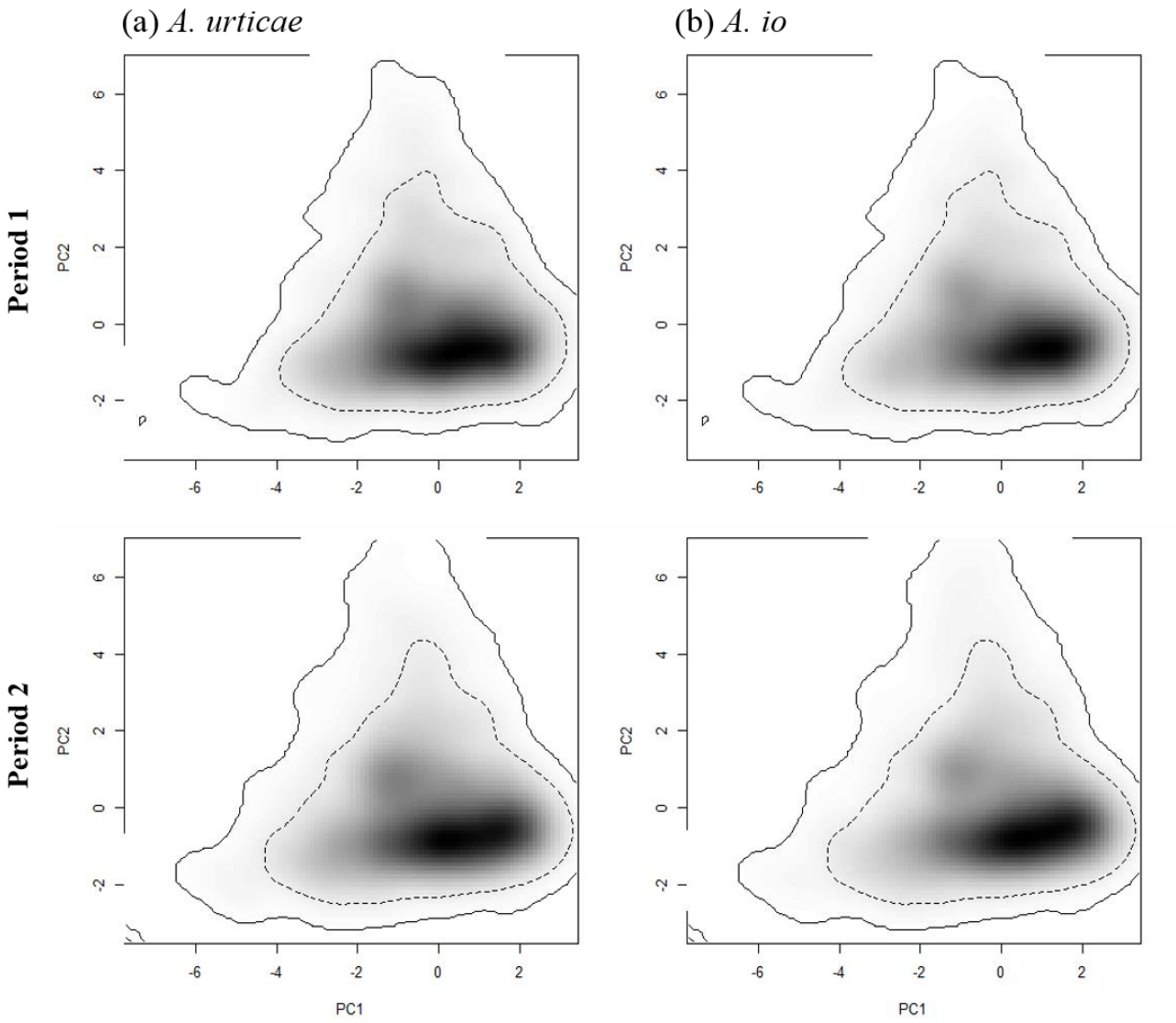
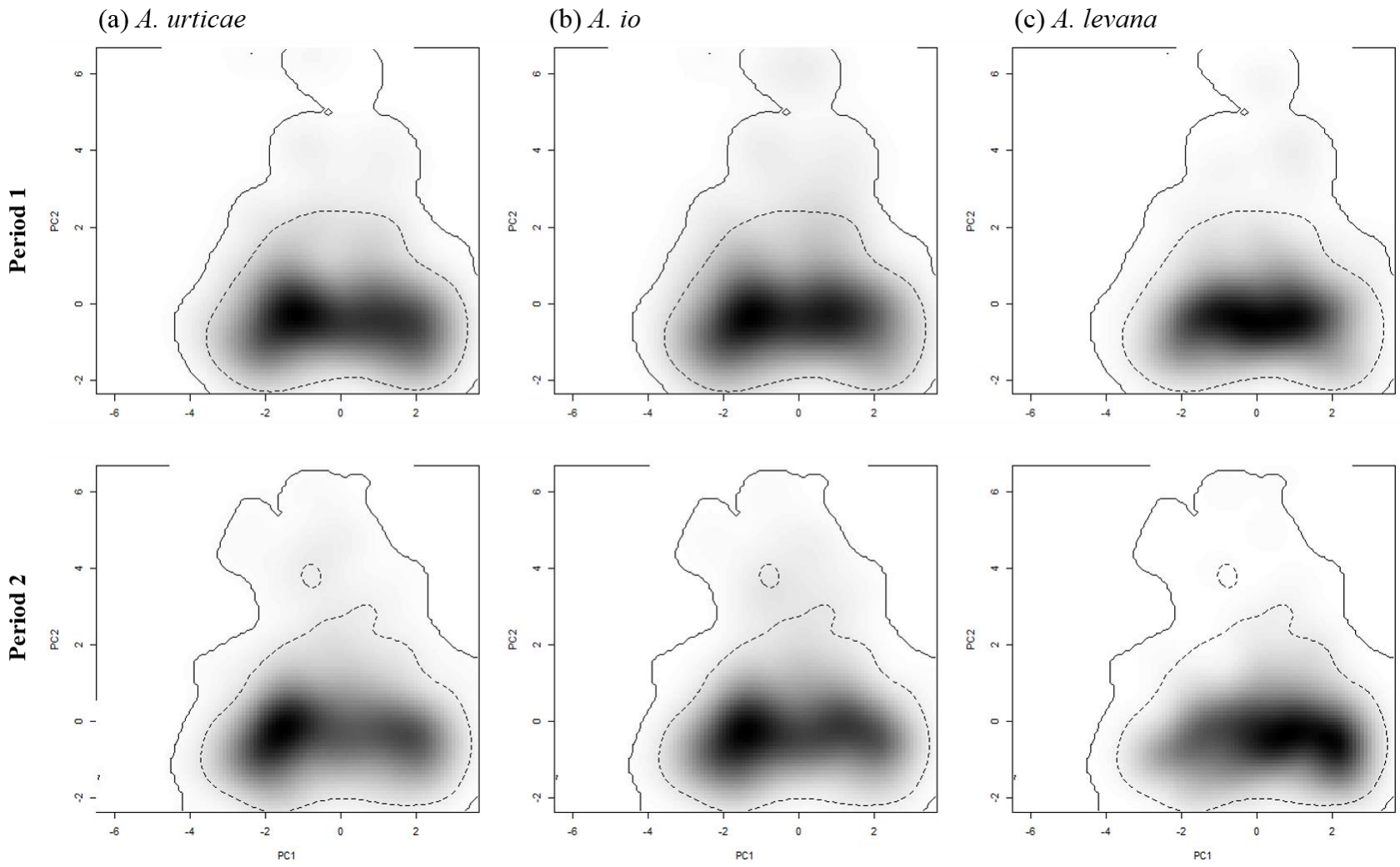


Figure 3



620 **Figure 4**

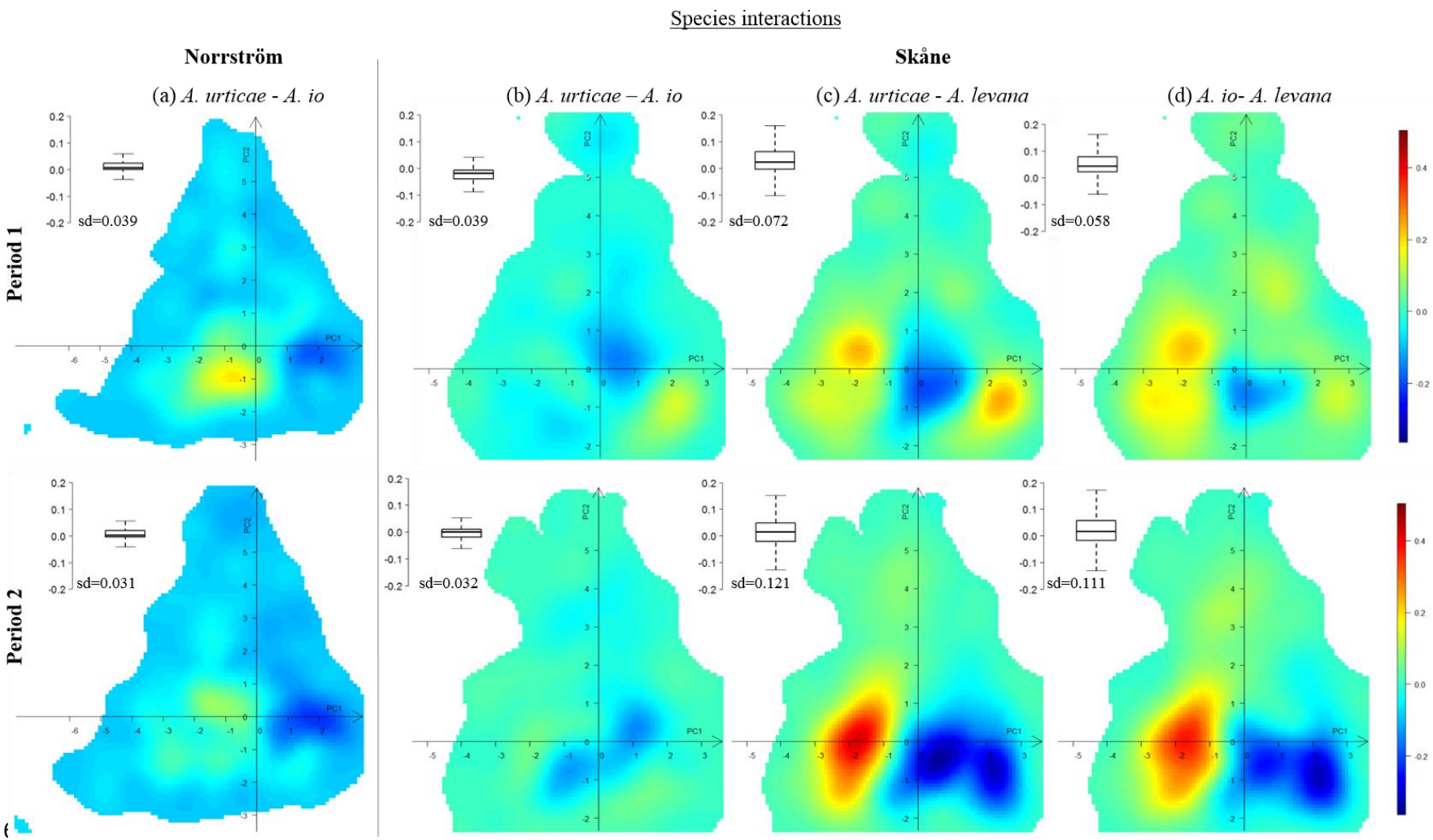
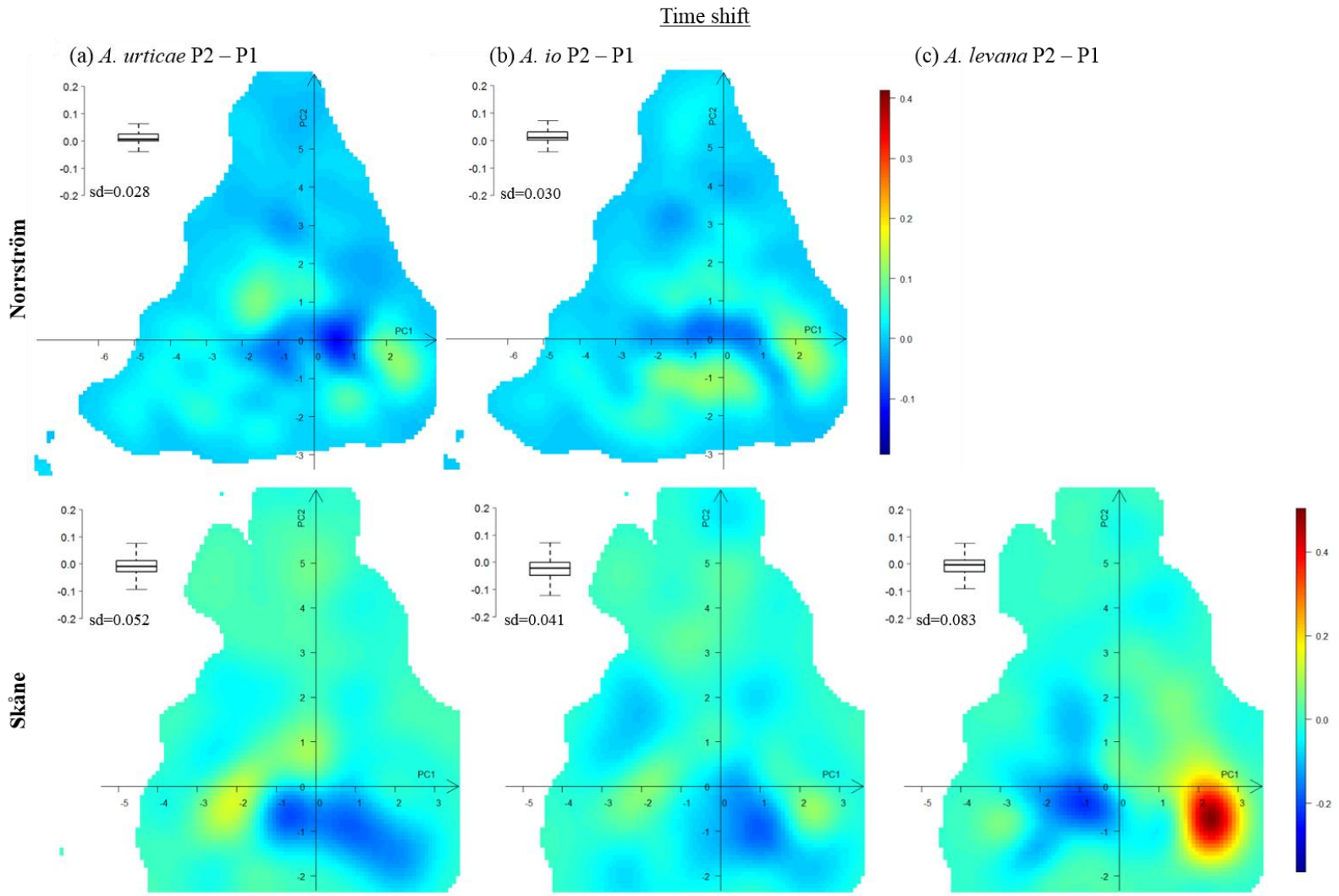

Species interactions
Norrström
Skåne
(a) A. urticae - A. io
(b) A. urticae – A. io
(c) A. urticae - A. levana
(d) A. io- A. levana
Period 1
Period 2
sd=0.039
sd=0.039
sd=0.072
sd=0.058
sd=0.031
sd=0.032
sd=0.121
sd=0.111
PC1
PC2

Figure 5


Time shift
(a) A. urticae P2 – P1
(b) A. io P2 – P1
(c) A. levana P2 – P1
Norrström
Skåne
sd=0.028
sd=0.030
sd=0.052
sd=0.041
sd=0.083
PC1
PC2

624