# Original article: Species range expansion constrains the ecological niches of resident butterflies.

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**Abstract**

- Changes in community composition resulting from climate change entail modifications of biotic interactions and reshape local species distributions. 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.
- 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) corresponding to before and after its establishment.
- We performed two distinct analyses in each region using the PCA-env and the framework described in Broennimann *et al.* (2012). We first described the main sources of variation in the environment. Second, we characterized, in each time-period and region, 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.
- We found indications of niche partitioning between native species, although niche differentiation was not clearly associated to specific environmental factors. Looking over time, we found a larger shift in species distributions of the resident species in Skåne than in Norrström. These shifts showed a consistent pattern of avoiding overlap with the environmental space occupied by *A. levana*, and it was stronger for *A. urticae* than for *A. io*.
- Interspecific interactions play a role in shaping species distributions. It seemed clear that the range expansion of *A. levana* modified local biotic interactions, and potentially induced shifts in resident species distribution. We suggest that parasite-driven apparent competition may mediate niche partitioning in this community.

**Key-words:** biotic interactions, community composition, environmental niche model, nettle-feeding butterflies, ordination technique, parasite-driven indirect competition, realized niche.

# Introduction

Changes in community composition resulting from climate change are expected to modify biotic interactions and thereby affect local species distributions. To better predict the widely recorded species geographical and environmental shifts (Parmesan, 2006; Walther *et al.*, 2002), it is crucial to first define and understand species environmental niches and their variability in light of their biotic contexts (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 climate change.

Northern regions offer a highly suitable model system to investigate shifts in niches and changes in species interactions. At high latitudes, the impacts of climate change are most pronounced (IPCC, 2014), making it more likely to detect a signature of species responses to changes over a relatively short time-scale. For example, Pöyry and *et al.* (2009) reported, over a ten-year period, changes in the latitudinal distribution of butterfly species of up to 300 km in Finland. Moreover, as poleward range shifts are unlikely to be synchronized across species, changes in community composition are expected to alter interspecific interactions (Devictor *et al.*, 2012; Kerbiriou *et al.*, 2009) and potentially lead to new interactions.

A good way to examine niche shifts and niche partitioning is to measure and test the overlap and the difference in the environmental space occupied (i.e. realized niche) over time and across species (Warren, Glor & Turelli, 2008; Broennimann *et al.*, 2012). Indeed, the realized niche reflects the action of both abiotic and biotic factors on species distribution. Significant improvement in our knowledge of the factors and processes shaping species realized niche is related to the rise of improved statistical methods and powerful computational techniques that have enabled better estimations of species-environment relationships. Fore-

most, Environmental Niche Models (ENMs) have been used to model and predict species distributions according to changes in climatic and environmental variables, considered to be the main drivers of species distribution at large and small spatial-scales (e.g. Berry *et al.*, 2002; Thuiller *et al.*, 2005). However, ENMs based on the relationship of climatic and environmental variables on species distribution have often shown some discrepancy between the potential and the realized niches, suggesting that other processes such as biotic interactions can have substantial effect on species distribution and therefore should be accounted (e.g. Leathwick, 1998; Pellissier *et al.*, 2012; Tingley *et al.*, 2014). Better consideration of biotic interactions in distribution models assessing species geographic range has greatly refined our predictions at both small and large scales (e.g. Leathwick, 2002; Heikkinen *et al.*, 2007; Araújo & Luoto, 2007). However, if ENMs and ordination techniques have been successfully used to further our understanding of the role of biotic interactions by comparing the realized niches of species (Anderson, Peterson & Gómez-Laverde, 2002; Schweiger *et al.*, 2012; Mason *et al.*, 2014), they have rarely been used to investigate the effects of changing biotic contexts (Wisz *et al.*, 2013).

Although computational techniques have been successfully used to study realized niches and have shown some potential to estimate interspecific interactions, their reliability and accuracy in predicting the importance of biotic interactions are often limited by the availability of extensive occurrence data. 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 the habitat covered, lacking independence between replicates, and having no explicit measures of sampling effort. Yet, considering the rapid expansion of programs collating data through volunteer contribution of citizen observers, the real potential of these large datasets is growing and remains largely under-exploited. This has led to increased

efforts being made to develop robust approaches to estimate and compare the realized niche from occurrence data 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, Glor & Turelli, 2008), using Principal Component Analysis to define the environmental space (PCA-env). Among other ENM methods, the PCA-env has been shown to be most reliable to define 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 (*Agais urticae*, *Agais 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 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*, which was absent from Sweden before 2006, 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. While no obvious direct competition has been documented, the three species are known to share common parasites (Hinz & Horstmann, 2007; Shaw, Stefanescu & Van Nouhuys, 2009), which can increase the potential of apparent competition among the species. Indeed, studies have shown that the community composition in herbivore insects can largely be shaped by parasites (Morris, Lewis & Godfray, 2004; van Veen, Morris & Godfray, 2006; Tylianakis, 2009).

The establishment of *A. levana* in southern Sweden may hence affect the population dynamic of parasites and indirectly entail modifications in the distribution of native butterfly species, making this system a unique opportunity to investigate the impact of such change over a relatively short time period. If competition, either direct or apparent, is an important determinant of spatial distribution across the landscape, its 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 use the PCA-env method applied within Broennimann's analysis framework (Broennimann *et al.*, 2012). For this aim, we gathered high-resolution data on land use (25m resolution) and topography (50m), and an index of nitrogen and phosphorus flows in the soil linked to agricultural practices (municipality). We perform these analyses over two time-periods (before and after 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 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, we expect the distribution of native (i.e. resident) species to be affected by the establishment of *A. levana*. We suggest that interspecific interactions, namely shared parasites in our study system, can play a substantial role in shaping species distributions. 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. 1), 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.

## Occurrence Data

We extracted occurrence data for *A. urticae*, *A. io*, and *A. levana* from the Swedish Species Information Centre at SLU (www.artportalen.se), a public database of species records in Sweden. The Artportalen database gathers opportunistic occurrence data (presence only) collected at 90% by amateurs with no specific required training in species identification (Gärdenfors *et al.*, 2014). For each species, we identify all grid cells for which the species was recorded in each of the two time-periods and the two study regions. For each period, we only considered species presence-absence across the selected grid cells, without accounting for variation in the number of observations per cell as our main interest was to determine species occurrence patterns across the total available environment. In this way, we reduced the potential bias associated with uneven sampling effort across sites (i.e. over-sampling of most frequently visited sites). We want to point out that both the number of observations and the corresponding number of grid cells visited increased between period one and two (see Appendix S1 in Supporting Information). The increase reflects an overall growing interest for citizen science. While increasing 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 two most reported butterfly species in Artportalen

and they were in the top fifteen most reported species according to the Swedish Butterfly Monitoring Scheme (records along transects, Pettersson, Mellbrand & Ottvall, 2013). As a newly established species in Sweden, *A. levana* is still in its initial phase of establishment and its current distribution is therefore likely to only reflect a subset of its potential environmental niche. In our final dataset, occurrence of *A. urticae* was recorded in 3309 grid cells, *A. io* in 2742, and *A. levana* in 273. Note that *A. levana* were only recorded in Skåne during the second time-period.

## 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 Lantmteriet at an original 25m resolution (http://www.lantmateriet.se/). The land use classification followed the Corine Land Cover. We extracted the percentage of the different types of land use (forest, open land, arable land, non-intensive agriculture, water body, and urban land) at 1km resolution grid cells. We also used estimates of soil nutrient flow (in nitrogen and phosphorus) which we used as a proxy for the amount of nutrients available for plant root absorption accessible from the SMED (Svenska Miljö Emission Data, http://www.smed.se/) at an original resolution of the sub-catchment. These estimates were modeled by means of simulation tools as well as measured data and

correspond to nitrogen and phosphorus loads to the water from diffuse sources across the whole sub-catchment (Brandt, Ejhed & Rapp, 2009). Nutrient loads to the water from the sub-catchment result from a combination of the run-off and leaching on the basis of assumptions on type-specific concentrations for each type of land use. From these estimates, we calculated nutrient flow through the 1km grid cells.

## Realized Niche Shifts and Overlaps

The spatial scale at which the statistical models are computed strongly determine the environmental variables that can potentially affect the distribution of species (Pearson & Dawson, 2003). While at large scales, species distribution is limited by physiological limitations, mainly determined by climatic variables, at small scales we expect distribution to be more related to local variables such as land use and topography (Pearson & Dawson, 2003), as well as by direct and indirect biotic interactions (e.g. predation, competition, resources). The interplay of factors acting on different scales constrains species distribution.

Considering the extent of our study areas, i.e. two regions of Sweden, we expected local-scale variables to be the most relevant factors for investigating niche differences between species and potential niche shifts. Therefore, we first extracted two axes that captured the maximum variation in land use and topography available to the species, using the PCA-env ordination method described in Broennimann *et al.* (2012). Second, we characterized, for each time-period and region, the realized niches of our study species (*A. urticae*, *A. io*, *A. levana*) in the environmental space defined by the topographic and land use gradients extracted above. Third, we quantified overlaps and differences for each species over time and between species in each period in how they distributed themselves in this environment. All analyses were computed with the ecospat (Broennimann *et al.*, 2015) package in R 3.1.3 (R Core Team, 2015). To reduce the risk of generating false absences in un-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 main sources of variation within region; the latter being the components of most interest for detecting niche partitioning. 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, Glor & Turelli, 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 from random reallocating of 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. Niche similarity is tested by comparing the overlap between the two realized niches to the expected distribution of overlap obtained by reallocating the density of occurrence of one entity across its range of occupancy, while the occurrence of the other remains constant. In other words, this test estimates the likelihood

that niche centroids are significantly different from each other. For both tests, expected distributions were based on 500 iterations of the randomization procedure.

# Results

## Description of the available environment and realized niches

The environmental space sampled in each region was described by the first two axes of the principal component analyses, capturing 41.6 and 43.0% of the environmental variation in Skåne and Norrström respectively (Figs 2 & 3, and see Appendix S2 in Supporting Information). In both Skåne and Norrström, the first PCA-axis was strongly associated to a gradient defined by grid cells having a higher amount of arable land at one end and more forest at the other. Note that in both cases the estimates of soil nitrogen and phosphorus flow explained a large part of the variance captured by the first PCA-axis and were associated with higher amount of arable land. In both Skåne and Norrström, the variance along the second axis reflected change in the mean aspect (varying from 0 degree North to 301 degrees at maximum).

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

## Interspecific interactions

In spite of the overall similarities, we detected significant differences between species realized niches. In most case, the null hypothesis of niche equivalency and similarity was rejected ($p<0.05$, Table 1), even though the three species displayed important overlap in their environmental space (Table 1, Figs 4 & 5).

In a two-dimensional environmental space, the two native species (*A. urticae* and *A. io*) strongly overlapped in both periods and regions (overlap between 0.88 and 0.91, Table 1). This is not surprising considering that *A. io* and *A. urticae* are often observed in sympatry with ecological niches that are known to be difficult to differentiate. While in the first period, *A. urticae* and *A. io* displayed equivalent niches in Skåne (paired-species comparisons of niche equivalency, p=1, Table 1), the null hypothesis of niche equivalency was rejected in the first period in Norrström and in both regions in the second period ($p<0.05$, Table 1). Thus, although the realized niches of *A. urticae* and *A. io* significantly overlapped, they 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. 4a bottom). In the second period, the prevalence of *A. urticae* slightly shifted from forested areas toward habitats with increasing amount of agricultural and urban lands (Fig. 4b top). 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 both *A. urticae* and A.io shifted significantly over time, their distribution in the environmental space being neither equivalent nor similar between the two time-periods (tests, $p<0.05$, Table 1). These shifts were relatively small, the overlap in the realized niche of each species between periods varied between 0.75 and 0.88 (Fig. 5), but noticeable considering the short time scale of the study. All shifts detected in the environmental space also corresponded to a geographical shift as only one layer of land use was available to cover

both time-periods. The largest changes between the two periods were observed in Skåne, in both *A. urticae* and *A. io* (Fig. 5a, b bottom). Moreover, the extent of the environmental shift observed in Skåne was species-specific, being larger for *A. urticae* (niche overlap=0.75) than for *A. io* (niche overlap=0.81). By shifting its distribution away from areas with larger amount of forest, *A. urticae* reduced its overlap with *A. levana*, which recently established in these environments across Skåne (niche overlap=0.69; Fig. 4c bottom). We observed the same pattern between *A. io* and *A. levana*, but to a lower extent (Fig. 4d bottom).

# Discussion

We found significant shifts in the realized niches of the two native species over time, in both Skåne and Norrström. These shifts in the environmental space 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. Such changes in occupancy of the environmental space could partly reflect species responses to climatic fluctuations over time between regions. However, as the amplitudes of climatic variations over time were comparable across the regions (see Appendix S3 in Supporting Information), the observed changes in species occupancy were systematically more pronounced in Skåne than in Norrström. The observed shifts in niche centroid over time could also be related to the increase in the number of reported observations through time. Yet, such an explanation 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, such as the recent establishment of *A. levana* in Skåne. In this region, we showed that the distribution of the native species dis-

played a seemingly consistent pattern of avoidance of overlap with the environmental space occupied by *A. levana*.

Based on our knowledge of the ecological niche of our focal species, we are highly confident in the description of species environmental niche and niche shifts evidenced by our models. The method developed by Broennimann *et al.* (Broennimann *et al.*, 2012) successfully identified the overall main characteristics of the realized niches of the three butterfly species, which are known to occupy open habitat and woodland, wood hedges, and hedgerows (Asher *et al.*, 2001).

Yet, the method also identified in each region variation in realized niches among species within time period 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 species interactions in shaping species distributions. The large overlap in the realized niches of the two native species 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 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 aspect, 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

of resources, potential asynchrony (temporal partitioning) in species phenology could also reduce the strength of spatial signal in the differentiation in species realized niches.

The distributions of our three focal species was described and compared along the two first axes of the environmental PCA, describing about 40% of the environmental variation available in both regions. The first axis was shaped along the same gradient from arable land to more forested land in both Skåne and Norrström (Figs 2&3). The second axis correlated with topographic parameters, specifically the mean aspect over the grid cells (Figs 2&3). 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 where recorded in urban areas, the highest densities of occurrence of the two native species based on the grid cell analysis were found in forest habitats (Figs 2&3). In addition, the lower number of species records in the first period did not seem to have affected our capacity to extract the main components of the realized niches as their shapes and centroids were consistent through time.

From our results, we believe that the shift in distribution of the native species is related to the arrival of *A. levana*, and that this response could have been mediated through the action of parasites (Dunn *et al.*, 2012). All three species are heavily parasitized (personal observation) and share many parasites (Hinz & Horstmann, 2007; Shaw, Stefanescu & Van Nouhuys, 2009). The population dynamics of these parasites is likely to have been positively affected by the increase in potential larval hosts (*A. levana*) between the two time-periods (Morris, Lewis & Godfray, 2004). Moreover, the differences in phenology between *A. urticae*, *A. io*, and *A. levana* may form a breeding ground to stimulate parasites population dynamics as it may also correlate with a prolonged temporal niche for parasites to achieve their reproductive cycle (Blitzer & Welter, 2011). In a scenario of parasite-driven apparent competition, the phenologically late species is expected to be the more vulnerable as its larval growth will coincide with an increase in parasite population size (Blitzer & Welter, 2011). Interestingly,

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 niche overlap. In addition, niche partitioning was stronger between *A. levana* and *A. urticae* than with *A. io*. At a first glance, this may seem counterintuitive, as, between the two native species, *A. urticae* is the earliest. But because *A. urticae* is bivoltine in Skåne, and produces a second brood later in the season, parasite populations may buildup over the season and result in the highest parasite load for the second brood of *A. urticae*. Although we have no direct data to support the hypothesis of parasite-driven niche differentiation, the circumstantial evidence is suggestive, and is further reinforced by the observation that *A. levana* appears to share more parasites with *A. urticae* than with *A. io* (Shaw, Stefanescu & Van Nouhuys, 2009).

Differences in life history may be another possible explanation for these differences in response between the two native species. Based on experimental studies, Merckx *et al.* (2015) suggested that because of its bivoltine life cycle, the plastic response of *A. urticae* to changes will be faster in comparison to the univoltine *A. io*. In that framework, a faster response of *A. urticae*, in comparison to *A. io*, to the arrival of *A. levana* would be expected. Interestingly, 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* (Audusseau, Kolb & Janz, 2015; Serruys & Van Dyck, 2014).

In conclusion, we believe that using occurrence records from citizen-science databases offer new opportunities to investigate the realized niches of species and differences between them, as long as the biological relevance of the modeling results is carefully considered. The method we used successfully identified the realized niches of our focal butterfly species, and we recommend using occurrence data associated with species and regions of high sampling effort in order to get more robust predictions. Such regions often correspond to more densely

populated areas as the reporting effort in citizen-based monitoring program is strongly related to the number of participants. With this in mind, our study showed that interspecific interactions play a role in shaping species distributions. While we found indications of niche partitioning between the two native species, we could not identify a specific environmental factor of niche differentiation. Interestingly, we also highlighted a current scenario of modification of the community composition that is happening as an indirect consequence of climate change. Looking over time and space, it seemed clear that the range expansion of *A. levana* modified biotic interactions, resulting in associated shifts in species distribution. Indeed, the larger shift in species distributions of the resident species in Skåne than in Norrström also showed a consistent pattern of avoiding overlap with the environmental space where *A. levana* has established. Based on our knowledge of the system, we suggest that the observed niche differentiation is driven by apparent competition mediated by shared parasites. The difference in the extent of the shift observed between *A. urticae* and *A. io* after the arrival of *A. levana* is potentially related to their differences in phenology, voltinism, and the highest number of shared parasites between *A. urticae* and *A. levana*. Because the number of records reporting the presence of *A. levana* in Skåne is still low in comparison with the other species, the recently established species has probably not yet reached its equilibrium in this environmental space. 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 appears insightful to study the role of biotic interactions on species distributions and better predict the outcome of their modifications on community composition and species-environment relationships.

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# References

Anderson, R.P., Peterson, A.T. & Gómez-Laverde, M. (2002) Using niche-based GIS modeling to test geographic predictions of competitive exclusion and competitive release in South American pocket mice. *Oikos*, **98**, 3–16.

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*.

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. *Proc. R. Soc. Lond. B Biol. Sci.*, **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. *et al.* (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.

Devictor, V., van Swaay, C., Brereton, T., Chamberlain, D., Heliölä, J., Herrando, S., Julliard, R., Kuussaari, M., Lindström, Å., Roy, D.B. *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. *et al.* (2012) Indirect effects of parasites in invasions. *Functional Ecology*, **26**, 1262–1274.

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.

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.

Kerbiriou, C., Le Viol, I., Jiguet, F. & Devictor, V. (2009) More species, fewer specialists: 100 years of changes in community composition in an island biogeographical study. *Diversity and Distributions*, **15**, 641–648.

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

Leathwick, J. (2002) Intra-generic competition among Nothofagus in New Zealand's primary indigenous forests. *Biodiversity & Conservation*, **11**, 2177–2187.

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 re-

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

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

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

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.*, **37**, 637–669.

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

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

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

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

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

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

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

Schweiger, O., Heikkinen, R.K., Harpke, A., Hickler, T., Klotz, S., Kudrna, O., Kühn, I., Pöyry, 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.

Taylor, K. (2009) Biological Flora of the British Isles: *Urtica dioica* L. *J Ecol.*, **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. *Annu. Rev. Entomol.*, **51**, 187–208.

Walther, G., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T., Fromentin, J., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.

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., Pellissier, L., Lenoir, J., Damgaard, C.F., Dormann, C.F., Forchhammer, M.C., Grytnes, J.A., Guisan, A. *et al.* (2013) The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews*, **88**, 15–30.

# Supporting information

**Appendix S1.** Data description and consideration of biases.

**Appendix S2.** Table showing the coordinates of each variable on the first three axes of the PCA-env and contribution of the axes in percentage of the total variance.

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

# Tables

Table 1: Showing niche overlap (D) within species over time (time shift) and between species in each period (species interactions) in Skåne and Norrtr´om, respectively, with the associated P-values obtained from the tests of niche equivalency and similarity.

| 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* | 0.75 | 0.004 | 0.002 | 0.032 |
| | | P1 -P2 | *A. io* | 0.81 | 0.004 | 0.002 | 0.004 |
| | Species interactions | P1 -P1 | *A. urticae -A.io* | 0.90 | 1 | 0.002 | 0.002 |
| | | P2 -P2 | *A. urticae -A. io* | 0.88 | 0.044 | 0.002 | 0.002 |
| | | P2 -P2 | *A. urticae -A. levana* | 0.69 | 0.004 | 0.002 | 0.002 |
| | | P2 -P2 | *A. io -A. levana* | 0.68 | 0.004 | 0.002 | 0.002 |
| Norrström | Time shift | P1 -P2 | *A. urticae* | 0.88 | 0.004 | 0.002 | 0.002 |
| | | P1 -P2 | *A. io* | 0.86 | 0.004 | 0.002 | 0.002 |
| | Species interactions | P1 -P1 | *A. urticae -A. io* | 0.91 | 0.036 | 0.002 | 0.002 |
| | | P2 -P2 | *A. urticae -A. io* | 0.89 | 0.004 | 0.002 | 0.002 |

# Figures

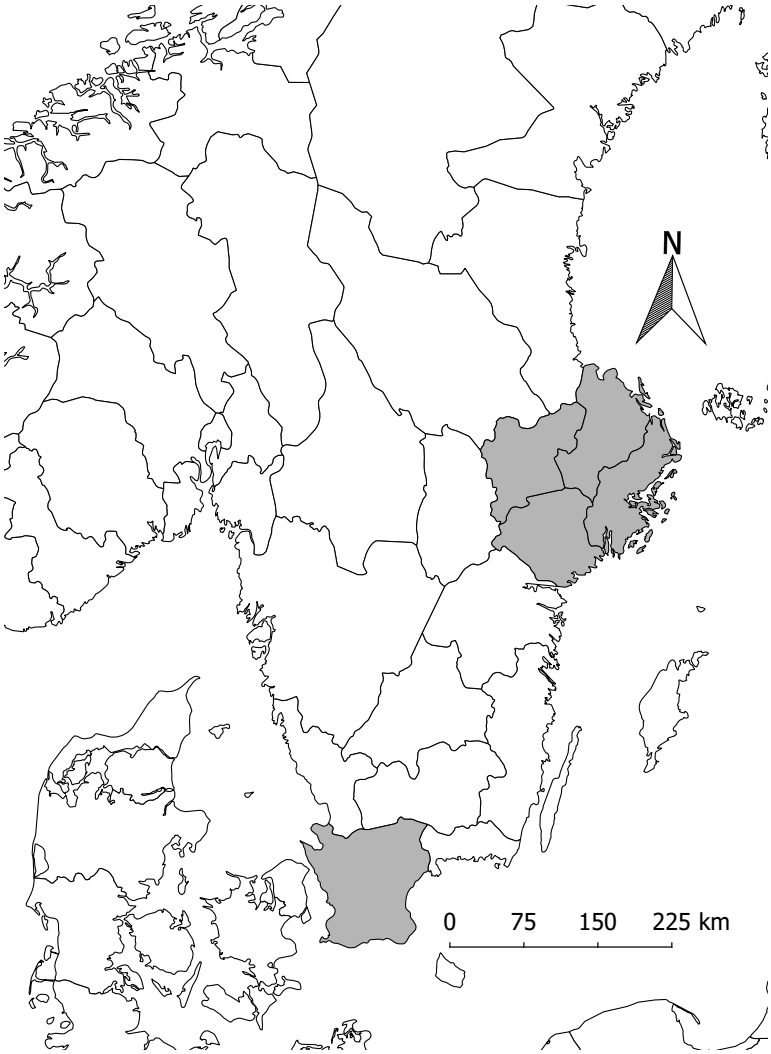


Figure 1: Map of the two study-regions, corresponding to the county of Skåne in Southern Sweden and the Norrström drainage basin in Central Sweden.

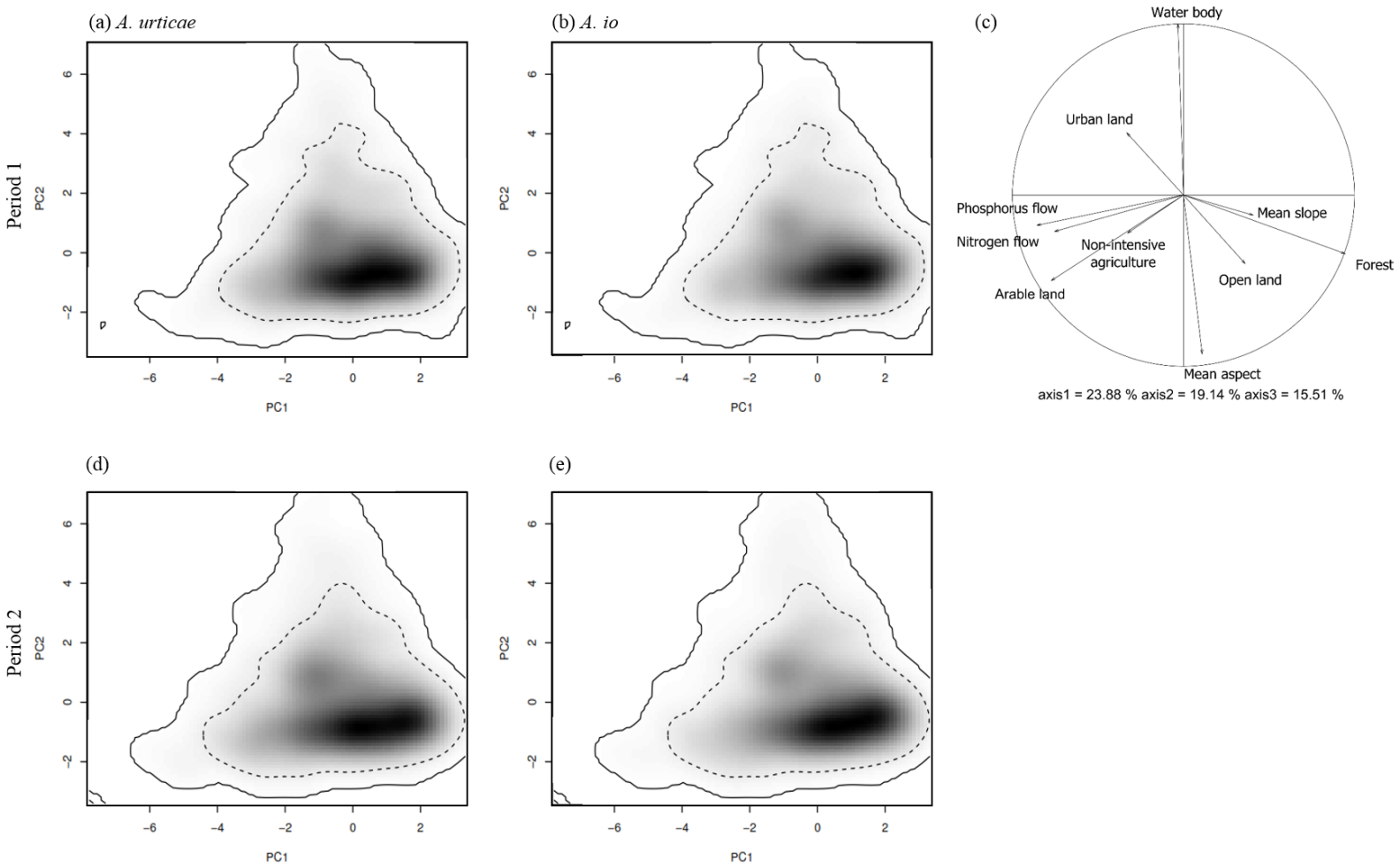


Figure 2: Density of species occurrence across the two-dimensional environmental space describing the Norrström region. In columns are the densities of occurrence of (a & d) *Agais urticae* and (b & e) *Agais io* and for each period (in rows). The black gradient corresponds to the increase in the density of occurrence of the species. The solid line corresponds to the limit of the environmental space available. The dashed line corresponds to the 50% more frequent available environmental conditions. (c) Correlation circle showing the contribution of the different variables to the two main axes of the PCA, which describe the environmental space in Norrström.

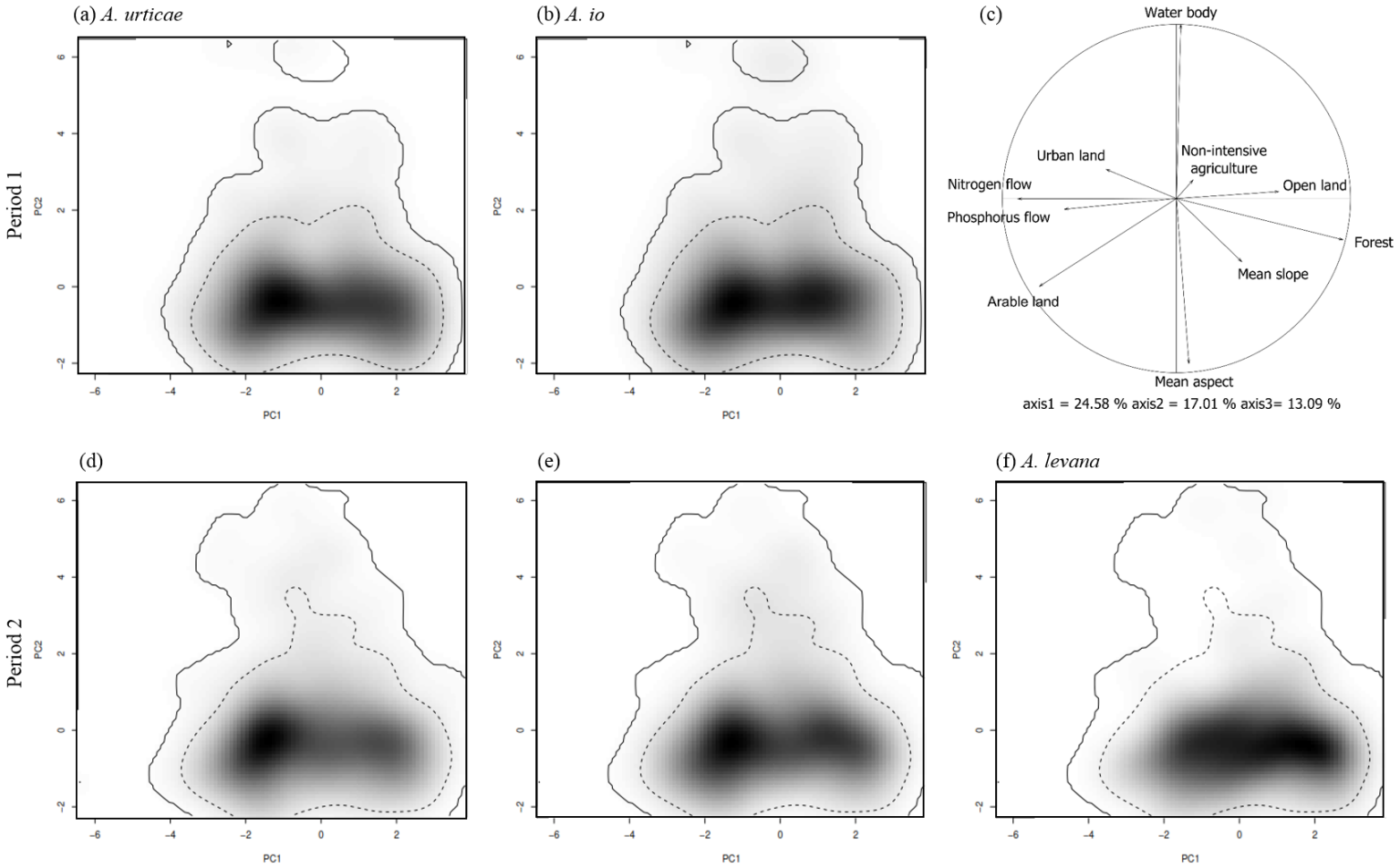


Figure 3: Density of species occurrence across the two-dimensional environmental space describing the Skåne region. In columns are the densities of occurrence of (a & d) *Agais urticae*, (b & e) *Agais io* and (f) *Araschnia levana* and for each period (in rows). Note that *A. levana* is only present in Skåne in the second period. The black gradient corresponds to the increase in the density of occurrence of the species. The solid line corresponds to the limit of the environmental space available. The dashed line corresponds to the 50% more frequent available environmental conditions. (c) Correlation circle showing the contribution of the different variables to the two main axes of the PCA, which describe the environmental space in Skåne.

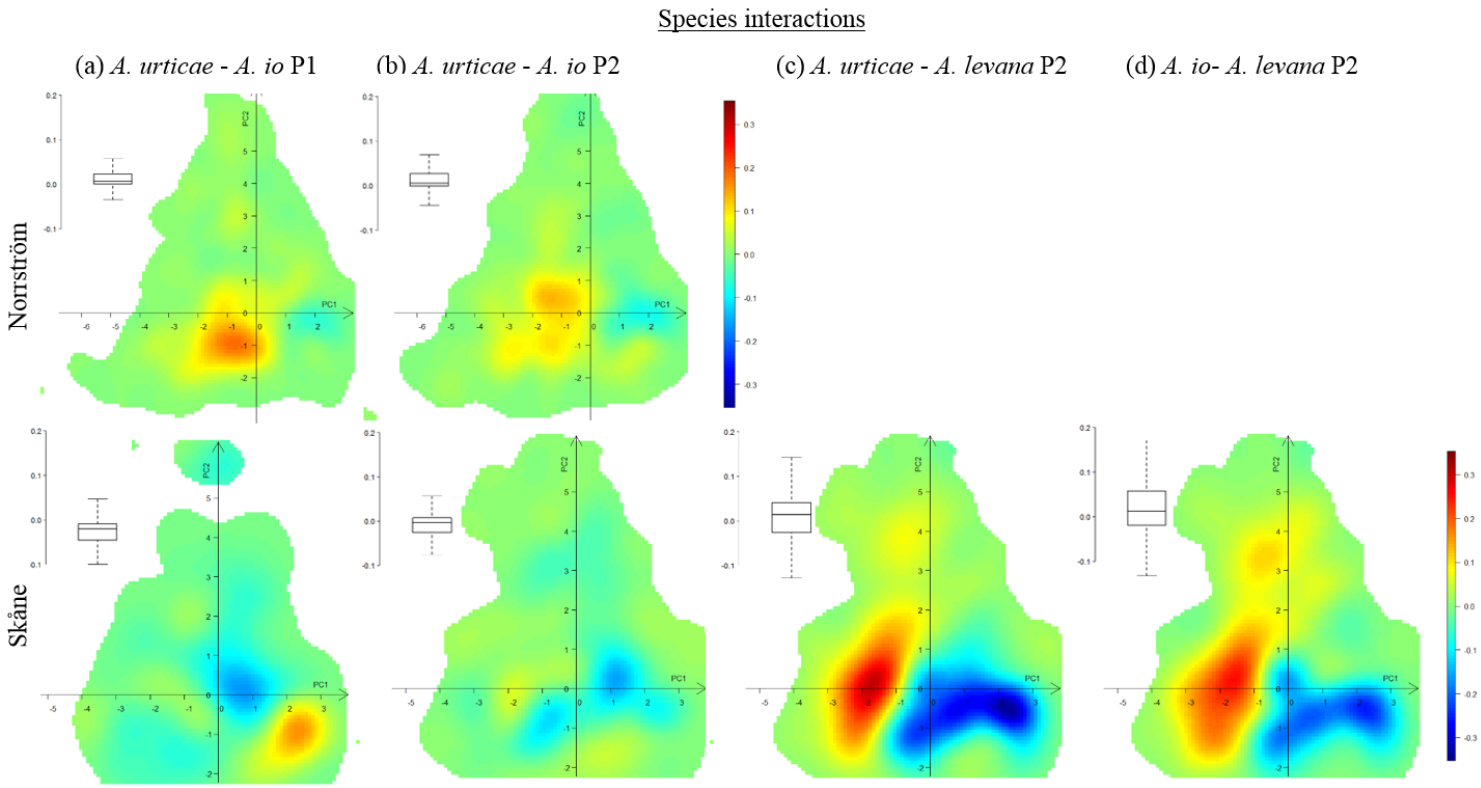


Figure 4: Plots of the differences in density of occurrence, for each region and time-period, between species. In columns are represented the differences in the density of occurrence of: (a) *Agais urticae* and *Agais io* in the first period, (b) *A. urticae* and *A. io* in the second period, (c) *A. urticae* and *A. levana* in the second period and (d) *A. io* and *A. levana* in the second period, and for each region (in rows), Norrström and Skåne respectively. 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 associated with each graph shows the variability of the differences observed across the available environment. The larger the box is the more contrasting the species are in their distribution. The values of niche overlap between the two species are also indicated.

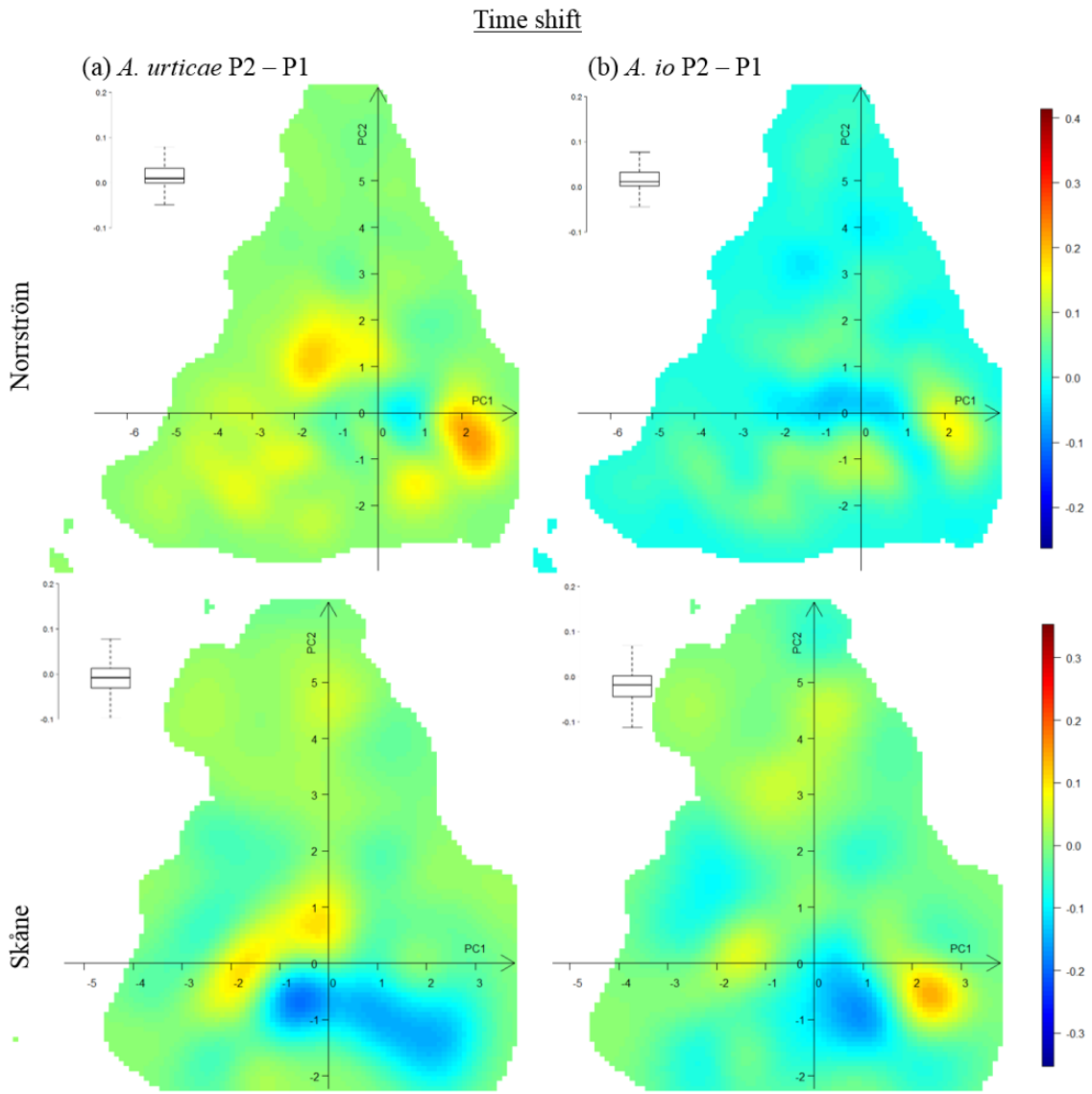


Figure 5: Plots of the differences in density of occurrence of each species over time, and for each region respectively. In columns are represented the differences in the density of occurrence of (a) *Agais urticae* and (b) *Agais io* over time and for each region (in rows), Norrström and Skåne respectively. 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 associated with each graph shows the variability of the differences observed across the available environment. The larger the box is, the more contrasting the species distributions are. The values of the overlap in species niche over time are also indicated.