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Climatic Niche Differentiation between the Invasive Hornet *Vespa velutina nigrithorax* and Two Native Hornets in Europe, *Vespa crabro* and *Vespa orientalis*

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Abstract: The introduction and expansion of the Asian yellow-legged hornet (*Vespa velutina nigrithorax*) in Europe poses concern for multiple reasons, including biodiversity conservation. In addition to the predation of native insects (e.g., bees and wasps), this species may compete with native hornets due to an overlap of their climatic and trophic niches. The aim of this study is to investigate the realised climatic niche of *V. v. nigrithorax* and its response to climatic conditions and to evaluate the degree of overlap with the niches of the two native *Vespa* species present in Europe, *Vespa crabro* and *Vespa orientalis*. The niches of both native species partially overlap with the niche of the invasive species (Schoener's D, 0.43 for *V. crabro* and 0.28 for *V. orientalis*), although some differences can be detected. *V. crabro* appears to be more adapted to cold and dry conditions than the invasive species, and *V. orientalis* is more adapted to arid climates. These differences may provide a competitive advantage to both native species in areas with a lower environmental suitability for *V. v. nigrithorax*, in the probable event that this species continues to spread, reaching all areas predicted to be suitable in Europe and in the Mediterranean basin.

Keywords: Asian yellow-legged hornet; European hornet; oriental hornet; Vespidae; competition; invasive wasps; climatic niche; multivariate niche analysis

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1. Introduction

The Asian yellow-legged hornet, *Vespa velutina*, is a Hymenoptera of the genus *Vespa* native to Southeast Asia [1]. Among the different subspecies present in Asia [2], the subspecies *V. v. nigrithorax* has been accidentally introduced through freight transport in other areas beyond its native range [3], namely Europe [4], South Korea [5] and Japan [6]. After its establishment in France in 2004, *V. v. nigrithorax* started to spread and by 2022 the species was observed in several European countries. Chronologically, these are France, Spain, Portugal, Belgium, Italy, Germany, the UK and Channel Islands, the Netherlands, Switzerland and Luxembourg [7].

The introduction of an invasive alien species can generate a range of environmental [8] and socio-economic impacts [9] of different magnitudes, and this may also occur with *V. v. nigrithorax* [10,11]. As many other eusocial hornets, *V. v. nigrithorax* is a generalist predator of insects, having a prey spectrum that encompasses bees (honey and wild bees), flies, wasps (mainly small size species of the genera *Vespula* and *Polistes*) and other taxa [12]. Predation toward honey bees weakens bee colonies and may lead to their collapse [13], with economic impacts on the beekeeping industry [11]. Predation toward other native insects may affect their abundance, although declines at the population level have yet to be demonstrated. Moreover, *V. v. nigrithorax* may jeopardize the ecological balance between species with effects also on ecosystems' services, as was shown for the pollination service [14].

The introduction of *V. v. nigrithorax* is also of concern for the conservation of other native wasp species that can be affected by competition mechanisms, particularly hornets of the genus *Vespa* with which the invasive species may share similar climatic or trophic niches [10]. Competition between hornets could occur for several reasons, notably for the use of space, including competition for colony foundation, or resources, including competition for prey [1]. For example, it has been demonstrated that *V. v. nigrithorax* could compete with other *Vespa* species in the invaded range of Asia [15,16]. Competition has also been supposed in Europe toward the European hornet *Vespa crabro*, despite in-field confirmations still lacking [17]. The reasons behind this hypothesis are the following: a substantial overlap in the trophic niches [18]; higher values in activity, boldness and exploration scores for the invasive species [19]; partial overlapping of the seasonal phenology, in which the invasive species could be facilitated by an earlier emergence of *V. v. nigrithorax* queens in spring [20]; and the precocity and higher potential fecundity of *V. v. nigrithorax* queens [21].

Another factor that may modulate competition between a native and an invasive species is the response of both species to the range of climatic conditions in the areas where the two species are occurring [22]. *V. v. nigrithorax* has demonstrated that it is well-adapted to the many climates present in Europe and, based on species distribution models, its potential distribution may range from Portugal to Italy and the Balkans as southern limits (including coastal Mediterranean areas of Africa), to the British Isles, Denmark and some coastal areas of Scandinavia as northern limits [23,24]. Therefore, if *V. v. nigrithorax* will be able to reach all the areas predicted to be suitable in Europe, it is possible that competition could occur with both native hornets, *V. crabro* and *Vespa orientalis*. Nevertheless, the knowledge on the ranges and climatic niches of the two native species, and their degree of overlap with the invasive hornet, is currently limited, although this information is important for evaluating the population status and effects after the *V. v. nigrithorax* invasion.

Consequently, this study aims to investigate the distribution of *V. v. nigrithorax*, *V. crabro* and *V. orientalis* in the European and Mediterranean areas predicted to be suitable for the invasive species to understand if the two native species may be favoured—or disadvantaged—over the invasive species under specific climatic conditions. This will be achieved by (i) characterising the realised climatic niches of the three species, (ii) evaluating the extent of their overlap and (iii) assessing the presence of differences in the current areas of co-occurrence.

2. Materials and Methods

2.1. Data Acquisition and Refinement

The records used to estimate the niches of the three species were obtained from the Global Biodiversity Information Facility [25–27]. Records of *V. v. nigrithorax* in the invaded range were integrated with data collected directly by the authors (2895 records for Italy, www.vespavelutina.eu accessed on 10 August 2021) together with information available from the literature [28,29] and from other online sources of information (British Beekeepers Association for UK and Channel Islands records).

Most GBIF records of the three species lack a differentiation between adults and nests. However, the spatial resolution at which analyses were performed is supposed to be higher than the action range of adults estimated in Europe [30,31], thus compensating for this lack of differentiation.

Collected data for the three species were cleaned by removing (i) wrong records, (ii) records without coordinates, (iii) duplicates, (iv) records with low coordinate precision (greater than 5 and 1 km, respectively, accordingly to the resolution of the two niche analyses performed) and (v) observations collected before the 1990 (these records were few and imprecise). This process generated 24,104 records for *V. velutina*, 28,330 records for *V. crabro* and 363 records for *V. orientalis* globally (Figure 1 and Table S1).

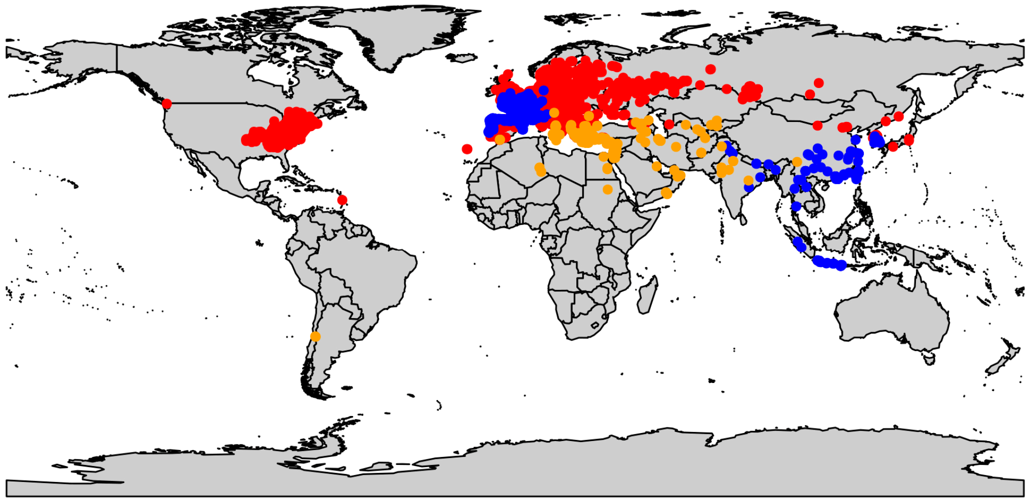

Figure 1. Global distribution of *Vespa velutina* (blue), *V. crabro* (red) and *V. orientalis* (orange). The temporal range of the data is 1990–2021.

Because *V. v. nigrithorax* is the only subspecies introduced in Europe [3], we limited the analyses to the western palearctic and saharo-arabian zoogeographic regions (from here on the study area) (Figure 2), to avoid introducing values of climatic variables associated with other subspecies that may be adapted to different climate conditions. This downscaled the number of records for the three species (see Table S1 for details on the number of records used at each step of the analyses).

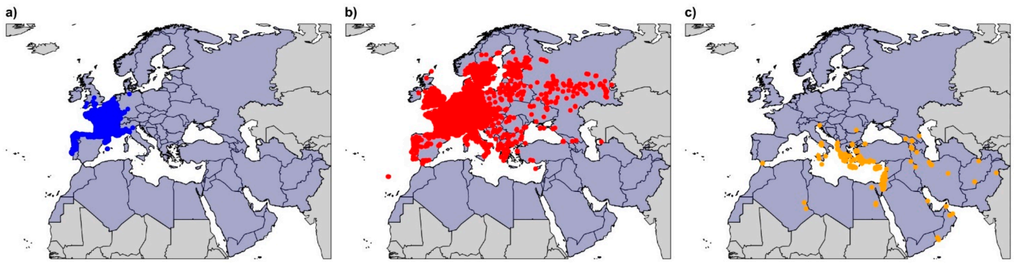

Figure 2. Distribution of *Vespa velutina nigrithorax* (**a**), *V. crabro* (**b**) and *V. orientalis* (**c**) in the western palearctic and saharo-arabian zoogeographic region (violet area of the map). The temporal range of the data is 1990–2021.

2.2. Climatic Niche Analysis for V. v. nigrithorax, V. crabro and V. orientalis at the Study Area Level

A thinning procedure was implemented on the records of the three species in the study area to cope with sampling biases (Table S1), by using the spThin R package [32] with a thinning distance of 10 km [33]. Latitudinal differences in the distribution of records for the three species were assessed with a Kruskal–Wallis test followed by a Dunn's test for multiple comparisons.

The niches of the three species were estimated by analysing the current climatic characteristics associated with the distribution data of *V. v. nigrithorax*, *V. crabro* and *V. orientalis*. For this purpose, the following variables were considered: (i) WorldClim bioclimatic variables (https://www.worldclim.org accessed on 10 December 2021) at 5 arc-minutes in resolution (11 variables associated with temperature and 8 variables associated with precipitation); (ii) elevation above sea level derived from the elevatr R package at a zoom level of 4 (that corresponds with a resolution comparable to the one of WorldClim); and (iii) aspect and slope, which were derived from the elevation raster.

The climatic niches of the three species were estimated following the procedure developed in previous studies [34], using the PCA-env approach that considers the climatic conditions associated with occurrence data calibrated with the conditions of the background environment. The latter were derived by extracting the climatic values in a buffer area of 100 km around the species observation limits (Figure S1) (ENMTools R package) [35]. PCA-env was implemented with the dudi.pca of the ade4 R package [36]. The climatic niche of the invasive species (*V. v. nigrithorax*) was compared with the niches of the two native *Vespa* species (*V. crabro* and *V. orientalis*), by plotting the niches using the ecospat R package [37] and by calculating their overlap with Schoener's D metric [38]. This index ranges from 0 (no overlapping) to 1 (complete overlapping).

For each considered variable, the overlapping of the density functions between the invasive and the two native hornets was estimated with a bootstrapping approach (1000 bootstrap draws) with the overlapping R package, while differences were assessed with a Wilcoxon test with Bonferroni correction.

2.3. Climatic Niche Analysis for V. v. nigrithorax and V. crabro in the Areas of Co-Occurrence

A fine scale analysis of climatic characteristics in relation to occurrence data was implemented in the areas of co-occurrence of *V. v. nigrithorax* and *V. crabro* to assess if the distribution of the invasive and the native species may already vary across the current range of the invasive species. This allows us to understand the degree of overlap between the niches of the two species in the range already colonised by *V. v. nigrithorax*, which is important information to deepen the knowledge on a possible competition effect between the two species. In contrast to the previous niche analysis at the study area level, this analysis was not implemented for *V. orientalis* because at the time the assessment was carried out, its range did not overlap with the range of the invasive species.

The area of co-occurrence was defined as the 100 km buffer area that encompasses all *V. v. nigrithorax* records within the main colonised countries of Europe, namely, France, Spain, Portugal, Italy and Belgium (Figure S2). The other countries (Germany, UK, Switzerland, Luxembourg and the Netherlands) were not included to avoid a bias due to a lower number of records of *V. v. nigrithorax* than records of *V. crabro*.

The variables that were considered for this second assessment were the ones previously used for the niche analysis at the study area level but increased in resolution: (i) WorldClim bioclimatic variables at 30 s in resolution; (ii) elevation above sea level at a zoom level of 7; and (iii) aspect and slope, which were derived from the elevation raster. Due to the higher resolution of these variables, the thinning distance was reduced to 1 km (Table S1).

The procedure previously described at the study area level for estimating the overlap of the niches was repeated for the analysis in the areas of co-occurrence. Considering that the conditions of the background environment, in this case, are not different between *V. v. nigrithorax* and *V. crabro*, the climatic niches of the two species were estimated using the PCA-occ approach [34].

3. Results

The distribution ranges of the three *Vespa* species in the study area tend to vary between species according to the latitudinal gradient, despite latitude overlaps being present (Figure 3). Generally, the *V. crabro* range is shifted to northern latitudes, the *V. orientalis* range to southern latitudes and the *V. v. nigrithorax* range falls in intermediate latitudes between the other two species (Kruskal–Wallis test: $H = 2216$, $df = 2$, $p < 0.001$; Dunn test with Bonferroni correction: $p < 0.001$ between all pairwise comparisons).

3.1. Climatic Niche Characterisation and Overlapping at the Study Area Level

The PCA-env approach allowed us to estimate the realised climatic niche of *V. v. nigrithorax* in Europe and compare it with those of *V. crabro* and *V. orientalis* (Figure 4). The first two principal components of both PCA-env explain most of the variability in the data (the overall explained variance is 63.7% for the PCA-env between *V. v. nigrithorax* and *V. crabro*, and 62.8% for the one between *V. v. nigrithorax* and *V. orientalis*).

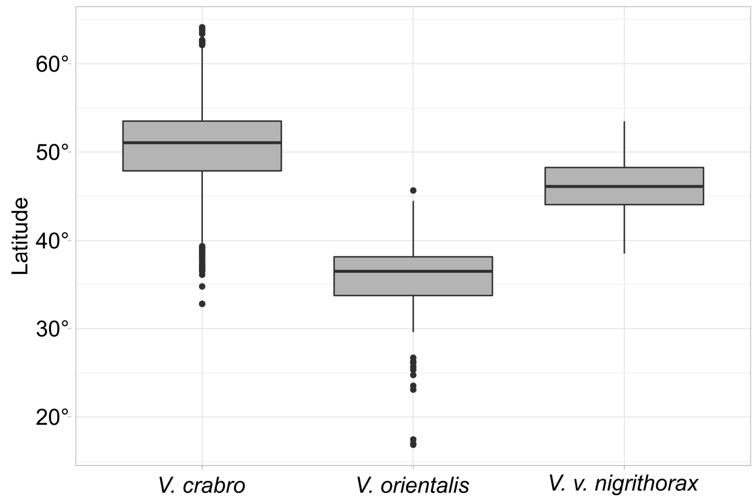

Figure 3. Distribution of *Vespa crabro*, *V. orientalis* and *V. v. nigrithorax* records along the latitudinal gradient of the study area, after considering the sampling bias.

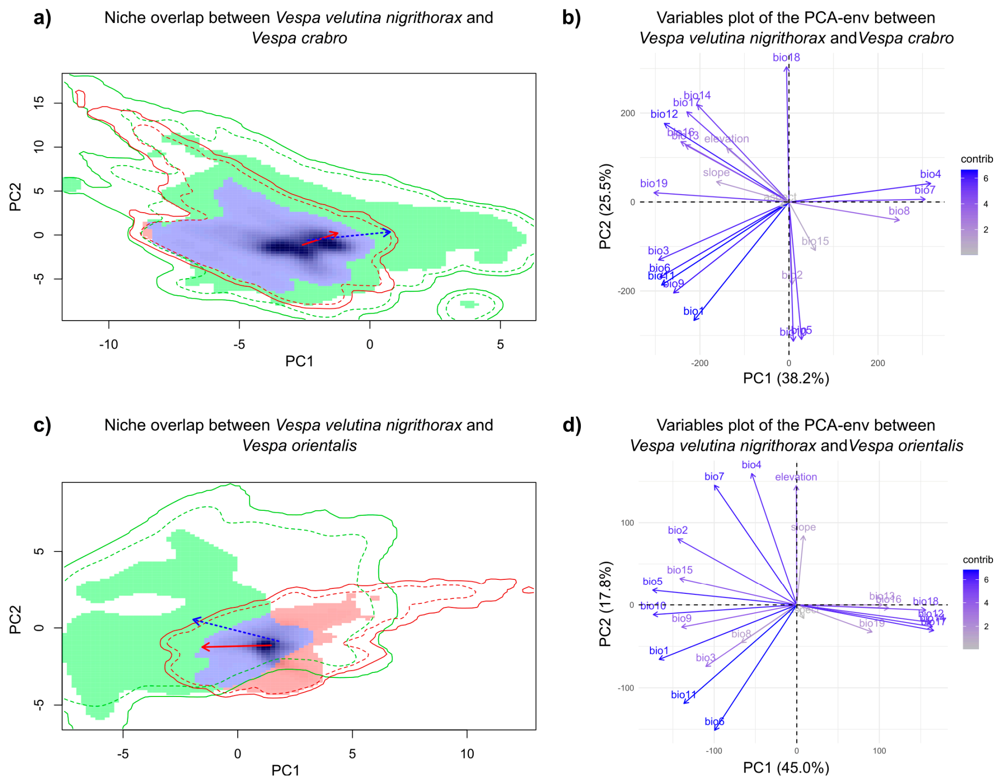

Figure 4. Results of the climatic niche analysis (PCA-env) at the study area level. (**a**,**c**) show the realised climatic niches of *Vespa velutina nigrithorax* (red) and the one of the two native species (green), respectively *V. crabro* and *V. orientalis*. Niche overlap is highlighted in blue. The solid and dashed contour lines illustrate, respectively, 100% and 50% of the available (background) environment. Arrows represent how the centre of the niche (red solid lines) and of the background (blue dashed line) change between species. (**b**,**d**) represent the variables plot of the PCA-env analysis along the first two principal components (PC1 and PC2).

The overlap in the niches between native and invasive species was higher with *V. crabro* (D = 0.43) than with *V. orientalis* (D = 0.28). Generally, the niche of *V. crabro* is shifted more toward areas with low values in temperature and precipitation than the one of *V. v. nigrithorax*, and high temperature ranges, both annual and seasonal (Figures 4a,b and 5a,b). On the contrary, the niche of *V. orientalis* is shifted toward areas with higher temperatures and lower precipitation than the one of *V. v. nigrithorax*, with high precipitation seasonality (Figures 4c,d and 5c,d). The density plots of each variable are reported in the supplementary materials (Figures S3–S8).

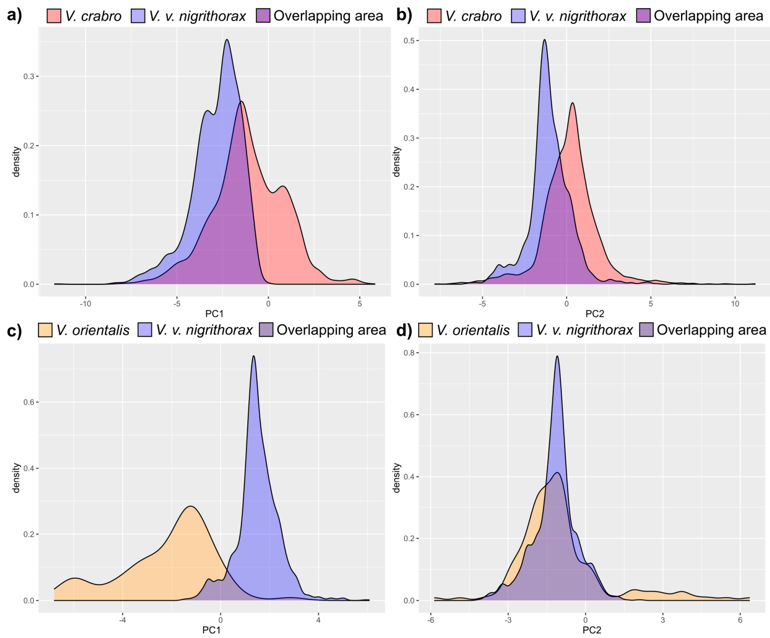

Figure 5. Density plots of the first two components (PC1 and PC2) of the PCA-env analyses between *Vespa velutina nigrithorax* (blue) and the two native *Vespa* species, respectively *V. crabro* (red, **a**,**b**) and *V. orientalis* (yellow, **c**,**d**).

The variables that show the lowest degree of overlap between *V. v. nigrithorax* and *V. crabro* are the annual mean temperature (Bio1) and the isothermality (Bio3), which both present values lower than 30% of overlap. Simultaneously, the comparison between *V. v. nigrithorax* and *V. orientalis* shows that 14 variables had a degree of overlap lower than 30%, indicating a higher divergence of the niches (Table 1).

Table 1. Overlapping of the density functions among species in the study area (*Vespa velutina nigrithorax* versus, respectively, *V. crabro* and *V. orientalis*) and in the areas of co-occurrence (*V. v. nigrithorax* versus *V. crabro*). For each variable, the percentage of overlapping and the standard error (SE) of the estimated overlap is reported (the mean and the standard deviation values are reported in Table S2).

Variables	Study Area				Area of Co-Occurrence	
	Overlapping VVN-VC		Overlapping VVN-VO		Overlapping VVN-VC	
	%	SE	%	SE	%	SE
Bio 01—Annual Mean Temperature (°C)	0.27 *	0.01	0.10 *	0.02	0.54 *	0.02
Bio 02—Mean Diurnal Range (°C)	0.48 *	0.01	0.50 *	0.03	0.52	0.02
Bio 03—Isothermality (%)	0.28 *	0.01	0.37 *	0.03	0.65 *	0.02
Bio 04—Temperature Seasonality (°C)	0.36 *	0.02	0.53 *	0.04	0.48 *	0.02
Bio 05—Max Temperature of Warmest Month (°C)	0.42 *	0.01	0.08 *	0.01	0.56	0.02
Bio 06—Min Temperature of Coldest Month (°C)	0.36 *	0.01	0.14 *	0.02	0.46 *	0.01
Bio 07—Temperature Annual Range (°C)	0.64 *	0.01	0.59 *	0.04	0.53 *	0.02
Bio 08—Mean Temperature of Wettest Quarter (°C)	0.49 *	0.01	0.39 *	0.03	0.51 *	0.01
Bio 09—Mean Temperature of Driest Quarter (°C)	0.32 *	0.01	0.08 *	0.01	0.50 *	0.02
Bio 10—Mean Temperature of Warmest Quarter (°C)	0.40 *	0.01	0.06 *	0.01	0.54 *	0.02
Bio 11—Mean Temperature of Coldest Quarter (°C)	0.33 *	0.01	0.13 *	0.02	0.42 *	0.01
Bio 12—Annual Precipitation (mm)	0.64 *	0.01	0.43 *	0.03	0.66 *	0.02
Bio 13—Precipitation of Wettest Month (mm)	0.72 *	0.02	0.23 *	0.02	0.64 *	0.02

Table 1. *Cont.*

Variables	Study Area				Area of Co-Occurrence	
	Overlapping VVN-VC		Overlapping VVN-VO		Overlapping VVN-VC	
Bio 14—Precipitation of Driest Month (mm)	0.54 *	0.01	0.06 *	0.01	0.81 *	0.02
Bio 15—Precipitation Seasonality (mm)	0.63 *	0.02	0.06 *	0.01	0.56 *	0.02
Bio 16—Precipitation of Wettest Quarter (mm)	0.80 *	0.02	0.25 *	0.02	0.59 *	0.02
Bio 17—Precipitation of Driest Quarter (mm)	0.55 *	0.01	0.04 *	0.01	0.66 *	0.02
Bio 18—Precipitation of Warmest Quarter (mm)	0.54 *	0.01	0.06 *	0.01	0.65 *	0.02
Bio 19—Precipitation of Coldest Quarter (mm)	0.50 *	0.01	0.26 *	0.02	0.55 *	0.02
Elevation (m a.s.l.)	0.82 *	0.02	0.57	0.04	0.72 *	0.02
Aspect (degrees)	0.82 *	0.02	0.76	0.04	0.91	0.02
Slope (degrees)	0.87 *	0.02	0.27 *	0.02	0.82 *	0.02

VVN: *V. v. nigrithorax*; VC: *V. crabro*; VO: *V. orientalis*. The symbol (*) indicate a significant difference among density functions accordingly to a Wilcoxon test with Bonferroni correction.

3.2. Climatic Niche Analysis in the Areas of Co-Occurrence of *V. v. nigrithorax* and *V. crabro*

Despite the higher overlap in the climatic variables observed between *V. v. nigrithorax* and *V. crabro* in the areas of co-occurrence than at the study area level (Table 1), the realised niches of the two species in the areas of co-occurrence were not totally equal (D = 0.43) (Figure 6). The niche of *V. crabro* appeared to be slightly shifted toward colder areas, in particular those areas with lower values in Bio 6 (minimum temperature of the coldest months), Bio 9 (mean temperature of the driest quarter) and Bio 11 (mean temperature of the coldest quarter) (Figures S9–S11). In fact, for these variables, the mean of *V. crabro* is 0.9 °C (Bio 6), 4.2 °C (Bio 9) and 1.2 °C (Bio 11) lower than the mean of *V. v. nigrithorax* (Table S2). These results are consistent with the results at the study area level. Among the remaining non-bioclimatic variables, a high overlap was observed for the elevation above sea level (72%) and the two derived variables, aspect (91%) and slope (82%) (Tables 1 and S2).

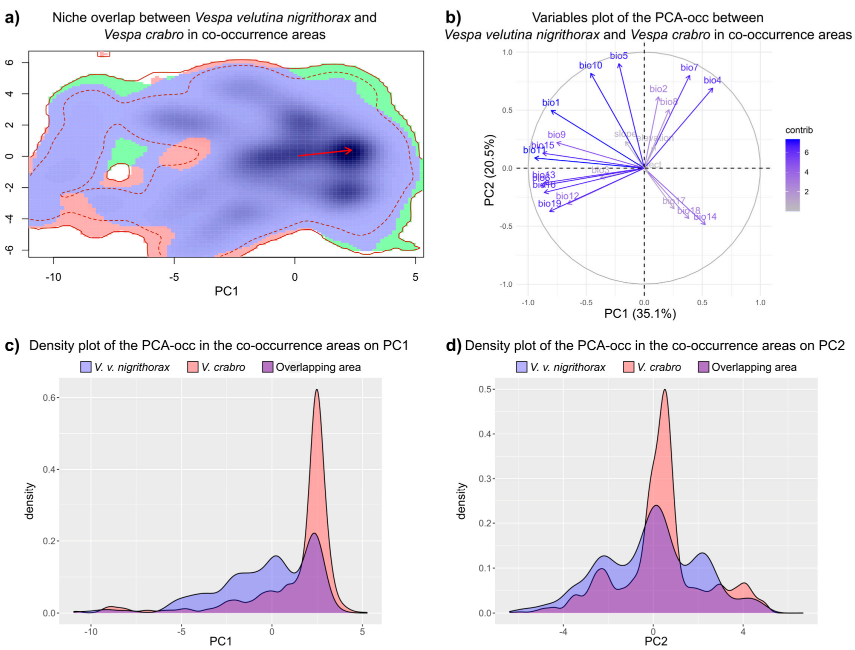

Figure 6. Results of the climatic niche analysis (PCA-occ) in the areas of co-occurrence of *Vespa velutina nigrithorax* and *V. crabro*. (**a**) shows the realised climatic niches of *V. v. nigrithorax* (red) and *V. crabro* (green). Niche overlap is highlighted in blue. The solid and dashed contour lines illustrate, respectively, 100 and 50% of the available (background) environment. The red arrow represents how the centre of the niche changes between species. (**b**) show the variables plot of the PCA-occ analysis along the first two principal components (PC1 and PC2). (**c**,**d**) report the density plots of the PCA-occ along the first two components, respectively, PC1 and PC2.

4. Discussion

This is the first study describing the climatic niches of three hornet species occurring in the western palearctic and saharo-arabian zoogeographic regions, where the two native hornets (*V. crabro* and *V. orientalis*) are potentially threatened by the biological invasion of *V. v. nigrithorax*. Consequently, the results of this study provide information on the climatic niche of *V. v. nigrithorax* in the invaded areas of Europe and quantify its overlap with the niches of the two native *Vespa* species.

The actual distribution of the invasive species along the latitudinal gradient is in an intermediate position between the distribution of *V. crabro* and *V. orientalis*. Moreover, the realised climatic niche of *V. v. nigrithorax* is already partially overlapped with those of the native species, to a greater extent with *V. crabro* than with *V. orientalis*. Therefore, if *V. v. nigrithorax* can colonise all of the areas predicted to be suitable for this species in continental Europe and in the Mediterranean basin [23,24], it is likely that in the near future, the overlap in the distribution ranges could increase both with *V. orientalis* and *V. crabro*.

Although the niches of the three species may correspond to a certain extent, some differences have been detected, both at the study area level and in the areas of co-occurrence. *V. crabro* appears to be more adapted to colder and drier climates than *V. v. nigrithorax*, while *V. orientalis* is more adapted to arid climates. These differences may provide some margins to the native species for avoiding competition with *V. v. nigrithorax*, at least in those areas with less favourable climatic conditions for the invasive species and in the case that *V. v. nigrithorax* does not further expand its niche [39].

Two additional factors, however, should be considered together with the previous considerations, which are the spatial sorting hypothesis and the climatic suitability at the extreme parts of species niches. Spatial sorting suggests that invasive species may face different selective pressures in areas of range expansion, which could favour specific traits such as dispersal and reproduction [40], thus differently affecting competition with native species. On the other hand, in the extreme parts of their niches, native *Vespa* species should probably afford non-optimal conditions for colony development, as observed for *V. orientalis* in arid climates [41]. Therefore, native species could be at an advantage in the extreme parts of their niches due to the low climatic suitability for *V. v. nigrithorax*, but their development (e.g., colony size) could also be limited by the climatic conditions.

The adopted methodological approach compensates for two critical aspects that should be considered when modelling species distribution data: (i) the sampling bias and (ii) the inclusion of data related to an invasive species that is currently under expansion. Sampling bias is a common issue with presence–absence data from citizen scientists that could be mitigated by adopting a thinning approach for filtering the nearest data [42]. Spatial thinning was implemented according to the precision of the coordinates of the records and to the resolution of the selected climatic variables to avoid errors due to spatial autocorrelation, similarly to the approaches already adopted for modelling the niche of other species [33,43,44]. *V. v. nigrithorax* is currently expanding its distribution range in continental Europe and in the Mediterranean basin, according to the suitability models developed at the early stage of invasion [45]. More specifically, *V. v. nigrithorax* expansion could lead to a limited increase of overlapping range areas with *V. crabro* in Germany, Belgium and the Netherlands, whereas the increase of an overlapping area could be with both *V. crabro* and *V. orientalis* in southern Europe, for example, in Italy. Therefore, it is possible that in the near future, the overlap of the niches with native *Vespa* species could change, altering the differences in the response to the climatic variables. For this reason, a fine-scale analysis has been carried out in the current areas of co-occurrence of *V. v. nigrithorax* and *V. crabro*, and the findings are consistent with the niche analysis performed at the study area level. In other words, even if *V. v. nigrithorax* increases its range, the differences in the response to the climatic variables may remain to a certain extent, as demonstrated by analysing the current distribution of the species in the area of co-occurrence.

In the future, the expansion of *V. v. nigrithorax* could also lead to an overlap with the *V. orientalis* European range. Low environmental niche overlap between the species suggests consistent difference in the response to the climatic variables. This result may slightly be biased by the low availability of distribution data of *V. orientalis*. This is likely connected to the countries in which *V. orientalis* is occurring, such as south-eastern European countries and the Middle East, areas where citizen science programs are less developed than northern European countries [46–48]. However, given the high environmental niche differences between *V. v. nigrithorax* and *V. orientalis* and the adaptability of the latter to arid climates [41], we do not expect that the above limitations could lead to significantly higher overlap between the two species.

Climate change may also play an important role in shaping the future competition between *Vespa* species. *V. v. nigrithorax* could further increase its range thanks to climate modifications [49] while, in the northern hemisphere, *V. orientalis* may expand its range toward higher latitudes [50]. These modifications could certainly increase the areas of co-occurrence and thus competition among species.

Nevertheless, the adaptability of the species to the climatic conditions is just one of the factors that might influence the interspecific competition in hornets. Other aspects to be considered are the interspecific hierarchies, the competition for prey items, the temporal overlap in the seasonal phenology and the competition for nesting sites [7].

Interspecific hierarchies among *Vespa* species, including *V. v. nigrithorax*, have been recently studied in an invaded area of Asia by analysing the aggressiveness and body size of the different species [16]. It has been demonstrated that *V. crabro* can outperform *V. v. nigrithorax* in direct fights, due to body size and aggressiveness. This is another factor that could help *V. crabro* populations avoid competition. However, the greater dimension of *V. v. nigrithorax* colonies [51] and the higher number of hornets at foraging sites (e.g., in apiaries) [52] may reduce the advantages that *V. crabro* have in single direct competitions. Information on interspecific hierarchies with *V. orientalis* are not available in the literature, but the smaller body size of this species compared to that of *V. crabro* suggests that *V. orientalis* could be disadvantaged in direct competition with the invasive species.

Hornets are known to be generalist insect predators, therefore, the trophic niche of these three species could correspond partially or totally. The trophic preferences of *V. v. nigrithorax* and *V. crabro* have been investigated in laboratory experiments [18]. The authors found that the preferences of both species highly overlap, with a marked dietary preference for honey bees. Notoriously, *V. orientalis* also prey on honey bees and is considered a nuisance for the beekeepers [53], therefore, it could be assumed that there is a high overlap in the trophic niche and competition at foraging sites for all *Vespa* species considered in this study.

Variations in the seasonal phenology between *V. v. nigrithorax* and *V. crabro* have been studied in France [20], finding that queens of the invasive species emerge from their overwintering sites earlier in spring. This temporal displacement may reduce competition because the two species are not directly competing for food resources at the same time; however, on the other hand, the earlier emergence of *V. v. nigrithorax* queens may favour the invasive species in the selection of nesting sites.

Differences in the locations of nesting sites between species may also influence the interspecific competition. Colonies of the two native species are often located in sheltered places, either subterranean or aerial, such as tree cavities, spaces inside rocks or walls, inside abandoned burrows of small animals, under ceilings or ledges, or inside empty beehives [1]. The colonies of *V. v. nigrithorax* also may be located in these areas (in particular the nests initiated by the queens during spring), leading to a partial overlap of the nesting sites, but more often, they are located (or relocated in the case of secondary nests) in tree canopies [54]. Furthermore, *V. v. nigrithorax* is a species well adapted to urban areas, while *V. crabro* appears to be a species mostly occurring in natural and forest landscapes [5]. Therefore, the differences in the adaptability of the three *Vespa* species to local landscape characteristics is an additional factor that could modulate species competition. Moreover, because the European regulation has set control/eradication measures for *V. v. nigrithorax* as mandatory, these strategies, which include adult trapping and nests' destruction [7], may play a role in driving competition with *V. crabro* in certain areas of co-occurrence.

Understanding how, and to what extent, all of the above-mentioned factors could affect the population of native species will help to understand the mechanisms of interspecific competition posed by the presence of *V. v. nigrithorax* in Europe, although negative impacts due to competition should be assessed by demonstrating an actual decline of native populations over time and/or space. A first effort in this sense has been implemented in Italy [17], but more effort is still needed in the implementation of multiple long-term monitoring programmes of wasp communities.

5. Conclusions

This study provides information on the climatic niches of three *Vespa* species present in continental Europe and in the Mediterranean basin, the invasive Asian yellow-legged hornet, *V. v. nigrithorax*, and two native species with which the invasive hornet might compete, the European hornet *V. crabro* and the oriental hornet *V. orientalis*. Overall, a certain degree of overlap in the (i) climatic niches and in the (ii) distribution of the species in response to climatic variables has been demonstrated. Nevertheless, some important differences were detected: *V. crabro* appears to be a species more adapted to cold and dry climatic conditions, whereas *V. orientalis* is a species more adapted to arid conditions. These differences may provide a margin of advantage to the native species in the case of competition with the invasive hornet, in particular in those areas characterised by a low environmental suitability for *V. v. nigrithorax*.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d15040495/s1, Figure S1: Buffer areas used for the niche analysis of the three species; Figure S2: Records of *V. v. nigrithorax* and *V. crabro* in the area of co-occurrence of the two species; Figures S3–S8: Density plots of the variables used in the niche analyses for *V. v. nigrithorax*, *V. crabro* and *V. orientalis* at the study area level; Figures S9–S11: Density plots of the variables used in the niche analyses for *V. v. nigrithorax* and *V. crabro* in the areas of co-occurrence of the two species; Table S1: Number of records of the three *Vespa* species used for the different sections of the analyses; Table S2: Mean and standard deviation of the climatic variables for the different species at the study area level and in the areas of co-occurrence.

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