



Modeling the effects of climate change scenarios on the potential distribution of *Vespa crabro* Linnaeus, 1758 (Hymenoptera: Vespidae) in a Mediterranean biodiversity hotspot

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ABSTRACT

Climate change poses unprecedented challenges to ecosystems and species, particularly in biodiversity hotspots like the European-Mediterranean regions. The ecological consequences are not easily discernible. Although the influence of climate on plants and vertebrates has been extensively studied, its impact on alien insects, especially social wasps, remains underexplored. To address this gap, this study identifies climatically suitable habitats for *Vespa crabro* under current conditions, projects its potential future distribution, and assesses potential range shifts driven by climate change to guide monitoring programs and management measures. We focused on Sardinia, a Mediterranean island with a heterogeneous morphological, geological, and climatic pattern, where *V. crabro* was accidentally introduced.

We used 316 verified citizen science occurrences, high-resolution bioclimatic variables (40 × 40 m) specifically developed for the island, and two future climate and socio-economic scenarios for two temporal horizons (2040 and 2060) to model climatic suitability using an ensemble framework with three machine learning algorithms: Artificial Neural Networks (ANN), Generalized Boosting Model (GBM), and Random Forest (RF). To ensure reliable predictions, we addressed several technical challenges, including correcting for sampling biases and spatial autocorrelation. The individual models were weighted based on spatial cross-validation performance and combined to obtain the ensemble model.

Performance varied among 150 individual models (3 algorithms × 10 replicates × 5 folds), depending on the algorithms, replicates, and subsets selected for training and testing. RF demonstrated the highest predictive performance, outperforming ANN and GBM. The ensemble model achieved even higher predictive accuracy with Receiver Operating Characteristics (ROC) = 0.95 ± 0.02 and True Skill Statistic (TSS) = 0.78 ± 0.06.

Key factors influencing *V. crabro* distribution included Annual Mean Temperature, Maximum Temperature of Warmest Month, Temperature Annual Range, Precipitation of Driest Month, and Precipitation Seasonality. Currently, climatically suitable habitats are predominantly in the northern part of the island, in most coastal areas, and in specific inland regions, especially those near or inside mountainous areas. Future projections indicate a distribution range contraction by the 2040s and 2060s, primarily driven by extreme variability in precipitation and rising temperatures approaching the species' thermal tolerance limits.

Our study demonstrates the value of integrating citizen science data, high-resolution climate data, and advanced modeling techniques to understand and manage alien species in the context of climate change. It highlights the importance of fine-scale studies to complement broader analyses, providing deeper insight into the impacts of climate change on species distribution, especially in heterogeneous areas like those in the Mediterranean.

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1. Introduction

Climate change presents unprecedented challenges to ecological, environmental, socio-political, and socio-economic systems worldwide (Abbass et al., 2022; Zhang et al., 2022). The changing climate will result in increased temperatures, reduced rainfall, diminished terrestrial water resources on land, and decreased river flow, thus leading to drier soils and more frequent or severe droughts (IPCC, 2022). Climate hotspots, such as the European-Mediterranean regions, are expected to experience warming rates that exceed the global average by 20 % and 50 % for the annual and summer periods, coupled with a 12 % reduction in rainfall under a 3 °C global warming scenario (Carnicer et al., 2022).

These climate alterations have profound ecological implications for species, populations, communities, and ecosystems (Grimm et al., 2008; IPBES, 2019; Schröter et al., 2005). Climate emerges as the predominant driving force behind species distribution shifts (Chen et al., 2011; Huang et al., 2024; Moritz et al., 2008; Román-Palacios and Wiens, 2020; Root et al., 2003; Thuiller et al., 2005a; Thuiller et al., 2005b). Distribution changes of native and non-native species (i.e., alien species, which are species introduced to regions outside their native range) as a response to ongoing climate change have been well-documented (Bellard et al., 2013; Hulme, 2017; Kuczynski et al., 2018; Robinson et al., 2020). In fact, meta-analyses of 334 species and global assessments of 1570 species revealed significant patterns of distribution range shifts aligning with observed climate warming trends throughout the twentieth century, thus providing strong evidence (>95 % confidence level) for a distinct global climate change signal (see Parmesan and Yohe, 2003).

Climate-induced range shifts vary among organisms, dependent on climatic exposure, species sensitivities, and adaptive capacities (Kuczynski et al., 2018; Ramalho et al., 2023), posing challenges for scientists and managers in developing effective management and adaptation strategies for biodiversity conservation and ecosystem resilience. The consequences for alien species are intricate, as climate influence are highly context-dependent and can vary throughout the invasion process (i.e., from initial introduction through establishment and spread) by modifying vectors, pathways, the abiotic features of the invaded environment, and influencing biotic interactions (Bellard et al., 2013, 2018; Kueffer et al., 2013; Novoa et al., 2020; Robinson et al., 2020). The rate and magnitude of these climate change effects on abiotic and biotic features can constrain or favor the invasion success, the post-establishment spread, and the long-term persistence of alien species later on (Hulme, 2017; Novoa et al., 2020; Robinson et al., 2020).

Due to the growing concern about the impacts of climate change, species distribution models (SDMs), also known as habitat suitability models, have been widely used to predict the potential geographic range of species based on presence data and environmental predictors (Elith et al., 2006; Guisan and Thuiller, 2005). However, SDMs face numerous technical challenges, including data retrieval at an appropriate scale, correct data processing, and the selection of appropriate statistical techniques (Chiaverini et al., 2023; Wan et al., 2016; Zhang et al., 2019). Issues such as spatial sampling biases, spatial autocorrelation, and algorithmic complexity and uncertainties must be addressed to obtain reliable predictions (Fourcade et al., 2014; Gutierrez-Velez and Wiese, 2020; Hao et al., 2020; Xu et al., 2024).

The selection of statistical techniques is crucial in SDM studies, as it introduces uncertainties depending on the algorithm employed (Hao et al., 2019, 2020; Marmion et al., 2009). Regression algorithms were used mainly in the early stages of species distribution modeling (Guisan et al., 2002), whereas machine learning algorithms have become more prominent in recent years (e.g., Chiaverini et al., 2023; Stupariu et al., 2022). To mitigate the algorithmic uncertainty, an ensemble approach has been developed. This approach combines multiple algorithms to produce an averaged prediction, which represents the central tendency of the distributions of single individual models (Araújo and New, 2007).

The scale of data (study extent and grain size of data) adds complexity to SDMs. These models reveal patterns and determinants

that vary with the temporal and spatial scale of the environmental predictors used, especially climate data (Gottschalk et al., 2011; Wan et al., 2016). Predictive power diminishes as the grain size becomes coarser, with coarse-grained global datasets failing to accurately predict species distributions in local contexts (Beck et al., 2014; Franklin et al., 2013; Gottschalk et al., 2011; Guisan et al., 2007a, 2007b; Song et al., 2013). Integrating citizen science data, which involves the active participation of the public in collecting and monitoring data for scientific research, can enhance SDM accuracy and extrapolate localized information to broader areas (Bosso et al., 2024; Florence et al., 2020). Most SDM studies have been conducted at the global or mainland scale using broad-grained climate data (from 30 s ~ 1 km² to 10 min ~ 340 km² at the equator) and coarse-grained occurrence records, which may oversimplify patterns and lack fundamental information for effective management (Bazzato et al., 2021; Beck et al., 2014; Bellard et al., 2013; Gottschalk et al., 2011; Gritti et al., 2006; Novoa et al., 2020; Robinson et al., 2020; Song et al., 2013). Fine-scale, high-resolution data are crucial for capturing environmental variability, particularly in complex landscapes (Franklin et al., 2013; Hijmans et al., 2005).

Implementing high-resolution modeling is therefore essential for improving our understanding of ecological systems, particularly in Mediterranean regions where historical climatic and geographical changes, combined with present environmental heterogeneities, have led to high biodiversity and complex biogeographical patterns (Médail, 2017). Such high-resolution models are fundamental for accurately forecasting invasion risks and understanding the spatial and temporal dynamics of alien species distributions, thus supporting the development of monitoring strategies and management actions (Kampichler and Sierdsema, 2018; Peterson, 2003; Peterson and Vieglais, 2001; Roura-Pascual et al., 2009; Thuiller et al., 2005b; van Rees et al., 2022). This is particularly important given the context-dependent nature of biological invasions in the face of climate change (Bellard et al., 2018; Cameron et al., 2016; Kueffer et al., 2013; Novoa et al., 2020; Robinson et al., 2020).

Furthermore, while much research has focused on the effects of climate change on plants and vertebrates, the responses of invertebrate to future climate conditions remain relatively underexplored (Cardoso et al., 2011; Polidori et al., 2020). Invertebrates, like other ectothermic organisms, exhibit heightened susceptibility to climate warming, primarily due to the influence of environmental temperature on their core physiological processes, such as locomotion, growth, and reproduction (Deutsch et al., 2008). Insects represent a major group of alien terrestrial invertebrates (Roques et al., 2009) and exhibit complex responses to climate change. These responses include changes in abundance, phenology, voltinism, morphology, physiology, behavior, and interactions with other species and communities (Musolin and Saulich, 2012). The multifaceted effects of climate change on insects vary with the rate of warming and the specific ecological traits of the species and the region under consideration (Deutsch et al., 2008; Hickling et al., 2006; Reemer et al., 2001; Walther et al., 2002).

Among insects, social hymenopterans (ants, wasps, and bees) are significantly influenced by variations in temperature, rainfall patterns, and humidity, which can affect their abundance and nesting behaviors (Dejean et al., 2011; Menzel and Feldmeyer, 2021). The survival of social hymenopterans may be constrained by low winter soil temperatures or temperatures surpassing their upper thermal limits (Brightwell et al., 2010; Menzel and Feldmeyer, 2021). Nevertheless, social hymenopterans can adapt to warming conditions by modifying their diurnal and seasonal foraging activities and patterns, a trait also observed in invasive or pest species (Menzel and Feldmeyer, 2021). Other social insects could benefit from climate warming, enhancing their potential for expansion and presenting challenges within the context of climate change (Bertelsmeier et al., 2016; Menzel and Feldmeyer, 2021). Alien social hymenopterans have exhibited remarkable success in invading new environments globally (Monceau et al., 2015) due to their proficient dispersal abilities, swift reproductive rates, versatile diets, and robust

competitive abilities against native biota (Beggs et al., 2011; Chapman and Bourke, 2001; Holway et al., 2002).

Several social hymenopterans have been established in Europe, being introduced from other continents into Europe or from continental Europe into various European islands (Rasplus et al., 2010; Roques et al., 2009). The majority of these introductions comprised social wasps, such as voracious generalist predators that are currently spreading throughout Europe (e.g., *Vespa velutina*) or invading European islands, such as *Vespula germanica* in Iceland, *Vespula vulgaris* in the Faroe Islands (Denmark), and *Vespa crabro* and congeneric species (i.e., *V. orientalis*) in Sardinia (Italy) (Pusceddu et al., 2022; Rasplus et al., 2010). Although several social wasps have invaded regions outside their native ranges (Otis et al., 2023), studies identifying the most suitable areas for the distribution and spread of some social wasps have mainly focused on *V. velutina* (Barbet-Massin et al., 2013, 2018; Bessa et al., 2016; Fournier et al., 2017; Herrera et al., 2023; Kim et al., 2021; Robinet et al., 2019; Villemant et al., 2011) or *V. orientalis* (Werenkraut et al., 2022).

The European hornet (*V. crabro*), a predator native to Eurasia, has been introduced to North and Central America (Landolt et al., 2010; Shaw and Weidhaas Jr., 1956), including Canada (Buck et al., 2008; Kimsey and Carpenter, 2012), and Sardinia (Pusceddu et al., 2019). However, to the best of our knowledge, no studies have yet examined the potential distribution and spread of *V. crabro* under climate change scenarios, either in Mediterranean regions or elsewhere. Mediterranean islands are particularly susceptible to the projected impacts of climate change and alien species invasions (Giorgi and Lionello, 2008; Hulme et al., 2008; Russell et al., 2017). Although these dual threats are expected to synergistically affect island ecosystems (Bellard et al., 2013), previous studies have shown that invasion patterns vary across geographic regions, with different taxa exhibiting variable increases or decreases in response to climate change (Bellard et al., 2018; Russell et al., 2017), underscoring the need for further research in these sensitive insular ecosystems.

Given that Sardinia is a critical biodiversity hotspot in the central Mediterranean, the introduction of *Vespa crabro* in 2010, with a limited but expanding distribution in the northern areas of the island (Pusceddu et al., 2019, 2022), causes considerable ecological concern. The potential for this species to establish and spread across Sardinia could have serious implications for the island's ecosystems, particularly due to its predatory nature, competitive interactions (Monceau et al., 2015), and potential impacts on honeybees and endemic insect species (Ikegami et al., 2020).

This study aimed to predict the potential distribution of *Vespa crabro* in Sardinia under current conditions and two future climate projections, each based on different socio-economic scenarios across two temporal horizons (2040 and 2060). We assessed changes in its range size to provide valuable insights to policymakers and managers regarding future vulnerable areas susceptible to this invader, helping to guide monitoring programs and management measures. By combining presence records gathered through a citizen science initiative with high-resolution climate data (fine grain, 40 × 40 m cells) under current conditions, we employed an ensemble approach using three machine learning algorithms. In addition to this approach, we addressed several technical challenges, including correcting for sampling biases and spatial autocorrelation, to ensure reliable predictions. This fine-scale modeling provides a deeper understanding of the potential distribution of *V. crabro*, identifying vulnerable areas within the island's ecosystem. The localized predictions generated by these models are crucial for decision-makers, offering essential support in guiding monitoring and management strategies across different temporal scales and ensuring that policymakers can make informed decisions to mitigate the impact of this alien species.

2. Materials and methods

2.1. Study area

The study was applied in Sardinia (Fig. 1), the third-largest Italian region and the second-largest island in the Mediterranean basin, encompassing about 24,000 km² and a diverse coastline of around 1900 km, featuring various landforms such as cliffs, sandy dunes, and beaches.

The island's extensive territory exhibits a complex and heterogeneous morphological, geological, and climatic pattern. Hills, plateaus, mountains, plains, and coasts are characterized by more than 600 formations and lithostratigraphic units, including Palaeozoic magmatic intrusive units, metamorphic complexes related to Hercynian Orogenesis, Mesozoic and Tertiary sedimentary successions, volcano-sedimentary successions, and Quaternary deposits of various origins (alluvial, aeolian, lacustrine, littoral, and slope movement-related) (Carmignani et al., 2016).

The climate is typically Mediterranean, with mild and relatively rainy winters, and warm and dry summers. High-resolution bioclimate map revealed a heterogeneous climate characterized by two macrobioclimates, four classes of continentality, eight thermotypic horizons, and seven ombrothermic horizons, resulting in 43 different isobioclimates (Canu et al., 2015). This complex and heterogeneous morphological, geological, and climatic pattern contributes to a high rate of endemism and many Potential Natural Vegetation types (sensu Farris et al., 2010).

2.2. Framework

We modeled climatic suitability within an ensemble framework (i.e., consensus modeling or ensemble forecasting), using three machine learning algorithms to address the inherent variability in predictive outcomes observed across different algorithms and individual models in previous studies (Elith et al., 2006; Guillaumot et al., 2019; Guisan and Thuiller, 2005; Hao et al., 2019, 2020; Roberts et al., 2017). The ensemble approach was implemented in R software version 4.0.2 (R core Team, 2020) by following four main modeling steps (Guisan et al., 2017; Peterson et al., 2011): (i) data preparation, (ii) model fitting and (iii) evaluation, and (iv) prediction (Fig. 2).

To improve clarity and consistency in our modeling process, we implemented the ODMAP protocol (Zurell et al., 2020), as detailed in Supplementary Appendix A1. Adopting ODMAP allowed us to align with standardized practices in species distribution modeling, ensuring that our methods are transparently communicated and straightforward to evaluate. This protocol is particularly valuable for addressing potential concerns regarding model transparency and uncertainty, both of which are essential for the broader application and acceptance of models in environmental decision-making (Zurell et al., 2020).

2.2.1. Data preparation

2.2.1.1. Occurrences and pseudo-absences. We obtained the occurrence records of *V. crabro* from a participative science program conducted throughout Sardinia in the Interreg project ALIEM, spanning from 2018 to 2023 (Pusceddu et al., 2019). Citizens were recruited through a variety of channels (i.e., online advertisements, leaflets distributed in public locations, public seminars and meetings, articles published in local newspapers, and informative documents sent via email to municipalities, research centers, environmental organizations, and institutions in Sardinia). The participants were asked to report the presence of nests and adults by sending coordinates and photographic documentation. Furthermore, participants were encouraged to place a homemade funnel-type trap on their own property (e.g., farm) to catch and monitor *V. crabro* adults. The participative science program yielded a total of 316

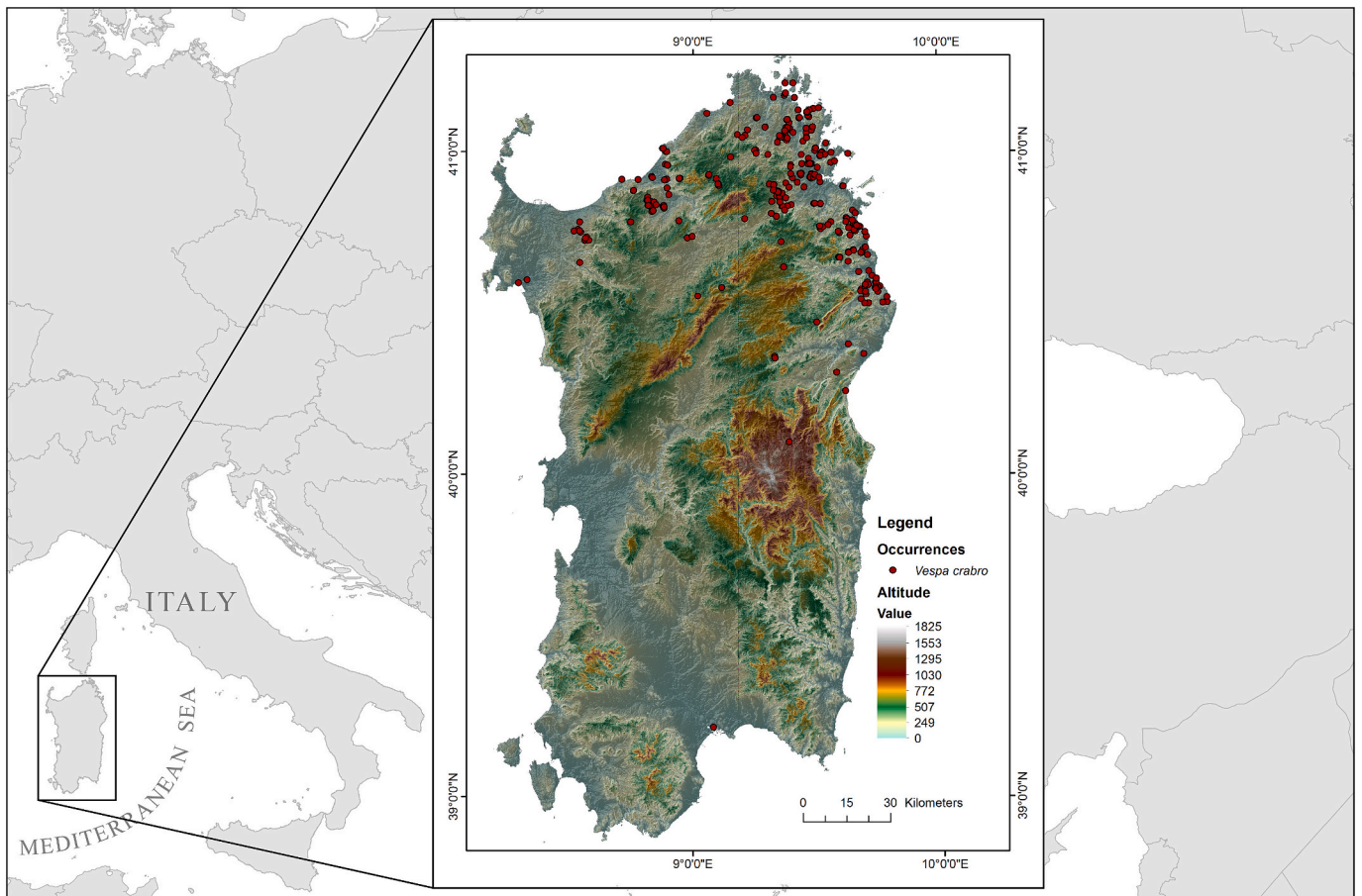


Fig. 1. Study area (Sardinia, Southern Italy) located in the western part of the Mediterranean Basin (coordinate systems WGS 84, EPSG: 4326).

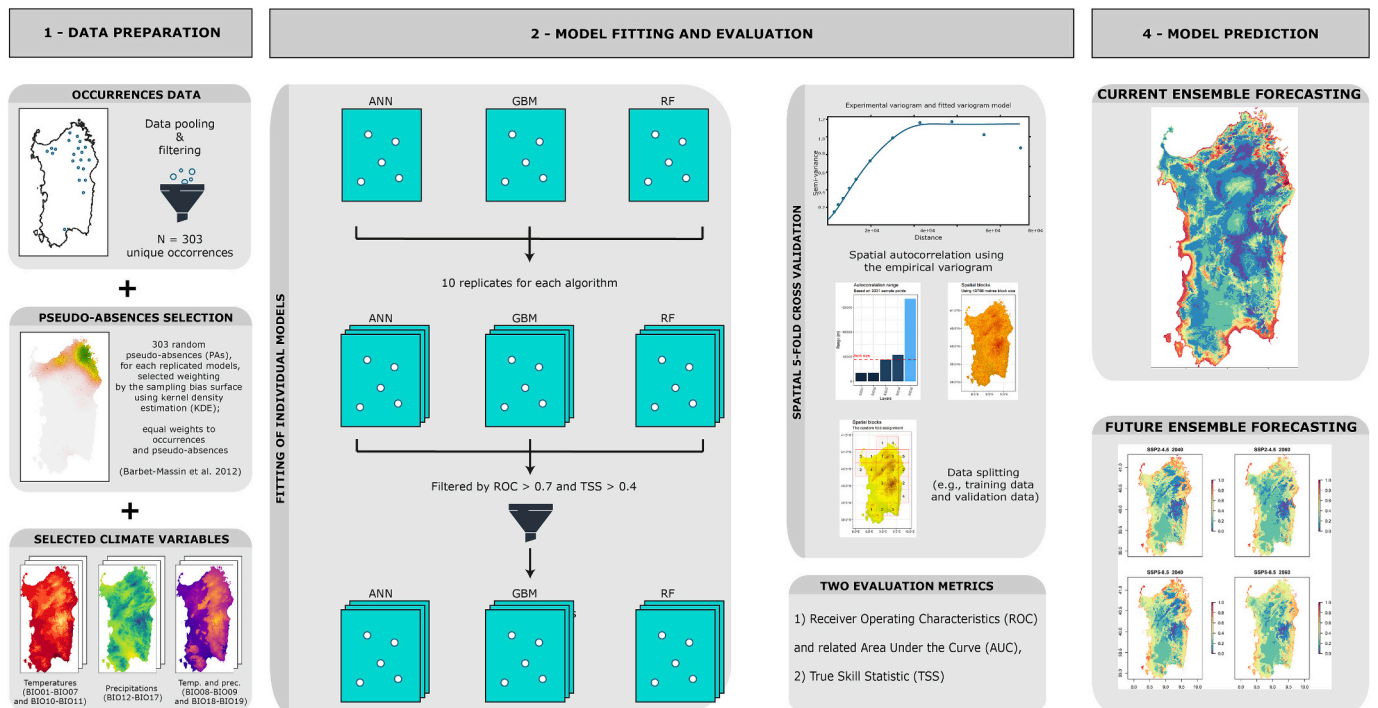


Fig. 2. Flowchart showing the approach adopted to predict *Vespa crabro* distribution under current conditions and two climate and socio-economic scenarios for two temporal horizons (2040 and 2060), using an ensemble framework with three machine learning algorithms: Artificial Neural Network (ANN), Generalized Boosting Model (GBM), and Random Forest (RF).

records of *V. crabro* nests and adults in Sardinia that were verified to ensure the correct species identification. Hence, we filtered the verified occurrence records by removing duplicated ones falling into the same pixel (40 × 40 m cells) of bioclimatic variables, thus obtaining 303 presence data for modeling. The 303 presence data points used for modeling in this study are provided in Supplementary Appendix A2 to enhance transparency and support further research.

Opportunistic species records exhibit significant bias, resulting from non-uniform sampling schemes and spatial biases towards more easily accessible areas (Baker et al., 2024; Bowler et al., 2022; Phillips et al., 2009; Ranc et al., 2017). Failing to address this bias could lead to inaccuracies in model fitting and/or erroneous interpretation and conclusions (Baker et al., 2024; Inman et al., 2021; Ranc et al., 2017). As spatially explicit knowledge of sampling effort is often lacking (Baker et al., 2024; Ranc et al., 2017), we adopted a background manipulation approach that utilizes presence data as background points to approximate unknown sampling effort through a sampling bias surface (Phillips et al., 2009). Under this approach, we generated a sampling bias surface using Kernel Density Estimation (Fig. A.1 in the Appendix A3) in the *sm* package (Bowman and Azzalini, 2021). Then, we selected ten replicate sets of pseudo-absences (Fig. A.1 in the Appendix A3) based on random locations proportional to the sampling bias surface (Phillips et al., 2009).

2.2.1.2. Current and future climate conditions. For the current conditions, we downloaded 19 bioclimatic variables from a high-resolution dataset (40 × 40 m, equivalent to approximately 1.69 arcsec) specifically developed for our study area by previous authors (Bazzato et al., 2021), based on high-quality long-term climate time series (averaged over the 1971–2000 period) of the regional climatic database of the Weather and Climate Department (ARPA Sardegna).

Then, we employed a data-driven variable selection procedure using the *SDMtune* package to reduce model complexity and collinearity within the climate dataset. This process involved iteratively assessing correlations among the most important variables (Vignali et al., 2020). When a correlation was identified, a leave-one-out Jackknife test was performed, starting with a full model, to determine which highly correlated variables ($R > 0.7$; Fig. A.2 in the Appendix A3) had minimal impact on the model (percent contribution <5 %; Fig. A.3 in the Appendix A3) and could be discarded (Vignali et al., 2020). This iterative process continued until correlations among retained variables contributing significantly to the model fell below the defined threshold. Finally, the retained set of uncorrelated bioclimatic variables (Fig. A.4 in the Appendix A3) was evaluated based on the current knowledge of the niche requirements before calibrating individual models (Lioy et al., 2023).

For the future conditions, we considered the bioclimatic variables listed above (Table 1) and two climate and socio-economic scenarios for two temporal horizons (2040 and 2060) as defined by Shared Socio-economic Pathways (SSPs) and the Representative Concentration Pathways (RCPs) (Kriegler et al., 2016; O'Neill et al., 2017; van Vuuren et al., 2017) under the Coupled Model Intercomparison Project Phase 6 (CMIP6; O'Neill et al., 2016). The two scenarios were the following: (1) SSP2–4.5, namely the “middle of the road”, an intermediate management regime in which social, economic, technological trends and greenhouse gas emissions are not expected to deviate significantly from historical patterns and environmental policy implementation will be moderate; (2) SSP5–8.5, namely the “Fossil-fueled Development”, a pessimistic management regime in which a high economic growth combined with material-intensive production and consumption pattern, and elevate greenhouse gas emissions will occur.

Different General circulation models (GCMs) have been developed to project plausible future climate forcing (Fajardo et al., 2020). While there is a general consensus among all GCMs regarding the overall trends, there is significant variance among them (Zappa and Shepherd,

Table 1

Bioclimatic variables considered in the study. The five variables selected by the variable selection procedure are indicated in bold. These variables were used for the calibration of individual models and for the ensemble model construction.

Variable code	Variable name and description	Unit
BIO01	Annual Mean Temperature	°C
BIO02	Mean Diurnal Range (Mean of monthly (max temp – min temp))	°C
BIO03	Isothermality (BIO02/BIO07) (x 100)	%
BIO04	Temperature Seasonality (standard deviation x 100)	Index
BIO05	Maximum Temperature of Warmest Month	°C
BIO06	Minimum Temperature of Coldest Month	°C
BIO07	Temperature Annual Range (BIO05–BIO06)	°C
BIO08	Mean Temperature of Wettest Quarter	°C
BIO09	Mean Temperature of Driest Quarter	°C
BIO10	Mean Temperature of Warmest Quarter	°C
BIO11	Mean Temperature of Coldest Quarter	°C
BIO12	Annual Precipitation	mm
BIO13	Precipitation of Wettest Month	mm
BIO14	Precipitation of Driest Month	mm
BIO15	Precipitation Seasonality (Coefficient of Variation)	%
BIO16	Precipitation of Wettest Quarter	mm
BIO17	Precipitation of Driest Quarter	mm
BIO18	Precipitation of Warmest Quarter	mm
BIO19	Precipitation of Coldest Quarter	mm

2017) due to differences in the modeled data, internal variability and the spatial structure of climate systems (van den Hurk et al., 2014).

Since the choice of the GCM has been identified as a source of variability and uncertainty in suitability models (Fajardo et al., 2020; Thuiller et al., 2019), we adopted the *GCM compareR* package (Fajardo et al., 2020) to compare the bioclimatic differences among all GCMs from CMIP6 (O'Neill et al., 2016) available at 30 arc-second resolution (~1 km²) in the Worldclim database version 2.0 (Fick and Hijmans, 2017; accessed August 24, 2023): ACCESS-CM2, CanESM5-CanOE, CMCC-ESM2, CNRM-CM6–1, CNRM-ESM2–1, EC-Earth3-Veg, HadGEM3-GC31-LL, MIROC6, MPI-ESM1–2-HR, MRI-ESM2–0. To ensure that the GCM employed effectively models the key climate variables influencing *V. crabro* distribution in our study area, we selected the MRI-ESM2.0 as the GCM exhibiting the smallest deviation from the multi-GCM ensemble mean (Fajardo et al., 2020). This selection was based on its balanced representation of temperature and precipitation variables that influence the current potential distribution of *Vespa crabro*, ensuring accurate predictions of the species' distribution under future climate and socio-economic scenarios for 2040 and 2060 (Fajardo et al., 2020). Finally, we provided summary statistics (mean, standard deviation (hereafter SD), minimum and maximum values, and coefficient of variation (hereafter CV, in percentage) for each current and future bioclimatic variable contributing to the models. Additionally, we included kernel density estimates (i.e., a smoothed curve of a histogram) to identify changes in bioclimatic variables under current and future scenarios.

2.2.2. Model fitting and evaluation

As it is recommended to select algorithms that exhibit similar responses to the same optimization method used for pseudo-absence selection (Barbet-Massin et al., 2012), we employed the following three non-linear and non-parametric machine learning algorithms to build individual models: Artificial Neural Network (ANN), Generalized Boosting Model (GBM), and Random Forest (RF). A careful model tuning procedure, through *biomod2* package (4.2–2 version) (Thuiller et al., 2020), was adopted to find optimum values for each modeling technique that minimize prediction error (Hao et al., 2019; Valavi et al., 2022). Tuning parameters adopted for each algorithm are summarized in Fig. A.5, Appendix A3. Each algorithm was replicated for each set of pseudo-absences (i.e., 10 replicates; Fig. A.6 in the Appendix A3), assigning the same weight to occurrences and pseudo-absences (Barbet-

Massin et al., 2012; Elith et al., 2010).

The predictive performance of individual models was evaluated through a block cross-validation procedure by spatially splitting data multiple times into different subsets used for calibrating (i.e., fitting or training) and validating (i.e., testing) models (Hijmans, 2012). The procedure takes into account potential spatial autocorrelation issues in model evaluation, improving independence between the two subsets (Hijmans, 2012; Muscarella et al., 2014; Roberts et al., 2017). We used the isotropic variogram (non-directional empirical variogram) from the *spatialAutoRange* function of *blockCV* package (Valavi et al., 2019) to identify the optimal separation distance over which residuals are approximately independent (Fig. A.7 in the Appendix A3), assuming that the data met the necessary geostatistical criteria (i.e., stationarity, having constant variance) (Valavi et al., 2019). The spatial autocorrelation structure associated with occurrences/pseudo-absences and climate data had a characteristic scale smaller than 44 km (Fig. A.7 in the Appendix A3). Thus, we used 19 equal-sized square blocks of $\sim 43 \times 43$ km each, to split the two subsets. The 19 blocks were randomly allocated into five folds, with a similar number of occurrences and pseudo-absence points in each fold, using the function *spatialBlock* in *blockCV* package (Valavi et al., 2019; Fig. A.8 in the Appendix A3).

The predictive performance of 150 individual models (3 algorithms \times 10 replicates \times 5 folds) was assessed using two evaluation metrics (Allouche et al., 2006): Receiver Operating Characteristics (ROC) and its Area Under the Curve (AUC), and True Skill Statistic (TSS). TSS, which represents the sum of sensitivity and specificity minus one, takes into account both omission and commission errors, as well as success due to random guessing (Barbet-Massin et al., 2012). The ROC curve plot sensitivity against the corresponding proportion of false positives (equal to 1 minus specificity), providing insight into the trade-off between sensitivity and specificity (Allouche et al., 2006; Pearce and Ferrier, 2000). TSS and AUC have been demonstrated to be highly effective measures for evaluating model performance, as they are not influenced by prevalence (i.e., the proportion of presences and absences across the prediction map) or the size of the validation set (Allouche et al., 2006; Barbet-Massin et al., 2012; Guisan et al., 2017; Jiménez-Valverde and Lobo, 2007). For TSS, a value of +1 indicates perfect performance, while values of 0 or less signify performance no better than random. For AUC, a value of +1 represents perfect prediction accuracy, while an AUC of 0 indicates a model with predictions that are entirely incorrect.

To avoid using poorly calibrated and validated models, we included only individual models with $AUC \geq 0.7$ and $TSS \geq 0.4$ in the ensemble model construction, following the thresholds suggested by a range of published work (Franklin, 2010; González-Irusta et al., 2015; Lahoz-Monfort et al., 2014; Manel et al., 2001; Osborne and Leitão, 2009).

Hence, the individual models were weighted, based on their calculated AUC and TSS evaluations, and averaged (EMwmean) through *biomod2* package (4.2–2 version) (Thuiller et al., 2020) to obtain the consensus distribution (i.e., the ensemble model) across individual predictions (Marmion et al., 2009) under the current scenario. The weighted average method has been shown to produce realistic estimates of model performance, particularly when a careful model tuning procedure and a block cross-validation procedure are implemented (Hao et al., 2019; Valavi et al., 2019). Finally, the obtained ensemble model was evaluated using the above-mentioned evaluation metrics and plotting the ROC curve.

2.2.3. Model prediction

We used the ensemble model to generate a spatially continuous suitability map under current climate conditions, showing the locations where there is a greater or lesser potential to observe the species. The potential presence and distribution are expressed as a spatial probability of species occurrence, ranging from zero (minimum probability) to one (maximum probability) based on the estimated overall prevalence and the local favorability of the species under the analyzed climate conditions (Real et al., 2017). We calculated the relative contribution of each

variable to the final ensemble model using 999 permutations in the function provided by *biomod2* package (Thuiller et al., 2020). Species response curves were estimated to investigate the relation between the probability of species occurrence and current climate variables.

Then, *V. crabro* distribution was projected, resulting in four future predictions of species occurrence probability (one for each temporal horizon in each scenario). As recommended for models based on presence-only data (Guisan et al., 2017; Liu et al., 2015), we converted each current and future occurrence probability of *V. crabro* into a binary classification (presence and absence) according to the threshold that maximizes the sum of sensitivity and specificity (max TSS = 0.73). This optimal threshold, determined using the *PresenceAbsence* package, yielded a sensitivity of 0.92 and a specificity of 0.88. Hence, we adopted the *BIOMOD_RangeSize* function (Thuiller et al., 2020) on the binary classification to quantify and measure the species distribution changes induced by the future forcing under a given management regime. The species distribution changes were computed to identify (i) climatically suitable or unsuitable areas occupied by *V. crabro* under current and future scenarios (i.e., stable presence or stable absence), and (ii) the loss or gain of climatically suitable habitats (i.e., decolonized or colonized areas) by *V. crabro* under future change scenarios. Finally, we computed three supplementary relative metrics to ascertain the loss (i.e., loss/(loss + stable)) and gain (gain/(loss + stable)) percentages, and the overall range change (i.e., gain percentage – loss percentage) (Guisan et al., 2017).

3. Results

3.1. Model fitting and evaluation

Individual model performances, obtained by spatial block cross-validation procedure, using two evaluation metrics (ROC, and TSS), showed high intra- and inter-model variability (Fig. 3; Table A.1 in the Appendix A3). The mean ROC values varied across algorithms, ranging from 0.72 for ANN to 1 for RF in the calibration, and from 0.5 for GBM or 0.52 for ANN to 0.57 for RF in the validation (Table A.1 in the Appendix A3). According to TSS, when the calibration was considered, the lowest mean values were obtained for ANN and GBM, while RF reached the highest mean values (Table A.1 in the Appendix A3). Considering the validation, the lowest mean TSS value was obtained for GBM, while ANN and RF reached the highest mean value (Table A.1 in the Appendix A3). Overall, these results highlighted that RF models were better calibrated compared to models based on ANN and GBM, considering all evaluation metrics (Fig. 3). The degree of model validity followed a similar pattern: the prediction performance of RF models was the highest, followed by ANN and GBM models (Fig. 3).

Choosing the individual models that performed best ($AUC \geq 0.7$ and $TSS \geq 0.4$) and excluding those poorly calibrated and validated, based on results of the spatial cross-validation procedure, yielded good performance on the ensemble model. The ensemble model was satisfactory and showed a low variability, considering all the evaluation metrics that ranged from the minimum value of 0.78 (± 0.06 SD) for TSS to the maximum value of 0.95 (± 0.02 SD) for ROC (Fig. A.9 in the Appendix A3).

3.2. Model prediction

3.2.1. Variable importance

As a result of the variable selection procedure, five of the 19 bioclimatic variables were retained as an optimal subset size for the individual models, showing that the current distribution of *V. crabro* was driven by many interrelated climate variables (Fig. A.2-A.3 in the Appendix A3). According to the permutation importance, these five bioclimatic variables contributed the most to the final ensemble model, explaining the suitable habitats for *V. crabro* under current climate conditions (Fig. 4). The current distribution of *V. crabro* was mainly influenced by the

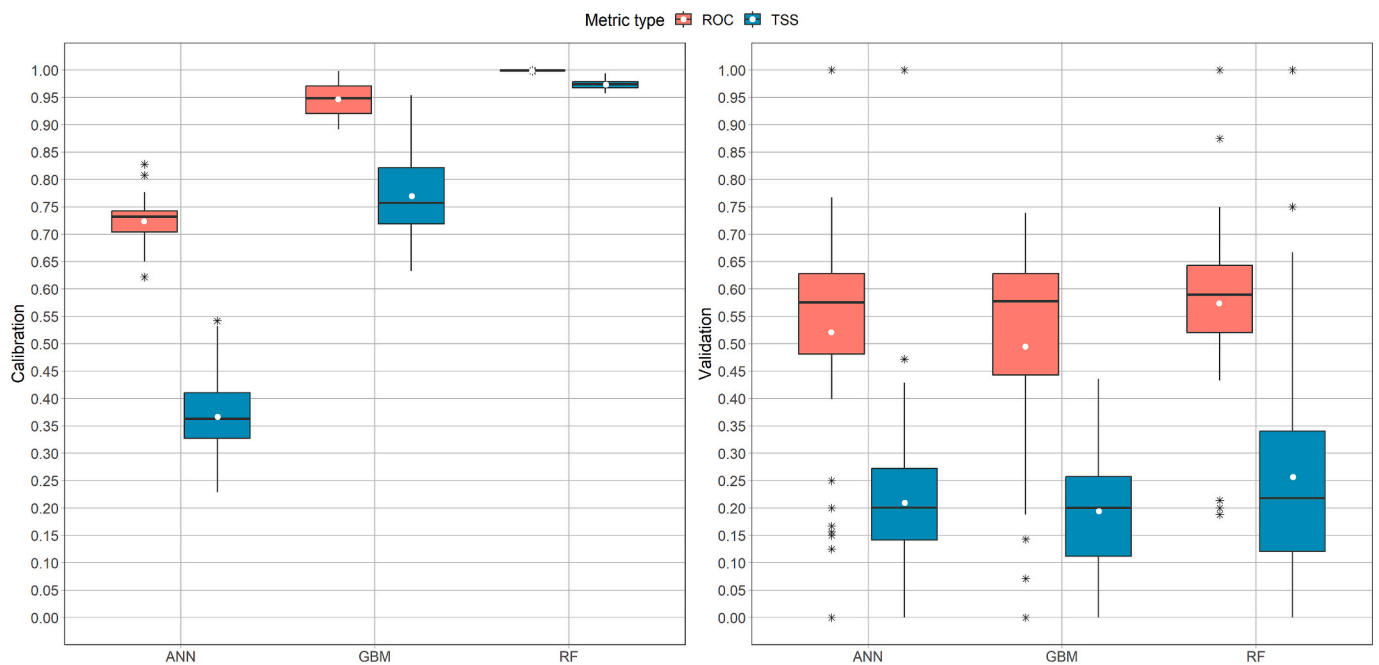


Fig. 3. Box plots representing the Receiver Operating Characteristics (ROC), and the True Skill Statistic (TSS) of 150 individual models (3 algorithms \times 10 replicates \times 5 folds) constructed for the current scenario using three machine learning algorithms: Artificial Neural Networks (ANN), Generalized Boosting Model (GBM), and Random Forest (RF). The boxes range from the 25th to the 75th percentile; the whiskers cover the 10th to the 90th percentile. The bar inside the box shows the median value of each evaluation metric, the white point indicates their mean values, and the star represents the outliers.

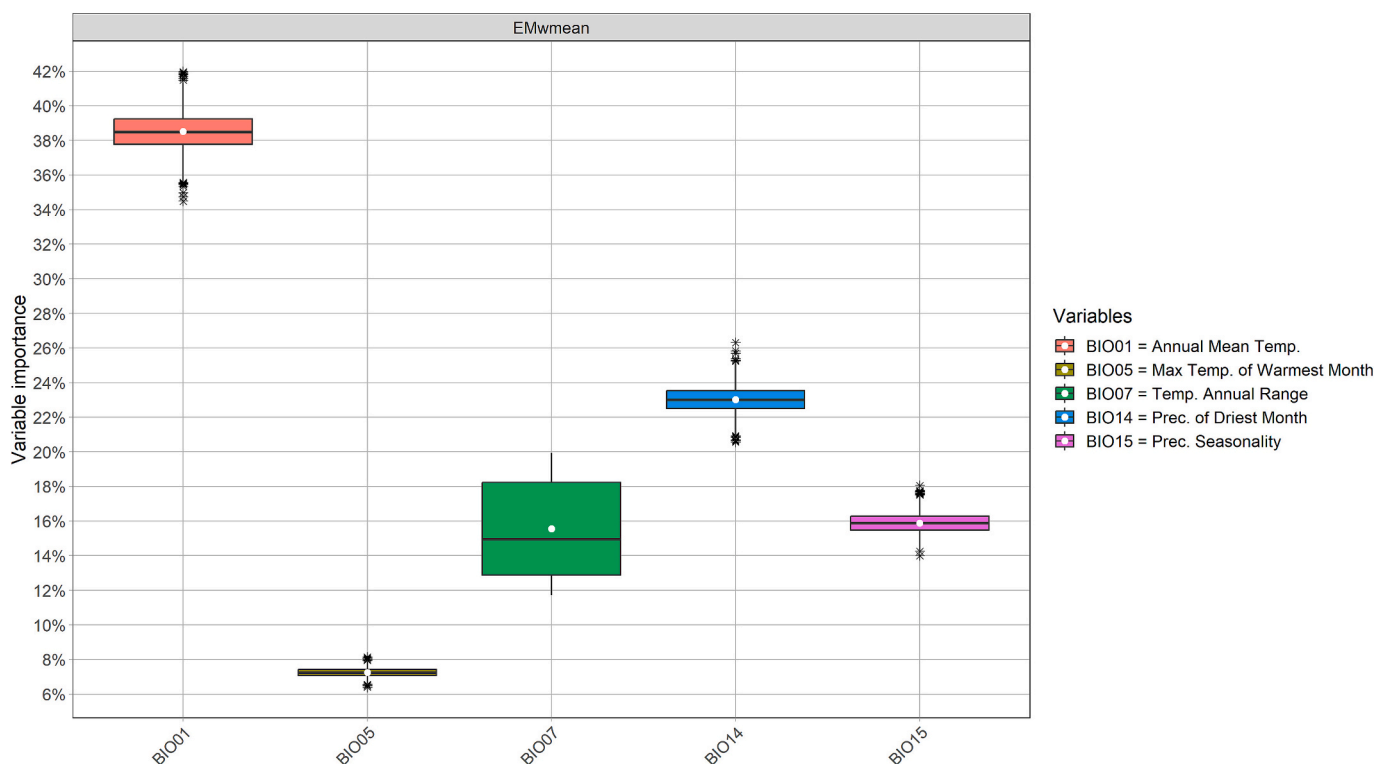


Fig. 4. Box plots representing the relative contributions of the bioclimatic variables to the final ensemble model, calculated using 999 permutations. The boxes extend from the 25th to the 75th percentile; the whiskers range from the 10th to the 90th percentile. The bar within each box shows the median value of each relative contributions, the white point indicates their mean values, and the star represents the outliers.

Annual Mean Temperature (BIO01) and Precipitation of Driest Month (BIO14), with a combined contribution of 61 % on average to the ensemble model (39 % \pm 1 SD and 23 % \pm 1 SD, respectively; Fig. 4). The Temperature Annual Range (BIO07) and Precipitation Seasonality

(BIO15) provided a mean cumulative contribution of 30 % (16 % \pm 3 SD and 16 % \pm 1 SD, respectively) to the ensemble model, whereas the Maximum Temperature of Warmest Month (BIO05) accounted for the remaining 7 % (Fig. 4).

3.2.2. Response curves

Response curves obtained from the ensemble model illustrated the relation among the probability of *V. crabro* occurrence and current climate parameters, explaining how each climate condition influenced the distribution of suitable habitats (Fig. 5). The response curve of the most important variables showed that the occurrence probability of the species directly increased as the Annual Mean Temperature (BIO01) and decreased as Precipitation of the Driest Month (BIO14; Fig. 5). In particular, a probability of species occurrence higher than 75 % (the threshold that maximizes TSS) was related to localities with average annual temperatures above 16 °C (a value close to the maximum one observed in the region) with a little amount of rainfall in the driest month compared to the range observed in the area of study (Table A.2 in the Appendix A3). The probability of species presence higher than 50 % seemed limited by a small amplitude of temperature range (25–26 °C; BIO07; Fig. 5) concerning the continentality values observed in the area of study, ranging from 17.45 °C to 31.16 °C (mean \pm SD = 26.02 \pm 1.89; Table A.2 in the Appendix A3). The probability of species occurrence above 50 % was limited to areas with precipitation seasonality (BIO15) values ranging from 42 % to 52 % (Fig. 5) which reflect values close to the mean (50.23 % \pm 3.66 SD) in current climate conditions (Table A.2

in the Appendix A3).

3.2.3. Bioclimatic variable changes under current and future scenarios

The statistical distribution of the five most important climatic variables across current and future scenarios is shown in Fig. 6. The future projections reveal that almost all bioclimatic variables will shift under the considered scenarios, but the greatest change will occur under the most pessimistic scenario (SSP5–8.5) regardless of the temporal horizon (2040 and 2060). Two temperature variables, i.e., Annual Mean Temperature (BIO01) and Maximum Temperature of Warmest Month (BIO05), will clearly shift towards higher values in the future (Fig. 6), respectively reaching average values of 17.68 °C (\pm 1.41 SD) and 32.59 °C (\pm 1.63 SD), and the maximum values of 20 °C and 36.40 °C in the pessimistic (SSP5–8.5) scenario by 2060 (Table A.2 in the Appendix A3). On the contrary, Temperature Annual Ranges (BIO07) will decrease slightly in the intermediate (SSP2–4.5) and pessimistic (SSP5–8.5) management regime for both the temporal horizons (Fig. 6). The statistical distribution of Precipitation of Driest Month (BIO14) will have more distinct and tighter peaks (i.e., multimodal distribution) in the future than in the current period, suggesting that in the future there will be more clearly defined and tightly clustered distribution of rainfall

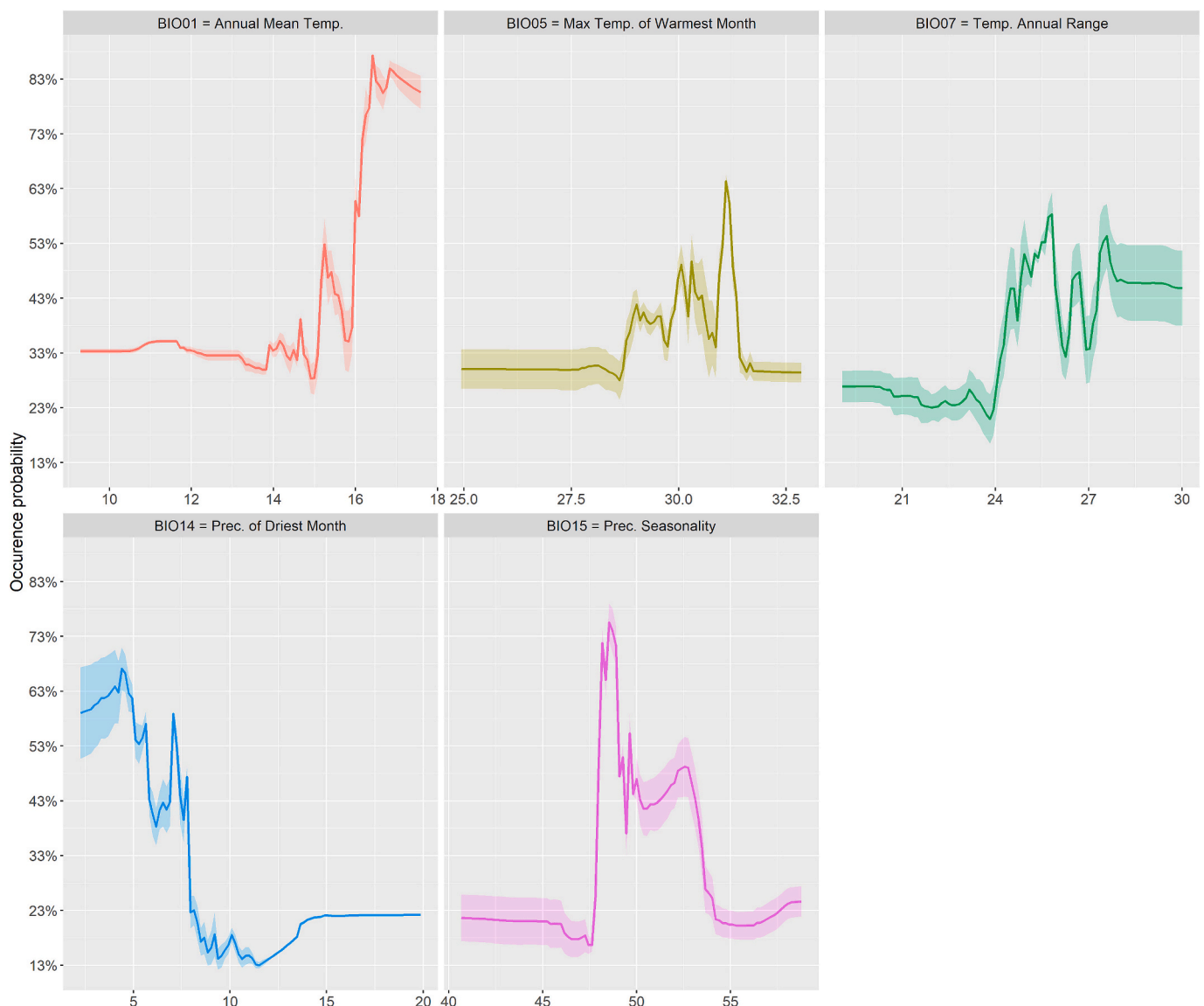


Fig. 5. Response curves of the most important bioclimatic variables: Annual Mean Temperature (°C; BIO01); Maximum Temperature of Warmest Month (°C; BIO05); Temperature Annual Range (°C; BIO07); Precipitation of Driest Month (mm; BIO14); Precipitation Seasonality (Coefficient of Variation in percentage; BIO15).

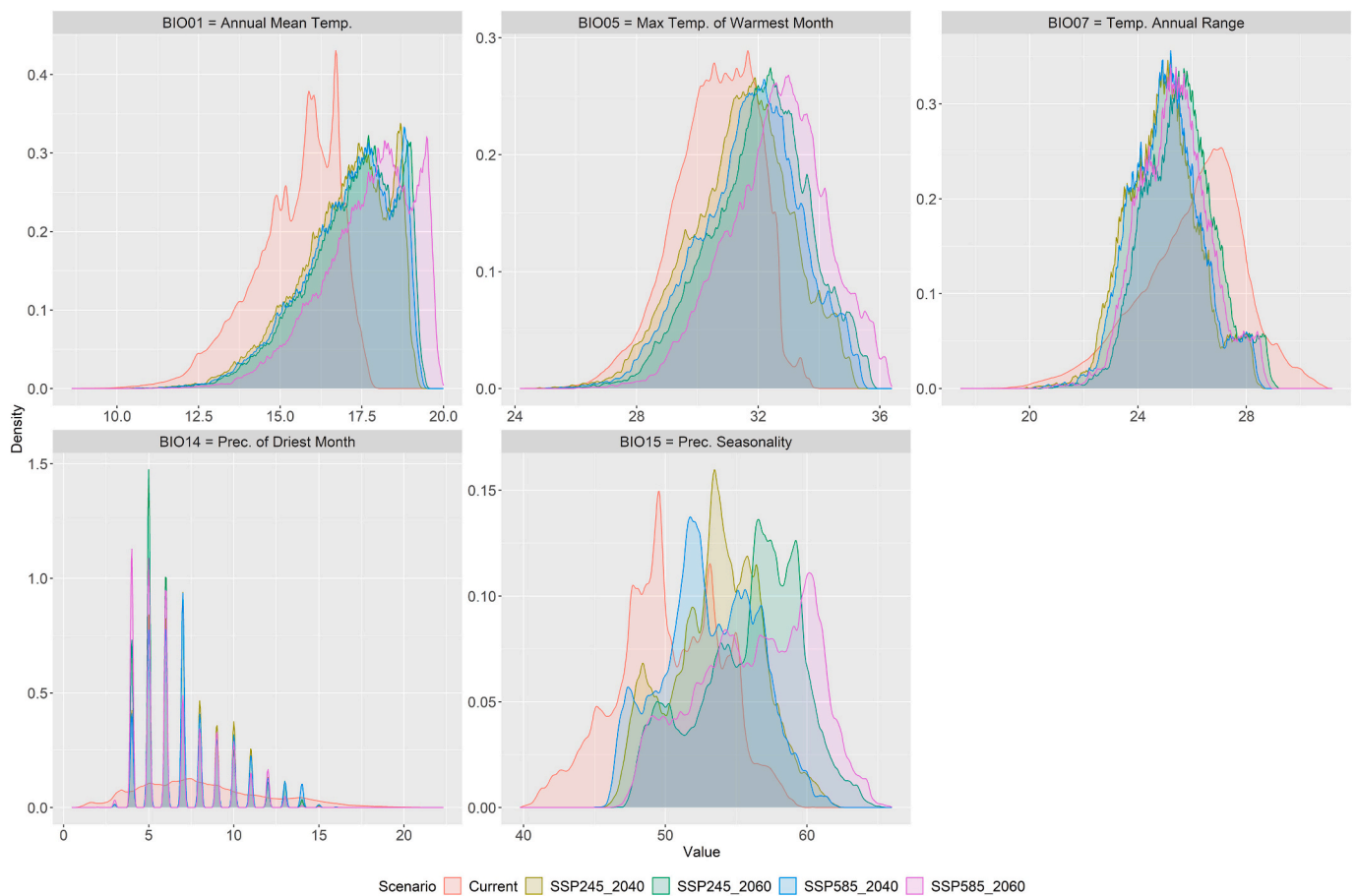


Fig. 6. Statistical distribution of the bioclimatic variables that contributed the most to the final ensemble model, explaining *Vespa crabro* distribution under (i) the current conditions, (ii) the intermediate management regime (SSP2–4.5) for the 2040 and 2060 horizons, and (iii) the pessimistic scenario (SSP5–8.5) for the 2040 and 2060 horizons.

amounts in different dense areas of the region compared to the current period (Fig. 6). Rainfall amounts of the driest month will vary towards lower maximum values and will show less variability in the future, with CV ranging from 32.73 % to 35.84 % in the intermediate (SSP2–4.5) scenario, and CV ranging from 34.57 % to 36.50 % in the pessimistic (SSP5–8.5) scenario by 2040 and 2060 compared to the current period (CV = 44.88 %) (Table A.2 in the Appendix A3). The seasonal variation in precipitation (BIO15, Precipitation Seasonality) will increase notably by 2060 (Fig. 6), reaching the average values of 55.92 % (± 3.63 SD) and 56.27 % (± 4.7 SD), and the maximum values of 65.40 % and 66 % in the intermediate (SSP2–4.5) and pessimistic (SSP5–8.5) scenario, respectively (Table A.2 in the Appendix A3).

3.2.4. Current occurrence probability maps

The ensemble model indicated that the current climatically suitable habitats in North Sardinia were basically consistent with the occurrence records of *V. crabro* collected during the participative science program (compare Fig. A.6 in the Appendix A3 and Fig. 7). In addition, the ensemble model predicted high climate suitability (probability values > 73 %, according to the threshold that maximizes TSS) for *V. crabro* in almost all coastal areas. High climate suitability (probability values > 73 %) was also predicted for the small islands around the region and in some inland areas (Fig. 7), where *V. crabro* has not yet been recorded (Fig. A.6 in the Appendix A3). In particular, only a few specific inland areas, especially those near or including mountainous regions, were also considered favorable for *V. crabro*. These areas include Monte Arci and Giara plateau (Giara di Gesturi) in central Sardinia, the limestone block of the Supramonte in eastern Sardinia, and Monte Arcosu and Monte dei

Sette Fratelli in southern Sardinia (Fig. 7).

3.2.5. Species distribution changes under future change scenarios

The range change analysis indicated that *V. crabro* distribution will undergo significant changes under future climate and socio-economic scenarios (Fig. 7 and Fig. 8). The spatial extent of climatically suitable habitats for *V. crabro* will decrease, particularly by 2060 (Fig. 8). This range reduction will be driven primarily by the loss of suitable habitats, especially along coastal areas (Fig. 7 and Table 2). Specifically, areas with a suitable climate for *V. crabro* are expected to decrease by approximately 91.02 % and 96.06 % under SSP2–4.5 change scenario by 2040 and 2060, respectively, when compared to current suitability (Table 2). The reduction in climatically suitable habitats under SSP5–8.5 will be of about 92.07 % and 98.98 % by 2040 and 2060, respectively (Table 2). This reduction will be more evident under SSP5–8.5 than under SSP2–4.5 (Table 2).

4. Discussion

In this study, we employed an ensemble approach to predict the current and future distribution of *Vespa crabro* in the island of Sardinia, a key Mediterranean biodiversity hotspot. By integrating presence records of citizen science programs with bioclimatic data, we aimed to identify areas of potential climate suitability for *V. crabro* under present conditions and two climate projections, each based on different socio-economic scenarios across two temporal horizons (2040 and 2060) to guide monitoring programs and management measures.

Recently, the contribution of volunteers and hobbyists to animal and

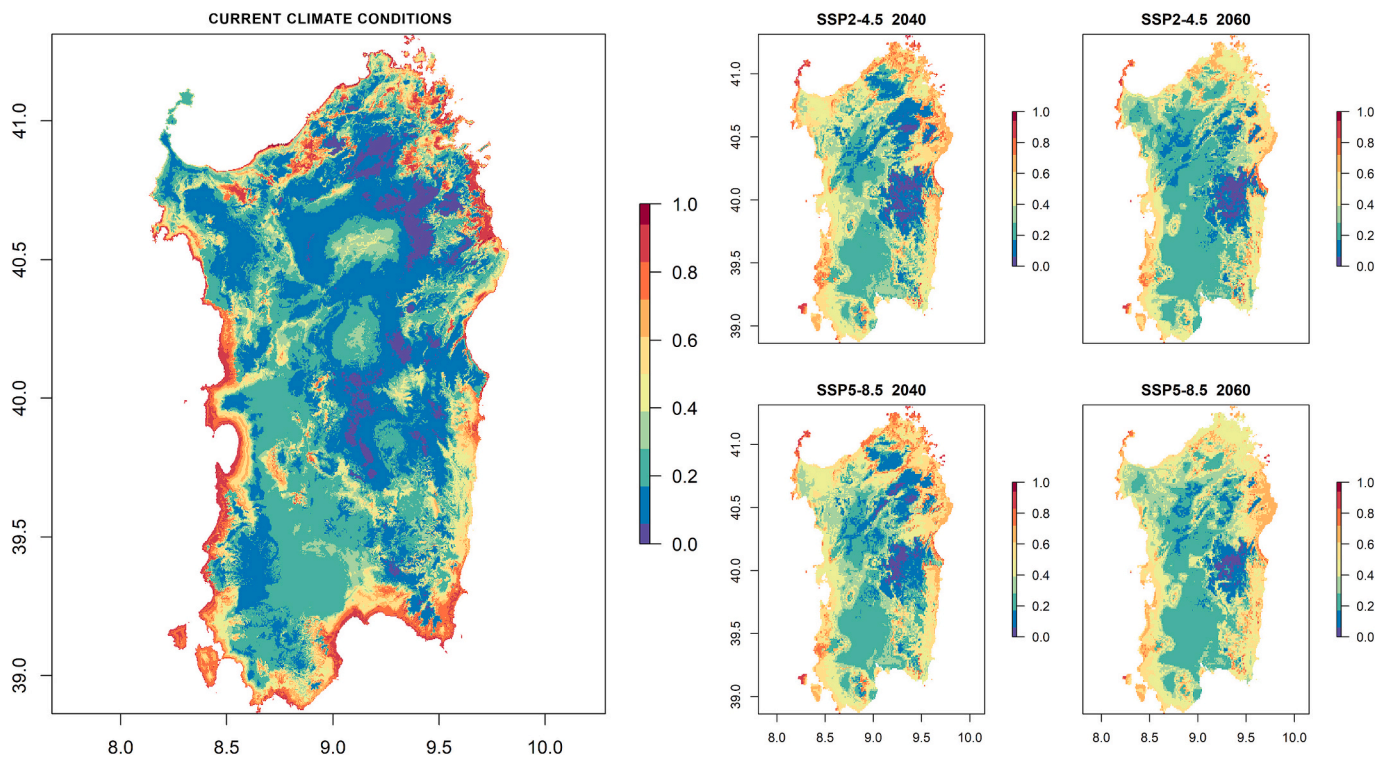


Fig. 7. Maps (coordinate systems WGS 84, EPSG: 4326) indicating geographical areas with potentially high climate suitability (i.e., occurrence probability values > 0.73, equal to 73 %, according to the threshold that maximizes TSS) for *Vespa crabro* under (i) the current conditions, (ii) the intermediate management regime (SSP2–4.5) for the 2040 and 2060 horizons, and (iii) the pessimistic scenario (SSP5–8.5) for the 2040 and 2060 horizons.

plant species reports has increased exponentially (Tiago et al., 2017; Zapponi et al., 2017). This has facilitated the timely detection of alien species that damage agricultural and forest ecosystems (Maistrello et al., 2016; Pocock et al., 2017). The establishment of alien species that are not relevant to human health of crops may remain undetected for years, particularly in the case of small-sized insects with cryptic habits (Cocco et al., 2021). Despite initial skepticism among researchers regarding the reliability of citizen science data, recent publications have indicated that datasets sourced from citizen scientists are as valid as data collected by professional scientists (Florence et al., 2020; Kosmala et al., 2016). Furthermore, such data can provide a valuable contribution to the implementation of suitability models (Florence et al., 2020; Guisan and Thuiller, 2005), especially for social wasps which are well-known and relatively easily distinguished species (Sumner et al., 2019).

Nevertheless, the quality of data obtained through participatory sciences varies, prompting the adoption of diverse methods to enhance data accuracy and address biases (Florence et al., 2020; Kosmala et al., 2016). In our dataset, data accuracy was first enhanced by volunteer training, and expert data validation (Pusceddu et al., 2019). In addition, observation data can exhibit variability in sampling intensity leading to inaccuracies in model fitting and/or false interpretation (Inman et al., 2021; Phillips et al., 2009), posing a significant concern for SDMs (Guillera-Aroita et al., 2015). Moreover, the spatial dependence (i.e., spatial autocorrelation) among training and validation subsets can favor overfitted or biased models, resulting in an underestimation of predictive error and overestimation of validation performance, potentially leading to erroneous scientific conclusions (Deppner and Cajias, 2022; Hao et al., 2020; Roberts et al., 2017; Rocchini et al., 2017). The increasing popularity of the spatial block cross-validation procedure over the past decade (Deppner and Cajias, 2022) has led to its application across a wide spectrum of algorithms, including machine learning ones, whether considered individually or combined in an ensemble model (El-Gabbas and Dormann, 2018; Hao et al., 2020). To address these issues, we accounted for bias resulting from heterogeneous

sampling effort by implementing a pseudo-absence sampling strategy (Barbet-Massin et al., 2012; Phillips et al., 2009) and ensured independence between training and testing subsets through a spatial block cross-validation procedure (Hijmans, 2012; Muscarella et al., 2014; Valavi et al., 2019). We implemented these strategies to calibrate and validate predictions of different tuned individual models before the ensemble model construction, obtaining a high variability in individual predictive performance depending on the algorithms, replicates, and subsets selected to train and test models. This finding aligns with previous research that reported substantial differences in model performance based on the choice of algorithms and their inherent complexity (Elith et al., 2006; Guillaumot et al., 2019; Guisan and Thuiller, 2005; Hao et al., 2019, 2020; Roberts et al., 2017).

In our case study, Random Forest (RF) outperformed other algorithms, including Artificial Neural Networks (ANN) and Generalized Boosted Models (GBM), in both calibration and validation phases. Our findings confirm previous studies (e.g., Stupariu et al., 2022) that highlight RF's superior performance compared to alternative algorithms (e.g., logistic regression, Generalized Additive Models, Support Vector Regression, and Decision Trees) across various applications, including species distribution modeling (Unnithan Kumar et al., 2021), prediction of canopy heights (Alvites et al., 2024; Alvites et al., 2025) or forest loss (Cushman et al., 2017), and soil nutrients (Jeong et al., 2017). Although RF demonstrated the highest predictive accuracy in our study and others, it is crucial to acknowledge that different algorithms may excel depending on the context. For example, MaxEnt is noted for its effectiveness in modeling species distributions with presence-only data, particularly for species with narrow ecological niches (Damaneh et al., 2022; Ghareghan et al., 2020; Kaky et al., 2020). Additionally, some research suggests that Generalized Linear Models may outperform RF at broader scales, revealing systematic differences in prediction accuracy across various scales and species (Chiaverini et al., 2023).

The use of the ensemble approach in our study mitigated the limitations associated with individual models by averaging the predictions

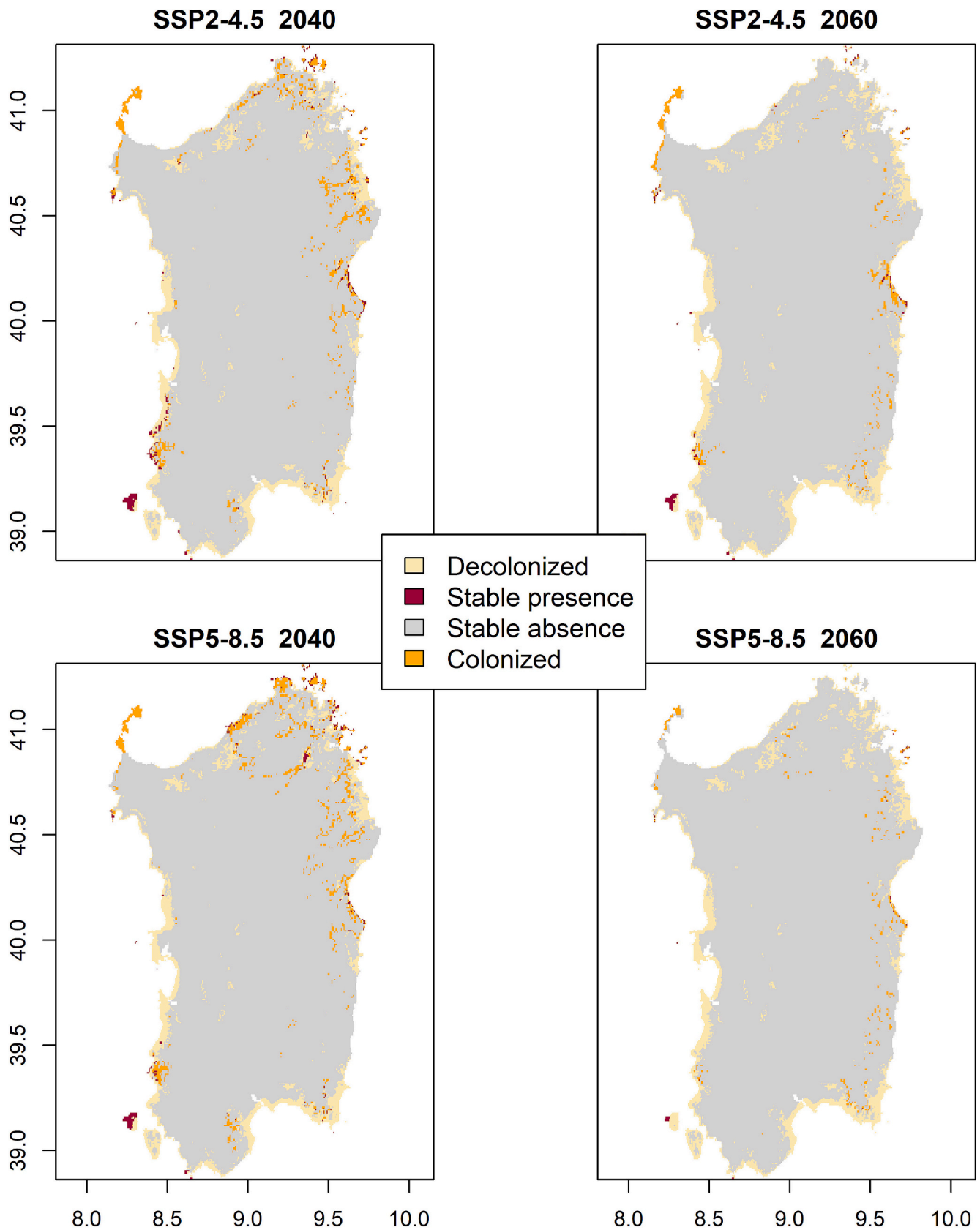


Fig. 8. Climatically suitable or unsuitable areas occupied by *Vespa crabro* under current and future scenarios (i.e., stable presence or stable absence), and the loss or gain of climatically suitable habitats (i.e., decolonized and colonized areas) by the species, as computed by *BIOMOD_RangeSize* function (Thuiller et al., 2020) on the binary classification maps (coordinate systems WGS 84, EPSG: 4326).

Table 2

Distribution changes of *Vespa crabro* (colonized, decolonized, and stable absence and presence areas, loss and gain percentages, and overall range change) obtained from the binary classification (presence and absence), according to the threshold that maximizes TSS (max TSS = 0.75), under different future scenarios compared to current conditions.

	Decolonized areas (km ²)	Stable absence (km ²)	Stable presence (km ²)	Colonized areas (km ²)	Loss percentage	Gain percentage	Overall range change percentage
SSP2-4.52040	1688.98	20,947.91	166.63	652.95	91.02	35.19	-55.83
SSP2-4.52060	1782.54	21,282.28	73.08	318.59	96.06	17.17	-78.89
SSP5-8.52040	1708.44	20,858.79	147.17	742.07	92.07	39.99	-52.08
SSP5-8.52060	1836.76	21,397.13	18.85	203.73	98.98	10.98	-88.01

across different algorithms, thereby reducing the likelihood of selecting a false hypothesis and enhancing overall accuracy. This approach is supported by the broader literature, which suggests that the ensemble approach often outperforms single algorithms by combining their strengths and compensating for individual weaknesses (Kalantar et al., 2020; Seni and Elder, 2010). This is particularly important considering that no single algorithm consistently outperforms others across all species, regions, and applications (Elith et al., 2006; Pearson et al., 2006; Segurado and Araújo, 2004). By combining the best-performing individual models to capture their central tendency, the ensemble strategy generally offers more reliable and robust predictions and enhances predictive accuracy, reducing prediction uncertainty (Amiri et al., 2020; Araújo and New, 2007; Hao et al., 2019, 2020; Liu et al., 2019; Marmion et al., 2009). In our study, the high predictive performance of the ensemble model was demonstrated by several commonly used statistical parameters, such as AUC and TSS. Overall, our findings contribute to the growing body of evidence that underscores the importance of algorithm selection and ensemble approaches in ecological modeling, particularly in areas like the Mediterranean regions, where fine-scale environmental heterogeneities may play a crucial role in species distribution.

The five bioclimatic variables were identified as most influential in determining the current distribution of *Vespa crabro* in our study, i.e., Annual Mean Temperature (BIO01) and Precipitation of the Driest Month (BIO14) (explaining 61 % to the ensemble model), followed by Temperature Annual Range (BIO07) and Precipitation Seasonality (BIO15) (explaining 30 %), and, to a lower extent, Maximum Temperature of Warmest Month (BIO05) (accounting for the remaining 7 %). These results are consistent with other studies on social wasps, reporting the critical role of temperature and precipitation in shaping species distributions (Bessa et al., 2016; Menzel and Feldmeyer, 2021; Robinet et al., 2019; Ruiz-Cristi et al., 2020; Dejean et al., 2011; Brightwell et al., 2010; Gibbs et al., 2003).

Our study showed that excessive precipitation during the driest month can be particularly detrimental to *V. crabro*, which favors relatively dry conditions. This is in accordance with previous studies demonstrating that dry periods may favor the abundance of social hymenopterans, as lower precipitation levels can support species survival and distribution (Dejean et al., 2011). Conversely, heavy rains and floods can negatively influence social hymenopteran populations and colonies, affecting their survival and distribution (Menzel and Feldmeyer, 2021; Ruiz-Cristi et al., 2020).

Our findings also indicated that high annual mean temperatures, as indicated by BIO01, are beneficial for *V. crabro*. However, future extreme temperature conditions could exceed the species' thermal tolerance. It has been shown that social hymenopterans may also face survival challenges due to low winter soil temperatures or when temperatures rise beyond their thermal limits (Brightwell et al., 2010; Menzel and Feldmeyer, 2021). The increase in drought periods, a major consequence of climate change, exacerbates these effects (IPCC, 2022). However, some insect species can reduce locomotor activity and metabolic rate as a mechanism of desiccation resistance (Gibbs et al., 2003).

Our fine-scale model for Sardinia revealed that *V. crabro* shows a high probability of occurrence in areas with the highest annual mean temperatures (BIO01), and the lowest precipitation during the driest

month (BIO14), with medium annual temperature range (BIO07) and precipitation seasonality (BIO15). This finding contrasts with a recent broad-scale study that suggested a shift in the niche of *V. crabro* towards colder and drier areas, as well as regions with a higher temperature range (i.e., more continental climatic areas sensu Rivas-Martínez et al., 2011), compared to that one of *V. velutina* (Lioy et al., 2023).

This discrepancy between our findings and those from the broader-scale study (Lioy et al., 2023) can largely be attributed to differences in the spatial and temporal scales of analysis, as found in other species distribution modeling studies on wasps (Bessa et al., 2016; Herrera et al., 2023). This finding highlights a key point of contention between broad-scale and fine-scale analyses, potentially suggesting that local climatic conditions may play a more relevant role in shaping species distributions than previously acknowledged.

Broad-scale studies may not fully capture the microclimatic variations present in heterogeneous environments, such as Sardinia, which is characterized by complex and diverse climatic patterns. In line with this insight, several authors have noted that global climate datasets may not always capture local climatic idiosyncrasies—unique, place-specific climatic characteristics that can significantly influence species-climate relationships and associated models (Baker et al., 2016; Bedia et al., 2013; Jeffress et al., 2013; Pliscoff et al., 2014; Rodríguez-Rey and Jiménez-Valverde, 2024; Soria-Auza et al., 2010). Such idiosyncrasies can be critical for species distribution and are often overlooked in broader assessments (Bellard et al., 2013; Franklin et al., 2013; Gardner et al., 2019; Gritti et al., 2006; Novoa et al., 2020; Robinson et al., 2020). As other studies suggest, high spatial and thematic resolution data can be crucial for accurately predicting species distribution patterns, especially when fine-grained occurrence data are available for species sensitive to specific habitat features (Beck et al., 2014; Gottschalk et al., 2011; Wan et al., 2016).

Fine-scale studies can be limited by focusing on a subset of the ecological conditions that a species encounters across its entire range. This subset may not encompass the full spectrum of physical or abiotic features a species can tolerate, leading to niche truncation (Broennimann and Guisan, 2008). This limitation can affect the estimation of response curves, particularly at the extremes of environmental ranges (Chevalier et al., 2021, 2022; Mateo et al., 2019; Scherrer et al., 2021; Thuiller et al., 2004). Therefore, although our fine-scale model offers valuable insights into the specific climatic preferences of *V. crabro* in a Mediterranean biodiversity hotspot, it may not fully represent the species response to broader-scale climatic trends. Further studies incorporating data from both native and invaded ranges could enhance the model predictability and provide a more comprehensive understanding of the species' potential distribution (Broennimann and Guisan, 2008).

We believe that there is a need for integrating both broad- and fine-scale analyses to achieve a complete perspective of species distribution dynamics. Considering multiple spatial scales can enhance our knowledge of how climatic factors interact with species' ecological requirements, improving SDM predictions and providing valuable insights for evaluating alien and invasive species risks (Wan et al., 2016). In addition, the variation in temperature over multiple temporal scales (e.g., days, months, years) should be considered as it influences species

responses. These fluctuations affecting both behavioral and physiological changes with ecological and biological consequences, especially on ectothermic animals, such as insects (Colinet et al., 2015; Danks, 2006; Marshall and Sinclair, 2012). Insect responses to temperature fluctuations at various scales can have significant implications, impacting not only thermal biology studies (Colinet et al., 2015) but also the prediction of future changes in species distributions (Kingsolver et al., 2013). Temperature variability, depending on its magnitude and the species' tolerance limits, can significantly influence species distributions and highlight the need for detailed, localized studies to complement broader-scale assessments (Bellard et al., 2018; Kingsolver et al., 2013).

Based on the relationship between the presence data and most influential predictors, our model predicted high climatically suitable habitats for *V. crabro* in nearly all coastal areas of northern Sardinia, in small islands around the main island, as well as in some inland regions, particularly those near or inside mountainous areas (i.e., Monte Arci and the Giarra plateau, Supramonte, Monte Arcosu and the Monte dei Sette Fratelli) where the species has not yet been recorded. The high suitability in coastal areas, as predicted by our model, contrasts with previous studies on *V. velutina*, that indicated a generally low potential for invasion in Mediterranean environments, particularly in warmer and drier southern regions, compared to continental ones (Bessa et al., 2016; Herrera et al., 2023; Robinet et al., 2019; Villemant et al., 2011). This discrepancy highlights the importance of species-specific studies, as *V. crabro* may be more adaptable to the Mediterranean climate of Sardinia compared to other invasive hornets.

Looking to the future, our projections indicate that nearly all the key bioclimatic variables that currently influence *V. crabro* distribution will undergo a notable shift. Under the pessimistic scenario (SSP5–8.5) in the farthest temporal horizon (2060), the expected substantial rise in Annual Mean Temperature (BIO01) and Maximum Temperature of Warmest Month (BIO05) may push *V. crabro* beyond its thermal optimum, potentially leading to a decline in fitness and survival. In fact, temperatures above 40 °C have been shown to compromise the vital capacities of *V. crabro*, with lethal effects observed at around 44.2 °C (Baracchi et al., 2010; Cappa et al., 2021). Additionally, *V. crabro* may be more sensitive to temperature than other species, possibly due to its nesting habits in hollow trees, which provide insulation from direct solar radiation and potential overheating. This lack of exposure to high temperatures may result in fewer adaptive responses to rising temperatures, in contrast to species whose colonies are commonly exposed to direct solar radiation (Heinrich, 1993; Tryjanowski et al., 2013). A negative influence of increasing temperatures on species distribution has been already observed in other ectotherms, including terrestrial insects and tropical species (Deutsch et al., 2008; Diamond and Chick, 2018; Huey et al., 2009, 2012; Kingsolver et al., 2013; Tewksbury et al., 2008).

Expected changes in other key bioclimatic variables, such as a slight decrease in Annual Temperature Range (BIO07) and a more pronounced multimodal distribution of Precipitation of the Driest Month (BIO14), which suggests a tighter clustering of rainfall amounts in certain Sardinian areas, may exert a further influence on *V. crabro*. This precipitation variability and the shift towards lower maximum values could further constrain the availability of suitable habitats for *V. crabro*, particularly in regions that become more arid under future climate conditions. In addition, the projected increase in Precipitation Seasonality (BIO15) by 2060, with average values of 55.92 % to 56.27 % under the intermediate and pessimistic scenarios, respectively, suggests that *V. crabro* may face increasingly variable and unpredictable precipitation patterns. This could exacerbate the challenges posed by rising temperatures, as the combination of higher temperatures and more extreme precipitation variability could limit the species' ability to adapt and thrive.

Coherently, the future projections for the distribution of *V. crabro* under various climate change scenarios indicate a substantial reduction in climatically suitable habitats, particularly by 2060. The most severe

reduction of approximately 98.98 % under the pessimistic SSP5–8.5 scenario (SSP5–8.5) by 2060, compared to current conditions, is primarily attributable to the loss of suitable habitats in coastal areas, which are currently favorable for the species. The projected decline in suitability in coastal areas indicates that *V. crabro* may encounter challenges in maintaining its current potential distribution as temperatures increase and precipitation patterns become more variable in Sardinia.

These findings align with other studies predicting range contractions at small scales (i.e., regional or local areas with an extension <1 million km²) for invertebrates under climate change (Bellard et al., 2018), particularly in Mediterranean and insular environments where the impacts of climate change are more pronounced (Carnicer et al., 2022). Differently, studies have forecasted that invertebrates may experience range expansion at larger scales (i.e., world or large regions with an extension >1 million km²; Bellard et al., 2018). This contrasts with the broader trend observed in alien plants and vertebrates, which often show predicted range decreases at larger scales but increases at smaller scales (Bellard et al., 2018).

The variability in these projections underscores the complexity of predicting climate change impacts across different taxa and scales (Bellard et al., 2018), highlighting the importance of conducting scale-specific analyses to fully understand the varying responses of species to climate change. In addition, to achieve greater clarity, especially regarding distributions of alien species, future studies could benefit from incorporating biological traits into their analyses. This approach would help account for factors such as acclimation, adaptation, dispersal, and behavioral or phenotypic plasticity, providing a more comprehensive understanding of how species may respond to changing climates (Deutsch et al., 2008; Rodrigues and Beldade, 2020).

From an application perspective, our findings could be useful in the management *V. crabro* in vulnerable insular ecosystems by providing insights into the direction and magnitude of its response under various future climate and socio-economic scenarios. Although social Vespidae like *V. crabro* are notoriously difficult to eradicate due to their high fertility (Beggs et al., 2011; Pusceddu et al., 2019), predictive modeling combined with local knowledge can offer valuable tools for policymakers and managers. These tools can help identify future vulnerable areas and prioritize them for monitoring and intervention. By concentrating on such zones, several management measures (e.g., prevention, rapid eradication, or long-term management) can be employed to mitigate the spread and impact of this alien species (Bellard et al., 2018; Bradley et al., 2009; Cuthbert et al., 2022). For example, short-term climate predictions (e.g., for 2040) can inform the creation of lists of alien species to be banned in specific geographical areas, anticipating areas at higher risk of invasion under changing conditions (Bellard et al., 2018). This forward-looking approach is crucial, as current risk assessments often rely solely on historical data without accounting for future climatic shifts (Kumschick and Richardson, 2013).

By focusing on areas projected to become unsuitable for the species under future climate scenarios, control or eradication efforts can be strategically implemented, leveraging the anticipated shifts in climate conditions to enhance the long-term success of these interventions (Cuthbert et al., 2022). In both artificial and natural habitats, the practicality of eradication programs depends heavily on the extent of the invasion, making localized efforts more feasible (Pluess et al., 2012). Targeting areas where the climate is expected to become unfavorable for *V. crabro* allows for more effective use of resources, as these areas may naturally limit the species' persistence.

The success of eradication programs depends on several key factors, including the speed of response, the extent of infestation, the depth of biological understanding, and readiness to act (House et al., 2020). A rapid response is particularly effective when populations are small or localized, as it increases the likelihood of successful eradication (Sandercock et al., 2023; Simberloff, 2003). Given that *V. crabro* is a relatively recent arrival in Sardinia and is expected to be limited under future scenarios, the prospects for successful eradication appear

promising. By aligning eradication efforts with areas expected to become climatically unsuitable, managers can optimize resources and improve the likelihood of long-term success in controlling this alien species.

Nevertheless, conventional cost/benefit analyses, which often prioritize economic over ecological considerations, may not adequately capture the benefits of early eradication efforts. These analyses typically focus on quantifiable economic gains, which may not be apparent during the initial stages of an invasion (House et al., 2020). Therefore, a broader evaluation of the ecological and long-term benefits of eradication is necessary.

Management responses to biological invasions are typically coordinated through national policies. However, local-level methodological approaches, such as those employed in this study, are valuable for informing stakeholders and supporting management measures across different temporal scales. Unlike broad global assessments, fine-scale studies offer new insights into the interaction between climate change and biological invasions, identify knowledge gaps, highlight species-specific responses, and provide potential management scenarios.

By focusing on the specific climatic and ecological contexts of the invasion, these localized analyses help to optimize resource allocation and improve the effectiveness of management strategies. The integration of detailed, site-specific data enables more precise and proactive measures, which are essential for mitigating the impacts of alien species in rapidly changing environments.

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CRedit authorship contribution statement

Erika Bazzato: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Formal analysis, Conceptualization. **Arturo Cocco:** Writing – review & editing, Visualization, Investigation, Data curation. **Emanuele Salaris:** Investigation, Data curation. **Ignazio Floris:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Alberto Satta:** Writing – review & editing, Visualization, Supervision, Resources, Conceptualization. **Michela Pusceddu:** Writing – review & editing, Supervision, Resources, Investigation, Data curation, Conceptualization.

Declaration of competing interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecoinf.2025.103006>.

Data availability

The data points used for modeling in this study are provided in Supplementary Appendix A2. Additionally, a detailed description of the modeling framework, including specifying functions and packages, is provided in accordance with the ODMAP protocol in Supplementary Appendix A1.

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