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Prediction and assessment of suitable habitats for paper wasps (Hymenoptera: Vespidae) based on the MaxEnt model for different climate scenarios

Прогнозирование и оценка подходящих мест обитания складчатокрылых ос (Hymenoptera: Vespidae) на основе модели MaxEnt для разных климатических сценариев

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Key words: MaxEnt, wasps, ecological niche modeling, climate change, potential distribution, habitat suitability.

Ключевые слова: MaxEnt, осы, моделирование экологической ниши, изменение климата, потенциальное распространение, пригодность местообитания.

Abstract. Climate change has a significant impact on the geographical distribution of species, making it critical to predict these changes for biodiversity conservation. This study modelled the current and future potential distribution of 10 species of wasps in the family Vespidae representing different biogeographical types, including Transpalearctic, East Asian, Nearctic and Mediterranean. Species occurrence data were obtained from the GBIF database as well as from original collections. 19 bioclimatic variables from WorldClim (resolution of 2.5 angular minutes) were used for current conditions and four scenarios of future climate change from the CMIP6 project (SSP2–4.5 and SSP5–8.5 for 2060 and 2100 using the ACCESS-CM2 global climate model). Species Distribution Modelling (SDM) was performed using the maximum entropy (MaxEnt) algorithm in the R environment. The results obtained allowed us to identify the current climatic niches of species and to predict changes in their potential habitats depending on the climate change scenario. We have shown that some species can significantly change their current habitats, while for some species, their habitats will remain unchanged. These findings will contribute to understanding the vulnerability of species to climate change and the development of conservation strategies.

Резюме. Изменение климата оказывает значительное влияние на географическое распространение видов, что делает прогнозирование этих изменений критически важным для сохранения биоразнообразия. В этом исследовании смоделировано текущее и будущее потенциальное распространение десяти видов ос семейства Vespidae, представляющих различные биогеографические типы, включая транспалеарктические, восточноазиатские, неарктические и средиземноморские. Данные о встречаемости видов были получены из базы данных GBIF, а также по собственным сборам. Для моделирования использовались 19 биоклиматических переменных из WorldClim (разрешение 2,5 угловых минут) для текущих условий и четыре сценария будущих климатических изменений из проекта CMIP6 (SSP2–4,5 и SSP5–8,5 на 2060 и 2100 годы глобальной климатической модели ACCESS-CM2). Моделирование распределения видов (Species Distribution Modelling, SDM) проводилось с применением алгоритма максимальной энтропии (MaxEnt) в среде R. Полученные результаты позволили выявить современные климатические ниши видов и спрогнозировать изменения в их потенциальных ареалах в зависимости от сценария климатических изменений. Мы доказали, что некоторые виды могут значительно изменять места современного обитания, для некоторых видов места обитания останутся неизменными. Полученные данные будут способствовать пониманию уязвимости видов к изменению климата и разработке стратегий сохранения.

Introduction

The resilience and integrity of terrestrial ecosystems are directly dependent on climate regimes. Climate change is currently considered one of the most pressing challenges facing humanity. Insects have evolved over 450 million years in response to fluctuating climates on Earth; however, the rapid, modern temperature and precipitation changes pose new challenges for them. These shifts are exacerbated by decades of anthropogenic factors, such as land conversion and degradation [Halsch et al., 2021]. Understanding and predicting the contribution of adaptation to insect species' resilience to climate change is therefore paramount for successful biodiversity management aimed at conservation, agriculture, and public health. To forecast species responses to climate change, it is necessary to understand how key traits and environmental factors interact to shape fitness

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in a changing world. Current trait-based models suggest that populations in low and mid-latitude regions are most at risk, although these models primarily focus on upper thermal limits, which may not be the most critical factor driving species distribution and adaptive capacity in the context of climate change.

Responses of insects to climate change are likely to be complex and difficult to capture fully in laboratory experiments. A shift towards well-established field experiments will not only allow the capture of this complexity but also enable the study of a greater diversity of species [Kellermann, van Heerwaarden, 2019].

Insects constitute one of the most pervasive forms of life on Earth, playing a significant role in ecosystem stability. Given the growing interest in investigating the effects of anthropogenic pollution on insects, this research will also incorporate an analysis of the potential role of invasive species (specifically, wasps) in transferring microplastics (MPs) into contaminated ecosystems [Liaqat et al., 2024].

Projected climate warming is expected to influence insect distribution in various ways. Increased temperatures and the degradation of permafrost in Russia will facilitate the expansion of the ranges of many insects in the north and east, leading to outbreaks of agricultural and forest pests in areas previously unaffected.

However, rising temperatures can also lead to the contraction of southern areas of the ranges of certain species. Range formation is dependent not only on temperature but also on numerous other factors, such as food availability, predation, pathogens, competition, and photoperiod characteristics [Yasyukevich, Davidovich, 2010].

As ectothermic organisms, insects cannot maintain a constant internal temperature and therefore respond to temperature changes differently depending on their physiological and ecological characteristics, seasonal cycles, trophic relationships. Currently, six categories of insect responses to climate change have been identified: 1) range shifts, 2) population changes, 3) phenological shifts, 4) voltinism, 5) morphological, physiological and behavioral changes, and 6) alterations in interspecific interactions and community structure.

Expansion of species ranges can enrich local faunas. Phenological responses include not only a shift in the timing of development earlier in the growing season, but also a shift in the timing of the later phases of development. In this case, the final phases of seasonal development are usually shifted to later times. This leads to an elongation of the active development period, which may have both positive and negative consequences for insect populations.

It is assumed that many insect species in temperate zones will benefit from warming temperatures. However, some experiments indicate that the situation may not be so clear-cut, and for some species or populations, the impact of warming may be negative even in temperate climates. It is likely that species or populations from regions with cold or temperate climates possess sufficient phenotypic plasticity to survive and thrive in warming conditions, while species or populations that are currently experiencing stress from high seasonal temperatures in temperate climates or in warmer climatic zones have very limited “room for maneuver” because the temperatures at which they exist are already close to the upper limits of their tolerance.

Without genetic adaptation, even modest warming would subject these species or populations to serious physiological stress. Current data suggest that insect and overall biota responses to warming will be complex and variable depending on both the rate of warming and the ecological characteristics of different species and the regions they inhabit. Even within a single species or population, responses affecting different aspects of their biology will vary in character and degree of expression, with an ambiguous resulting intensity in different seasons.

It is important to remember that insect species will experience the effects of warming climate not in isolation; temperature is not the only changing factor in the environment, and changes will not be uniform throughout the seasons. Plants, insects, their competitors, predators, parasites, symbionts, and pathogens will all react to seasonal changes in many physical and biological factors, individually and in a complex interaction. All this makes it extremely difficult to predict the consequences of warming or any change in external conditions.

Expected reactions will be specific to different species and populations and will affect all aspects of their biology. Reactions will range from difficult-to-capture changes at the cellular level to large-scale range shifts and even the extinction of species in certain areas. The intensity of reactions will depend on the degree and rate of warming. A minor warming is likely to trigger responses only in some insect species with plastic seasonal cycles, while more significant warming can lead to changes in a large number of species from different ecological groups.

For constructing predictive models of range shifts, we have selected the paper wasps (Vespidae). These wasps are widespread due to human influence and play an important role in forest and agro-ecosystems. Paper wasps rapidly reproduce and have a highly diverse diet, many species are closely associated with human settlements. With the help of wasps, the Vespidae family can be used to assess the influence of various factors not only on range shifts, but also on the distribution of MPs and anthropogenic fibers in nature.

The goal of this study is to forecast the potential range shifts of mass wasp species (Vespidae) under different climate scenarios in the future. These forecasts will allow us to identify species whose range shifts may be associated with an increase in their role in biotic migration and the accumulation of microplastics in terrestrial ecosystems.

Material and Methods

This study investigates the contemporary and potential distribution of 10 wasp species: *Dolichovespula me-*

dia (Retzius, 1783)*, D. pacifica* (Birula, 1930)*, Polistes gallicus* (Linnaeus, 1767), *P. nimpha* (Christ, 1791)*, P. mandarinus* Saussure, 1853*, Vespa crabro* Linnaeus, 1758*, V. dybowskii* André, 1884*, Vespula germanica* (Fabricius, 1793)*, V. koreensis* (Radoszkowski, 1887)*, V. vulgaris* (Linnaeus, 1758). Current species distribution was assessed using two datasets: original field collections and data from the GBIF database [GBIF.org, 2024]. Field collections consisted of geographically-referenced sightings obtained during field investigations. GBIF data were utilized following taxonomic verification, removal of duplicate records, records lacking coordinates, and clearly erroneous points. All records were standardized to a common format and employed in the construction of species distribution models.

For predicting future distribution, we utilized the MaxEnt algorithm, implemented within the dismo package of R [Phillips et al., 2006; Hijmans et al., 2017]. The analysis incorporated two categories of environmental predictors: a set of 19 bioclimatic variables (bio_1–19), representing mean monthly values, extreme conditions, and seasonal fluctuations in temperature (°C) and precipitation (mm). To account for the energetic regime of the area, we used mean monthly sums of incoming shortwave solar radiation on a horizontal surface (srad — incident solar radiation), expressed as kilojoules per square meter per day ($kJ \cdot m^{-2} \cdot day^{-1}$). These values were obtained from the WorldClim version 2.1 dataset [Fick, Hijmans, 2017] with a spatial resolution of 2.5 arc minutes (~4.5 km^2 at the equator).

Prior to model construction, a preliminary data filtering process was undertaken to mitigate multicollinearity using Variance Inflation Factor (VIF) analysis. Highly correlated predictors were excluded, and only variables passing this redundancy check were retained in the final set.

Following predictor selection, models were constructed independently for each species using presence locations as input points. Background points were randomly generated within the study area to represent null space. Spatial overdispersion was addressed by removing closely positioned presence points as needed.

To assess potential distribution under future climate conditions, we employed four scenarios derived from the ACCESS-CM1.5 global climate model project [Ziehn et al., 2020], based on greenhouse gas emission trajectories and varying levels of climate warming. SSP2–4.5 (2041–2060) — a moderate scenario representing average emissions and a relatively stabilized socioeconomic trajectory; reflects mid-21st-century climatic conditions under intermediate radiative forcing. SSP5–8.5 (2041–2060) — a high-emission scenario depicting more pronounced warming by mid-century driven by continued fossil fuel use and high radiative forcing. SSP2–4.5 (2081–2100) — a moderate scenario for the end of the 21st century, reflecting potential climate changes with partial emission stabilization and milder warming. SSP5–8.5 (2081–2100) — an extreme scenario for the end of the 21st century characterizing the most significant changes in temperature and precipitation patterns under sustained high emissions.

These climate scenarios were utilized to construct predictive models of future species distributions and to evaluate potential shifts in their spatial ranges. Models for both contemporary and future climates were compared using maps of potential habitat suitability. Model quality was evaluated using standard MaxEnt metrics, including Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) curve, as well as by assessing the congruence of model predictions with known occurrence records.

The present work is registered in ZooBank (www.zoobank.org) under urn:lsid:zoobank.org:pub:96BF148B-E9F5-4D10-B4D7-7CE-4CEE7A857

Results

Following multicollinearity analysis, 10 bioclimatic variables and the incoming solar radiation (srad) data were selected: annual mean temperature (bio_1), thermal homogeneity (bio_3), thermal seasonality (bio_4), maximum monthly temperature (bio_5), minimum monthly temperature (bio_6), mean summer temperature (bio_9), mean summer temperature (bio_10), monthly rainfall (bio_13), thermal seasonality (bio_15), summer rainfall (bio_18), winter rainfall (bio_19), January solar radiation (srad_1), July solar radiation (srsd_7), and October solar radiation (srad_10).

Model quality was assessed using the Area Under the Receiver Operating Characteristic Curve (AUC). Models exhibited high predictive capacity for all 10 wasp species: the mean Test AUC was 0.937 (92.7–96.3%), and the Training AUC was 0.985 (94.1–99.9%). The difference between Training and Test AUC was minor (mean 0.039, maximum 0.046), indicating a lack of overfitting and high predictive generalization ability.

Predicted habitat suitability generally aligned with species distributions. The investigated species are distributed across various natural zones, primarily in temperate and colder regions [Gorodkov, 1991].

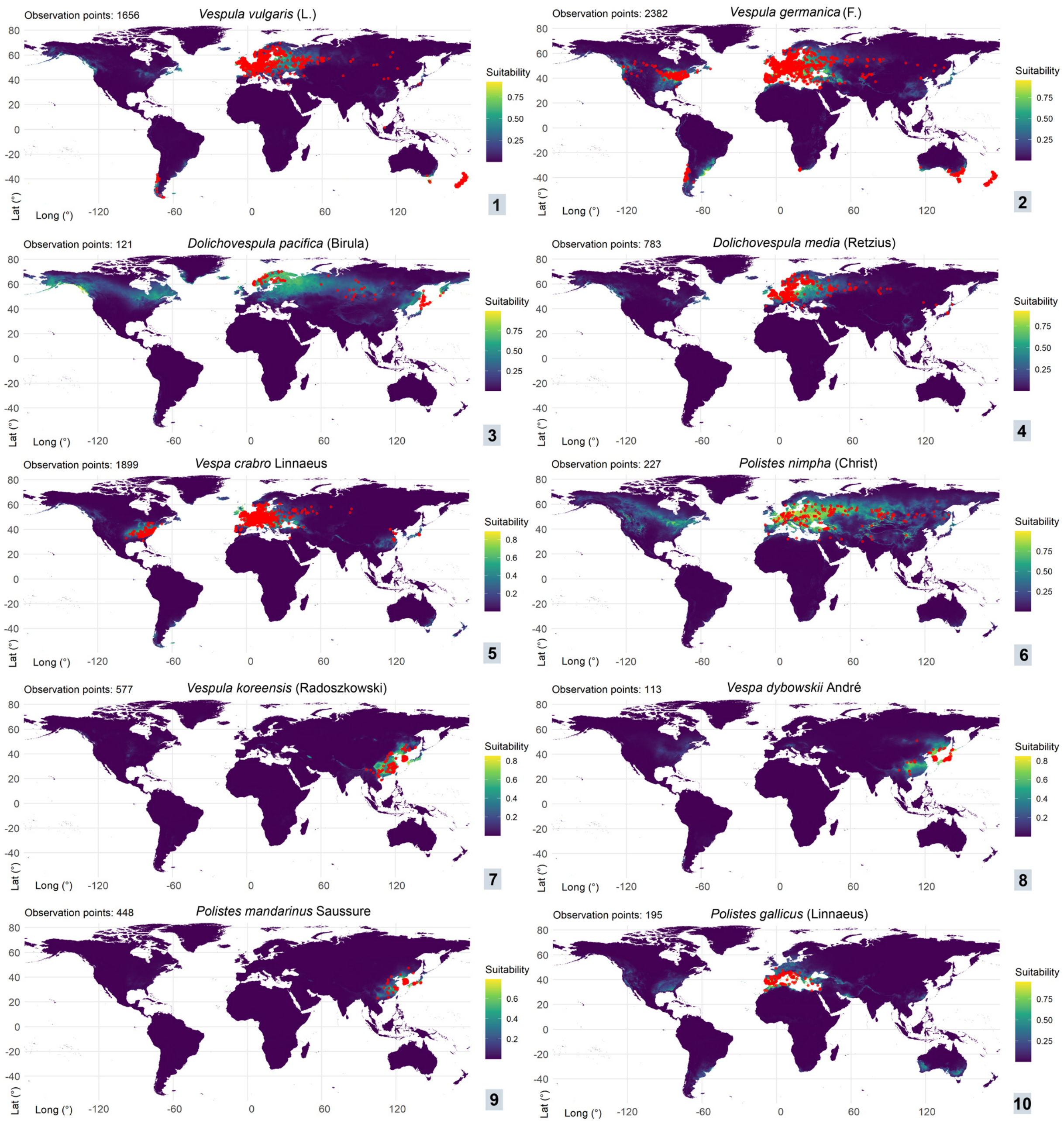
Six wasp species are trans-Palearctic in distribution, *Dolichovespula media* (polytropical, temperate and cold region), *D. pacifica* (boreal), *P. nimpha* (sub-boreal), *V. germanica* (arctic, widely invasive cosmopolitan), *V. crabro* (arctic polytropical), and *V. vulgaris* (polytropical), exhibiting broad ranges and correspondingly extensive habitat suitability, particularly *D. pacifica* and *P. nimpha* (Figs 1–6).

Three East Asian species, *P. mandarinus* (temperate warm-region), *V. dybowskii* (non-temperate), and *V. koreensis* (temperate), are characterized by restricted and fragmented areas of high suitability. The largest predicted area for *V. dybowskii* is observed (Figs 7–9).

One Mediterranean species, *P. gallicus*, currently has a limited range, but possesses significant potential for expansion, primarily in the north-western and central regions of the study area, under favorable environmental conditions (Fig. 10).

An analysis of the contribution of variables (Fig. 11) revealed that for transpalearctic species, the key limiting factors are temperature variables determining the overall level of thermal energy, which are critical for defining thermal zones (arctic, boreal, temperate, tropical) — bio_1 (mean annual temperature), bio_6 (a key factor in determining frost resistance), and bio_10 (mean temperature of the warmest quarter).

For the successful dispersal of East Asian species, the most important factors are isothermality (bio_3 shows what proportion of annual temperature variability is accounted for by diurnal fluctuations) and the amount



Figs. 1–10. Maps of predicted habitat suitability for 10 wasp species (Hymenoptera: Vespidae) based on MaxEnt models. 1 — *Vespula vulgaris* (Linnaeus); 2 — *Vespula germanica* (Fabricius, 1793); 3 — *Dolichovespula pacifica* (Birula, 1930); 4 — *Dolichovespula media* (Retzius, 1783); 5 — *Vespa crabro* Linnaeus, 1758; 6 — *Polistes nimpha* (Christ, 1791); 7 — *Vespula koreensis* (Radoszkowski, 1887); 8 — *Vespa dybowskii* André, 1884; 9 — *Polistes mandarinus* Saussure, 1853; 10 — *Polistes gallicus* (Linnaeus, 1767). Designations: The colour scale represents the probability of species occurrence, 0 — unsuitable to 1 — high-suitability habitat, red points represent the presence locations of the species.

Рис. 1–10. Карты потенциальной пригодности местообитаний для 10 видов ос (Hymenoptera: Vespidae) на основе моделей MaxEnt. 1 — *Vespula vulgaris* (Linnaeus); 2 — *Vespula germanica* (Fabricius, 1793); 3 — *Dolichovespula pacifica* (Birula, 1930); 4 — *Dolichovespula media* (Retzius, 1783); 5 — *Vespa crabro* Linnaeus, 1758; 6 — *Polistes nimpha* (Christ, 1791); 7 — *Vespula koreensis* (Radoszkowski, 1887); 8 — *Vespa dybowskii* André, 1884; 9 — *Polistes mandarinus* Saussure, 1853; 10 — *Polistes gallicus* (Linnaeus, 1767). Обозначения: цветовая шкала показывает вероятность присутствия вида от 0 — непригодные до 1 — высокопригодные местообитания, красные точки — места присутствия вида.

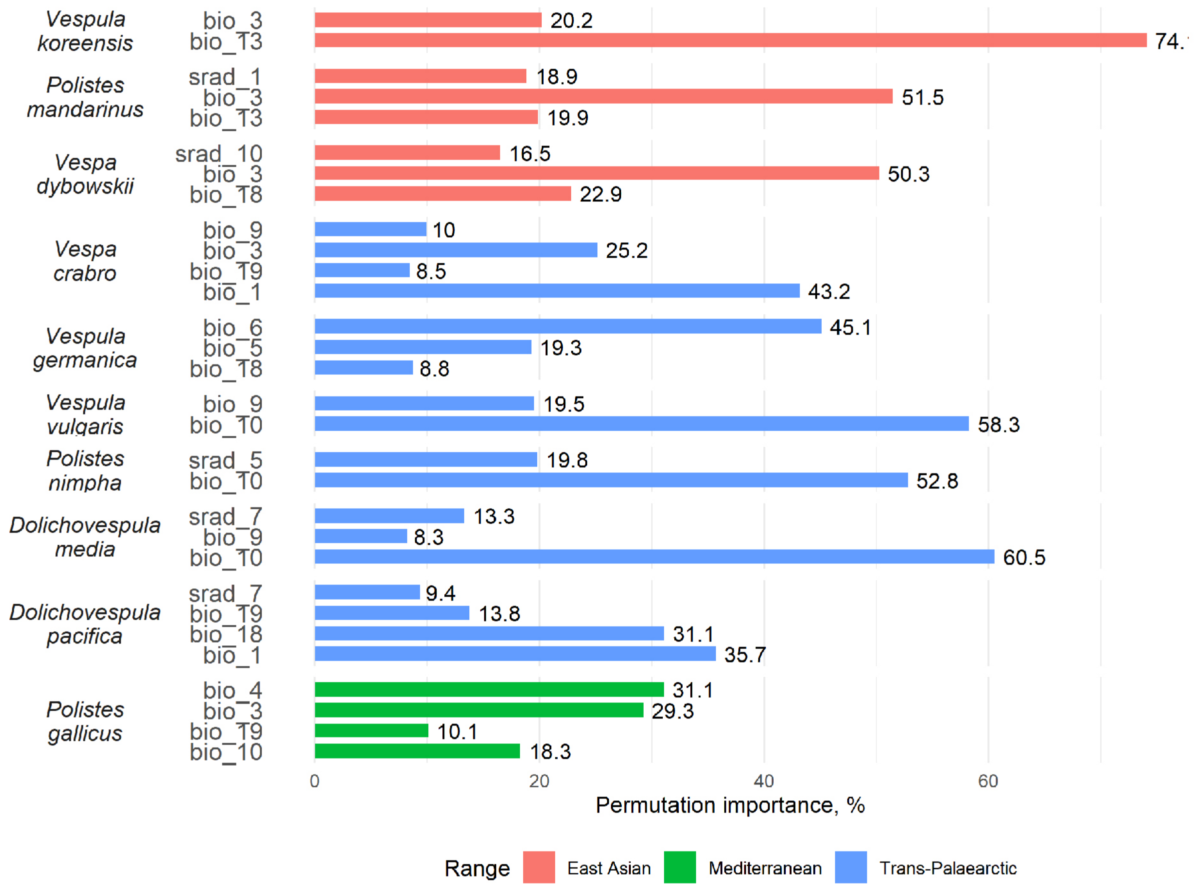


Fig. 11. Permutation importance for MaxEnt models of 10 wasp species (Hymenoptera: Vespidae).
Рис. 11. Важность предикторов (permutation importance) для моделей MaxEnt 10 видов ос (Hymenoptera: Vespidae).

of precipitation in the wettest month (bio_13 shows the risk of flooding and maximum water availability). The Central Asian species *P. gallicus* is also associated with the temperature predictors isothermality (bio_3) and seasonal variability (bio_4). The identified differences in the significance of the predictors are consistent with differences in the ecology of the species and the origin of their ranges.

In addition to temperature predictors, solar radiation (srad) had a significant effect on species distribution, with the contribution of solar radiation varying significantly across species depending on the season. For species with an early onset of the active season (*Polistes nimpha*), May radiation (srad_5) was key; for species with a midsummer peak (*D. media* and *D. pacifica*), July radiation (srad_7) was key; and for species apparently sensitive to wintering conditions (*Polistes mandarinus*), January radiation (srad_1) was key. The identified seasonal differentiation indicates differences in the phenology and ecology of the studied species.

Modelled ecological niches for the 10 wasp species allowed the prediction of changes in their potential ranges by 2060 and 2100 under two climate change scenarios: a moderate scenario (SSP2–4.5) and a pessimistic scenario (SSP5–8.5) (Fig. 12).

Species projected to experience range expansion: *Vespa crabro*, *V. germanica*, and *V. vulgaris*, these species already demonstrate high adaptability and invasive potential resulting from deliberate or unintentional introductions.

A key characteristic of the forecast is the non-linear dynamic: by 2060, a reduction in the area of suitable habitat is expected for many species, likely linked to approaching their thermal limits and increased precipitation variability. However, by 2100, particularly under the pessimistic scenario (SSP5–8.5), a significant expansion of ranges is predicted compared to the current level, indicative of potential species adaptation or a shift of climatic zones towards higher latitudes or polar regions.

Species projected to experience range contraction: *Dolichovespula pacifica*, *Vespula koreensis*, and *Polistes gallicus*. For these species, changes in climatic conditions are likely to result in the loss of suitable habitat, elevating the risk of local extinction.

Species exhibiting stable ranges: *Dolichovespula media*, *Polistes nimpha*, *Polistes mandarinus*, and *Vespa dybowskii*. The stability of these species' ranges may be explained by their broad ecological plasticity or by the persistence of their specific habitat requirements (e.g.,

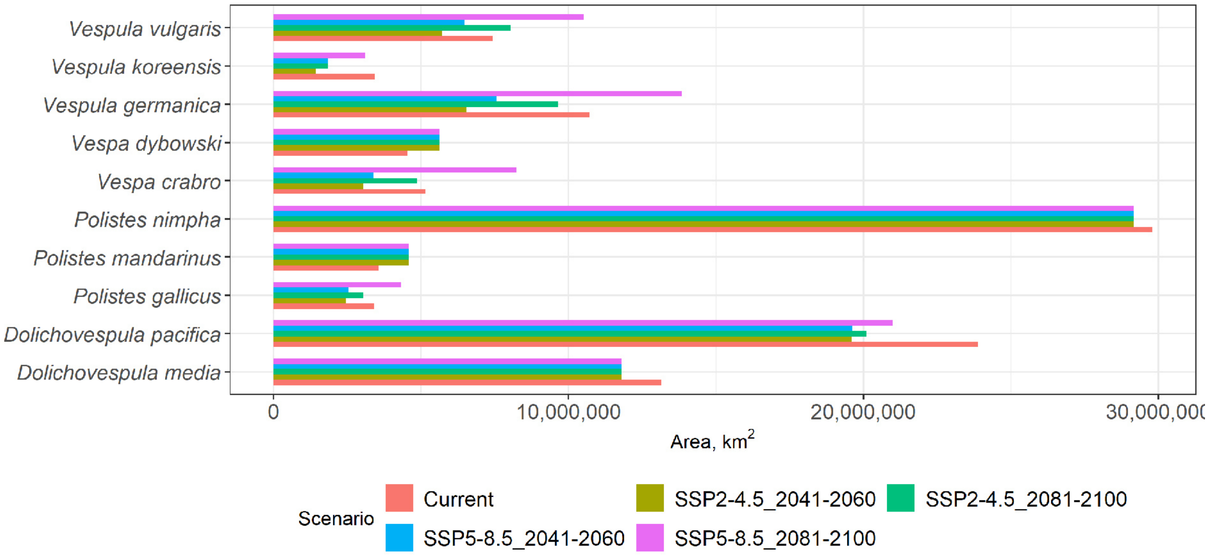


Fig. 12. Change in the distribution areas of 10 species of Vespidae under scenarios SSP2-4.5 and SSP5-8.5 (2060, 2100).
Рис. 12. Изменение площади ареалов 10 видов Vespidae при сценариях SSP2-4.5 и SSP5-8.5 (2060, 2100 гг.).

their restriction to temperate and subtropical zones) even under global climatic changes.

Therefore, expansion is predicted for three species, *V. crabro*, *V. germanica* and *V. vulgaris*, contraction for three species, *D. pacifica*, *V. koreensis* and *P. gallicus*, and stability for four species, *D. media*, *P. nimpha*, *P. mandarinus*, and *V. dybowskii*. A U-shaped dynamic was observed for most species: a decrease by 2060 followed by a subsequent increase by 2100. Species already demonstrating invasive potential will benefit and be able to significantly expand their ranges by the end of the century, aligning with the general pattern of range boundary shifts driven by global warming.

Discussion

The findings of this study, predicting future distributional shifts for wasp species under a range of climate change scenarios, underscore the significant vulnerability of insect communities to current and projected environmental changes. The high predictive capacity of MaxEnt models, combined with the U-shaped dynamic predicted for many species, highlights the complexity of insect responses to climate change, accentuating the potential for range shifts driven by temperature gradients, precipitation patterns, and solar radiation levels. Investigated wasp species demonstrated diverse ecological strategies in response to these global climate factors.

Several species, namely: *D. media, P. nimpha, P. mandarinus*, and *V. dybowskii,* exhibit stability in their predicted ranges, potentially reflecting a degree of adaptive capacity to their habitat. However, the predicted contraction of *D. pacifica, V. koreensis,* and *P. gallicus* requires particular attention, as these species appear sensitive to climate change and are at an elevated risk of local extinction.

The dominance of temperature as a key predictor, particularly through variables such as mean summer temperature and thermal homogeneity, aligns with established insect physiology, reflecting their ectothermic nature and dependence on temperature regulation. The influence of seasonal precipitation patterns, highlighted by variables such as summer rainfall, further underscores the importance of moisture availability in shaping species distributions.

Of particular concern is the fact that invasive species, such as *V. crabro, V. germanica,* and *V. vulgaris*, are predicted to significantly expand their ranges under future climate conditions, given their established ecological impact and demonstrated capacity for rapid colonization [Zhang et al., 2024; Bazzato et al., 2025]. These results convincingly support the need for enhanced monitoring and management strategies directed toward these high-risk species.

This study indirectly addresses a growing issue: the potential role of insects, specifically wasps, in the dispersal of microplastics (MPs) within terrestrial ecosystems [Rodrigues et al., 2023]. Predicted range shifts of *V. crabro, V. germanica,* and *V. vulgaris,* particularly in areas with increasing anthropogenic activity, raise concerns regarding their potential to accumulate and transport MPs, given the demonstrated foraging plasticity of these wasps [Lee et al., 2024, 2025]. Beyond potential MP accumulation in the guts and subsequent translocation within wasp ontogeny, the incorporation of synthetic fibres into nest construction by some social wasp species has also been noted [Maciel et al., 2025].

Global climate change influences physical, biological, and ecological processes in the environment, potentially impacting MP uptake and fate within biota and food chains through various mechanisms [De Wit et al., 2022]. Predictably, climate change, particularly in the northern extent of the range (shifts in the ranges of subarctic and temperate terrestrial species), may alter many processes, potentially leading to either reduced or increased pollutant exposure at the base of food chains and changes in trophic structure [Liaqat et al., 2024].

Future research should deliberately investigate the prevalence of microplastics within wasp guts and nest material, as well as model the potential for MP translocation during nest building and foraging activities. This link between climate-driven range shifts and the potential for microplastic dispersal represents a critical, often overlooked, pathway for understanding the cascading consequences of environmental change on biodiversity and ecosystem health.

This study provides a foundation for understanding the vulnerability of wasp communities to climate change and defining key areas for future research. Further investigations should focus on including more detailed ecological data, encompassing soil moisture, land-use changes, and the impact of invasive species, and the explicit modelling of the microplastic dispersal pathway adds a critically important dimension to this analysis.

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