

Global niche dynamics of two invasive *Aedes* mosquitoes, *Aedes japonicus* and *Aedes koreicus* (Diptera: Culicidae), using comprehensive native and non-native occurrence data

Sangwoo Seok

seok.s@ufl.edu

University of Florida

Jiyeong Shin

Seoul National University

Woo Jun Bang

Seoul National University

Motoyoshi Mogi

Saga University

Yoosook Lee

University of Florida

Research Article

Keywords: niche convergence, niche dynamics, species distribution models, invasive mosquitoes

Posted Date: May 21st, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-9381631/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Additional Declarations: No competing interests reported.

Version of Record: A version of this preprint was published at Parasites & Vectors on August 3rd, 2026.
See the published version at <https://doi.org/10.1186/s13071-026-07596-7>.

Abstract

Background

Identifying areas at risk of invasion is essential for effective surveillance and management of invasive species. Two invasive mosquito species originating from East Asia, *Aedes japonicus* and *Aedes koreicus*, are of importance in Europe and America. Whether these invasive mosquitoes retain their environmental niches after introduction remains uncertain. Moreover, niche dynamics of these species, particularly for *Ae. koreicus*, remain poorly understood. This study aimed to quantify niche dynamics of both species by comparing environmental niches between native and non-native populations.

Methods

We compiled occurrence records of *Ae. japonicus* and *Ae. koreicus* after from published sources, databases, and field collections, and applied data clearing and spatial filtering to reduce sampling bias. The final dataset included 2,623 for *Ae. japonicus* and 501 for *Ae. koreicus*. Environmental space was defined using selected bioclimatic variables and elevation. Within this space, we quantified niche overlap and dynamics using Schoener's D and metrics of stability, expansion, and unfilling across species, regions, and invasion statues.

Results

The two species occupied distinct niches in their native ranges but showed niche convergence in their non-native ranges. For both species, niche comparisons between native and non-native populations revealed subtle but significant niche differentiation. Niche dynamic analyses indicate high niche stability (0.821 in *Ae. japonicus* and 0.776 in *Ae. koreicus*) with low niche overlap values. Native subpopulation comparisons suggested potential invasion origins, with the Japanese population likely representing the source of *Ae. japonicus* and the Chinese population representing a potential additional source for *Ae. koreicus*.

Conclusion

Our results show that these two invasive mosquito species exhibit convergent niche shifts after introduction. Niche comparisons between native and non-native populations show niche differentiation for both species and also provide insights into invasion origins. Incorporating comprehensive native occurrence data is critical for improving predictions of invasion risk and supporting surveillance and management of invasive mosquito species.

Background

Identifying areas at risk of invasion is crucial for the effective surveillance and management of invasive species. Early detection and rapid response are key components of invasion management because interventions implemented at early stages of invasion are more likely to be successful and cost-effective [1]. For example, the early detection of *Aedes aegypti* in Australia was followed by rapid management actions, resulting in successful elimination [2]. Moreover, continuous surveillance of disease-associated mosquitoes is generally more cost-effective than responding after pathogen introduction, which often requires substantially higher management and response costs [3].

To aid early detection of invasive species in non-native ranges, species distribution models (SDMs) are widely used to predict invasion risk areas of invasive species [4–8]. These models typically combine occurrence data, particularly from the native range of the target species, with climate variables to estimate the realized environmental niche. Such projections rely on niche conservatism, which assumes that the target species maintain similar environmental niches when they establish in non-native ranges [9]. Therefore, before applying SDMs to predict their potential invasion areas, it is important to verify whether invasive species retain their environmental niche and whether the available data adequately represent their native distribution [10].

Two closely related *Aedes* mosquito species, *Aedes japonicus* (Theobald, 1901) and *Aedes koreicus* (Edwards, 1917), originate from East Asia [11, 12]. Both species are members of the Japonicus group, which also includes several species formerly regarded as subspecies of *Ae. japonicus* before being elevated to species status, such as *Ae. shintienensis* [13]. *Aedes japonicus* (often referred to as *Aedes japonicus japonicus* in earlier literature) has established invasive populations in America in 1998 and Europe in 2000 [11, 14]. *Aedes koreicus* has established invasive populations in Europe in 2008 [8, 15, 16]. Although neither species is currently regarded as a primary vector of arthropod-borne viruses (arboviruses) circulating in Europe and/or America, both *Ae. japonicus* and *Ae. koreicus* have demonstrated competence for several arboviruses in experimental studies, indicating their potential contribution to pathogen transmission [17, 18].

Although several SDM studies have examined the potential distribution of *Ae. japonicus* and *Ae. koreicus*, studies explicitly addressing their niche conservatism remain very limited [4–8]. One study has examined niche dynamics of *Ae. japonicus*, reporting high niche stability and low niche expansion during invasion [4]. However, the study did not define the native environmental niche using empirical occurrence data. Instead, the model assumed that *Ae. japonicus* is distributed across the entire Palearctic region of Japan and South Korea. This assumption may include environmentally unsuitable areas with extreme climatic, potentially leading to overestimation of the environmental niche occupied by the species in its native range. Consequently, the extent to which environmental niches differ between native and non-native populations of *Ae. japonicus* remains uncertain. In addition, to our knowledge, no study has yet investigated niche dynamics of *Ae. koreicus*. From a management perspective, such uncertainty can lead to inaccurate SDM-based risk assessment, thereby resulting in misidentification of areas at risk of invasion and inefficient surveillance and control strategies.

The inconsistency in niche dynamics reported in other invasive *Aedes* species makes it difficult to draw universal conclusions [19–21]. Some studies suggested a niche shift in *Ae. albopictus* [19, 21], whereas another study supported niche conservatism in *Ae. albopictus* [20]. One study suggested niche conservatism in *Ae. aegypti* [20], while a following study using a more comprehensive occurrence dataset again reported niche shifts in *Ae. aegypti* [21]. These contrasting findings suggest that conclusions about niche dynamics may be sensitive to the completeness and representativeness of occurrence data. Consequently, incorporating a comprehensive dataset is critical for accurately characterizing environmental niches and assessing niche dynamics during biological invasions.

To address this uncertainty, this study aims to compare environmental niches of native and non-native populations of *Ae. japonicus* and *Ae. koreicus* using comprehensive occurrence datasets. Specifically, we (1) evaluate niche differentiation between the two species, (2) examine geographic niche variation among native subpopulations, and (3) assess niche dynamics between native and non-native populations during invasions.

Methods

Occurrence records

Occurrence records of *Ae. japonicus* since 1980 were collected from research articles [22–113] and an online database [114]. Occurrence data for *Ae. koreicus* were obtained from datasets used in previous SDM studies [7, 8], as well as from subsequently published articles [30, 115, 116] and an online database [117]. In addition, we incorporated personal collection records of both species collected in Korea and Japan between 1980 and July 2025 by the authors (SS, JS, WJB, and MM). These specimens were obtained using various collection methods, including larval sampling, BG traps, aspiration, sweeping, and ovitraps. Sampling sites covered a wide range of environments, from urban areas to natural habitats, and from seacoasts to mountainous areas (up to 2,000 m).

We retained only coordinates reported to at least two decimal places in the WGS 84 geographic coordinate system, representing a spatial resolution on the order of hundreds of meters to about one kilometer. Duplicate records were subsequently removed. The compiled dataset included records of *Ae. japonicus* from the Oriental region, such as southern China, Hong Kong, Ryukyu Islands (Japan), and Philippines. However, *Ae. japonicus* is a species native to the Palearctic region [97], and records reported from the Oriental region are likely to represent other morphologically similar species belonging to the Japonicus group. Records of *Ae. japonicus* from southern China may reflect *Ae. shintienensis*, a species formerly treated as a subspecies of *Ae. japonicus* before being elevated to species status [13]. These records with taxonomic uncertainty were therefore excluded for both species. Several records of *Ae. koreicus* from Canada were removed because no published studies have documented the occurrence of *Ae. koreicus* in North America. To minimize potential sampling bias caused by high sampling density, we further applied spatial thinning by treating occurrence points located within 3 km of each other as

duplicates, and only one record was retained using *spThin* package version 0.2.0 [118]. This threshold was chosen based on the average flight distance of female *Ae. japonicus* is approximately 2 km [119].

Environmental space and principal components analysis

To define a unified geographical extent, we first combined occurrence coordinates of *Ae. japonicus* and *Ae. koreicus* from both native and non-native ranges. We then added a spatial buffer of 1 degree to the minimum and maximum values of longitude and latitude of the combined coordinates. The resulting extent defined the environmental extent for all subsequent analyses. Within the defined environmental extent, we randomly sampled 10,000 background points to represent background environmental conditions.

We obtained nineteen bioclimatic variables from the WorldClim database version 2.1 [120], representing average climatic conditions from 1970 to 2000. All climatic variables had a spatial resolution of 30 arc seconds (approximately 1 km at the equator). Elevation variable with 1 km resolution was obtained from the EarthEnv database [121], derived from the global digital elevation model GMTED2010 [122]. To reduce multicollinearity among the 20 variables, we calculated variance inflation factors (VIFs) using background environmental data and excluded variables with VIF values greater than 5. The remaining eight variables used for further analysis were Bio2, Bio3, Bio8, Bio9, Bio14, Bio15, Bio18, Bio19, Elevation (Supplementary Table S1).

We extracted the nine environmental variables at both background points and occurrence locations of the two species. Occurrence records lacking complete environmental data were excluded. Following the PCA-env framework [123], we performed principal component analysis (PCA) on the combined dataset of background and occurrence environmental variables to reduce dimensionality and define a shared environmental space. The first two principal components (PC1 and PC2) were retained because they explained the majority of environmental variance. We examined variable loadings on each principal component to interpret the environmental gradients represented by PC1 and PC2. This two-dimensional environmental space was subsequently used for all niche comparisons among species, populations, and subpopulations.

Niche analyses

We evaluated niche relationships across multiple comparison types defined by species (*Ae. japonicus* and *Ae. koreicus*), distribution status (native and non-native), and geographic subdivision (Japan, Korea, China, America, and Europe). First, we conducted interspecific niche comparisons between *Ae. japonicus* and *Ae. koreicus* to assess overall niche differentiation between the two species. Second, we performed intraspecific comparisons between native subpopulations to evaluate geographic niche differentiation within each species. For *Ae. japonicus*, native populations were subdivided into Japanese and Korean subpopulations. For *Ae. koreicus*, native populations were subdivided into Chinese and Korean

subpopulations. Third, we compared native and non-native populations within each species to assess niche conservatism during invasion. For *Ae. japonicus*, non-native populations were subdivided into American and European subpopulations, and each was compared with the native population. For *Ae. koreicus*, the non-native population was compared with the native population. Occurrence records from Russia Far East and North Korea were excluded from niche analysis because of insufficient sample size ($N < 3$).

Ecological niche overlaps were quantified using Schoener's D, which measures the overlap between probability distribution of two niches in environmental space and ranges from 0 (no overlap) to 1 (complete overlap) [123]. Because niche overlap value alone does not fully describe how niches change during invasion, niche dynamics were additionally quantified using three complementary metrics: niche stability, niche expansion, and niche unfilling [124]. Niche stability represents the proportion of overlap between native and non-native niches relative to the non-native niche, niche expansion indicates the occupation of novel environmental conditions in the non-native ranges, and niche unfilling represents portions of the native niches that remain unoccupied in the non-native ranges relative to the native niche (Fig. 1).

We calculated niche overlap using Schoener's D within a PCA-based environmental space. We also conducted niche equivalency tests and bidirectional niche similarity tests to determine whether observed niche overlaps differed from random expectations [125]. Niche dynamics (stability, expansion, and unfilling) were calculated for comparisons between native and non-native populations. All niche analyses were performed using *ecospat* package version 4.1.2 [126] in R version 4.5.0 [127].

Results

Occurrence records

After all data preprocessing steps, the dataset comprised 2,623 occurrence records for *Ae. japonicus* (171 native and 2,452 non-native occurrence records) and 501 occurrence records for *Ae. koreicus* (138 native and 363 non-native occurrence records) (Supplementary Table S2) (Fig. 2). *Aedes japonicus* is distributed across its native range in Japan and Korean Peninsula and widely established throughout Europe and America. In this study, records from Hawaiian Islands were regarded as American population. *Aedes koreicus* is distributed across continental East Asia and parts of Europe. The distributions of the two species geographically overlap in the Korean Peninsula and in some parts of Europe.

Environmental space and principal components analysis

The two principal components captured 56.9% of environmental variance (PC1: 38.2%, and PC2: 18.7%) (Fig. 3). The three variables most strongly associated with PC1 were Bio14 (precipitation of driest month: 0.887), Bio2 (mean diurnal range: -0.777), and Bio15 (precipitation seasonality: -0.775). PC2 was

mainly associated with Bio9 (mean temperature of driest quarter: -0.819), Bio3 (isothermality: -0.639), and Elevation (elevation: 0.534) (Supplementary Table S1). The environmental space defined by these two axes was used in subsequent niche comparisons between native and non-native populations of *Ae. japonicus* and *Ae. koreicus*.

Niche analysis between *Ae. japonicus* and *Ae. koreicus*

Interspecific niche comparisons revealed contrasting patterns depending on whether native or non-native populations were included. When all global occurrence records were included, the two species showed high niche overlap ($D = 0.424$) with no evidence of niche differentiation, and similarity tests indicated significant niche similarity in both directions ($p = 0.007$ and $p = 0.034$) (Table 1). In native populations, significant niche differentiation was detected ($D = 0.102$, $p < 0.001$), whereas non-native populations showed no significant differentiation ($D = 0.327$, $p = 0.138$), with significant niche similarity in both directions ($p = 0.016$ and $p = 0.035$), indicating niche convergence in non-native ranges. Similar contrasting niche patterns were also observed in PCA-based environmental space. When non-native populations or all global populations were compared, the 95% confidence ellipses of the two species overlapped extensively (Fig. 4A, 4C). In contrast, when only native populations were considered, partial overlap was observed (Fig. 4B).

Table 1

Interspecific niche overlaps and statistical tests between *Aedes japonicus* and *Aedes koreicus* across global, native, and non-native populations. Schoener's D (D) indicates niche overlap (0 = no overlap, 1 = complete overlap). Equivalency (Eq.) tests assess whether the niches of the two species are statistically equivalent. Similarity (Sim.) tests evaluate whether niche overlap is greater than expected by chance in both directions: from *Ae. japonicus* to *Ae. koreicus* (1→2) and from *Ae. koreicus* to *Ae. japonicus* (2→1).

<i>Aedes japonicus</i>	<i>Aedes koreicus</i>	D	Eq. p value	Sim. (1→2) p value	Sim. (2→1) p value
Global	Global	0.424	1	0.007	0.034
Native	Native	0.102	< 0.001	0.237	0.456
Non-native	Non-native	0.327	0.1379	0.016	0.035

Niche analysis among *Ae. japonicus* subpopulations

Niche overlap analysis revealed clear differentiation among *Ae. japonicus* subpopulations. The Japanese and Korean native populations showed low niche overlap ($D = 0.125$), and the niche equivalency test indicated that their niches were significantly different ($p < 0.001$) (Table 2). Similarity tests were not significant in either direction ($p > 0.05$), suggesting that the niches of these native subpopulations were not more similar than from random distribution. Native subpopulations in PCA-based environmental space showed partial overlap, with the Japanese population extending toward positive values along PC1 and negative values along PC2 (Fig. 5A), indicating higher precipitation of driest month and coldest quarters.

Comparisons between native and non-native populations showed moderate niche overlap ($D = 0.205\text{--}0.216$), with equivalency tests consistently showing significant niche differentiation across all comparisons ($p < 0.001$) (Table 2). Niche dynamic analysis revealed high niche stability ($0.693\text{--}0.909$) and relatively low unfilling ($0.095\text{--}0.192$), indicating that a large portion of the native niche was retained in the non-native range. The 95% confidence ellipses of native and non-native populations of *Ae. japonicus* in PCA-based environmental space largely overlapped (Fig. 5B). In the non-native population, occurrences were more broadly distributed along the negative PC2 axis compared with the native populations. This pattern was more apparent when only the American *Ae. japonicus* population was considered (Fig. 5C), whereas the niche of the European *Ae. japonicus* population largely overlapped with the native *Ae. japonicus* population (Fig. 5D).

Comparisons among subpopulations generally showed low to moderate niche overlap ($D = 0.106\text{--}0.226$), and all equivalency tests indicated significant differences between niches of the subpopulations (Table 2). Notably, comparisons involving the Japanese *Ae. japonicus* population as a native subpopulation generally exhibited higher niche stability ($0.711\text{--}0.829$) than those involving the Korean *Ae. japonicus* subpopulation ($0.221\text{--}0.326$). Similarly, in PCA-based environmental space, the non-native *Ae. japonicus* population overlapped more with the Japanese *Ae. japonicus* population than with the Korean *Ae. japonicus* population (Fig. S1).

Niche analysis among *Ae. koreicus* subpopulations

Niche overlap analysis revealed clear differentiation between the native subpopulations of *Ae. koreicus*. The Chinese and Korean *Ae. koreicus* populations showed very low niche overlap ($D = 0.066$), and the niche equivalency test indicated that their niches were significantly different ($p < 0.001$) (Table 2). The similarity tests were not significant in either direction ($p > 0.05$), indicating that the niches of these native *Ae. koreicus* subpopulations were not more similar than expected. In PCA-based environmental space, the Korean *Ae. koreicus* population had a considerably narrower niche than the Chinese *Ae. koreicus* population (Fig. 6A).

Comparisons between native and non-native *Ae. koreicus* populations showed very low niche overlap ($D = 0.083$), and the equivalency test showed significant niche differentiation ($p < 0.001$) (Table 2). Niche dynamics analysis indicated moderate niche stability (0.776), with substantial niche unfilling (0.562) for *Ae. koreicus*. Most non-native *Ae. koreicus* occurrences fell within the native niche and were located relatively toward the positive side of PC1 and the negative side of PC2, suggesting that precipitation of driest month (Bio14) and precipitation of coldest quarter (Bio19) are most contributing variables for the non-native *Ae. koreicus* population (Fig. 6B).

Comparisons among *Ae. koreicus* subpopulations also showed low niche overlap ($D = 0.049\text{--}0.144$), and all equivalency tests indicated significant differences between niches (Table 2). Niche stability and expansion were similar between the Chinese and Korean *Ae. koreicus* subpopulations. Non-native *Ae. koreicus* occurrences did not fall clearly within either niche of native populations but instead overlapped to a similar extent with the niches of both the Chinese and Korean *Ae. koreicus* populations (Fig. S2).

Table 2

Intraspecific niche overlaps and statistical tests between subpopulations of *Aedes japonicus* and *Aedes koreicus*. Schoener's D (D) indicates niche overlap (0 = no overlap, 1 = complete overlap). Equivalency (Eq.) tests assess whether the niches of the two species are statistically equivalent. Similarity (Sim.) tests evaluate whether niche overlap is greater than expected by chance in both directions: from the first population (Pop 1) to the second population (Pop 2) (1→2) and from Pop 2 to Pop 1 (2→1).

Pop 1	Pop 2	D	Eq. p value	Sim. (1→2) p value	Sim. (2→1) p value	Stability	Expansion	Unfilling
<i>Aedes japonicus</i>								
Japanese	Korean	0.125	< 0.001	0.914	0.388			
Native	Non-native	0.205	< 0.001	0.541	0.747	0.821	0.179	0.099
Native	American	0.215	< 0.001	0.402	0.613	0.693	0.307	0.095
Native	European	0.216	< 0.001	0.684	0.837	0.909	0.091	0.192
Japanese	Non-native	0.209	< 0.001	0.544	0.729	0.829	0.171	0.107
Japanese	American	0.186	< 0.001	0.465	0.686	0.711	0.289	0.115
Japanese	European	0.226	< 0.001	0.682	0.768	0.916	0.084	0.178
Korean	Non-native	0.122	0.003	0.392	0.882	0.278	0.722	0.035
Korean	American	0.134	0.003	0.294	0.691	0.221	0.779	0.012
Korean	European	0.106	< 0.001	0.208	0.985	0.326	0.674	0.298
<i>Aedes koreicus</i>								
Chinese	Korean	0.066	< 0.001	0.736	0.647			
Native	Non-native	0.083	< 0.001	0.511	0.759	0.776	0.224	0.562
Chinese	Non-native	0.049	< 0.001	0.406	0.878	0.522	0.478	0.827
Korean	Non-native	0.144	< 0.001	0.381	0.881	0.456	0.544	0.195

Discussion

Environmental factors affecting distribution of *Ae. japonicus* and *Ae. koreicus*

Considering the variable loading and the distribution patterns in the PCA-based environmental space, niche differentiation between the two species is likely associated with elevation and precipitation-related variables: precipitation of driest month (Bio14), precipitation seasonality (Bio15), and precipitation of coldest quarter (Bio19) (Fig. 3). *Aedes japonicus* tended to occupy environments with higher precipitation during the driest month and coldest quarter and lower precipitation seasonality, indicating a preference for humid habitats with relatively stable moisture conditions throughout the year. In contrast, *Ae. koreicus* was more associated with higher seasonal precipitation and higher elevations. This pattern is well reflected in the distribution observed in Korea, where the two species co-occur but *Ae. koreicus* is predominant while *Ae. japonicus* is relatively rare [128]. The Korean Peninsula is characterized by its extensive mountainous terrain and highly seasonal precipitation, which closely align with the favorable environmental niche of *Ae. koreicus*.

Niche convergence of *Ae. japonicus* and *Ae. koreicus* in their non-native ranges.

Although *Ae. japonicus* and *Ae. koreicus* occupy statistically different environmental niches within their native ranges, their niches partially overlap in environmental space (Fig. 4). This partial overlap indicates that the two species are not completely ecologically segregated in their native environments and may have facilitated the niche convergence of the two species observed after introduction into non-native habitat. When introduced into non-native regions, both species likely encountered climatic conditions that differ from those in their native habitats, potentially promoting rapid niche shifts [129]. In addition to these shifts, the observed convergence may also arise from shared ecological constraints among closely related species during establishment in non-native regions. Closely related taxa often exhibit similar physiological tolerances and climatic requirements due to phylogenetic niche conservatism [130]. Both *Ae. japonicus* and *Ae. koreicus* belong to the Japonicus Group [13] and share key ecological traits, including container-breeding life histories and association with temperate climates [11, 128]. Also, both species co-occur in the same habitats in parts of their native [128, 131] and non-native ranges [24]. These shared characteristics may restrict the range of environmental conditions that both species can successfully exploit, thereby producing overlapping realized niches in non-native regions. How stable their niches will be in non-native ranges and whether their range will shift closer to the native niche over a longer period of time in non-native ranges remains to be determined.

Niche shift of *Ae. japonicus* and *Ae. koreicus*

Niche overlaps and dynamics reveal consistently high stability but low Schoener's D across multiple population comparisons (Table 2). The high stability values indicate that invasive populations remain within the environmental niche space that their native populations occupy rather than expanding into non-native environmental ranges for *Ae. japonicus* and *Ae. koreicus*. Nonetheless, Schoener's D values in this study, under previously proposed classification criteria [129], were classified as very limited overlap

or low overlap, indicating subtle differences in environmental preferences between *Ae. japonicus* and *Ae. koreicus*. This implies that the specific combinations or gradients of environmental conditions preferred by non-native populations may have shifted. Such differentiation may reflect local adaptation during the establishment process in non-native regions [132]. Alternatively, non-native populations may originate from specific native subpopulations rather than representing the full native distributions, resulting in the occupation of only a subset of the native environmental niche [133].

In *Ae. japonicus*, niche dynamic analyses revealed slightly higher niche expansion in American populations than in European populations (Table 3), consistent with findings from previous niche study [4]. This pattern may be associated with multiple independent introduction events into Hawai'i, eastern North America and western North America [37, 134], with distinct genetic lineages potentially contributing to a broader environmental niche range.

In *Ae. koreicus*, the non-native population in Europe occupied a much narrower niche range than the native population, with low expansion and high unfilling values (Table 3). This pattern implies that only a small portion of the native population was introduced, resulting in occupation of only a limited part of the entire native niche. Alternatively, the shorter invasion history of *Ae. koreicus* (first report in 2008) compared to *Ae. japonicus* (first report in 1998) may explain high unfilling [14, 15]. Of note, this species has not been observed in the American continent as of March 2026. The high unfilling value may indicate the potential for further expansion as invasion progresses [125].

Inference on source population of *Ae. japonicus* and *Ae. koreicus*

Niche analysis can provide insights into the identification of potential source populations [135]. For *Ae. japonicus*, higher stability values of the Japanese subpopulation compared to the Korean subpopulations may suggest that the Japanese *Ae. japonicus* subpopulation represent a potential source of the non-native *Ae. japonicus* subpopulations in America and Europe (Table 2). This is consistent with previous findings that North American populations of *Ae. japonicus* are genetically more closely related to the Japanese population than to the Korean population [136].

For *Ae. koreicus*, our results raise questions about the prevailing hypothesis that the European population originated solely from the two Korean *Ae. koreicus* populations: the Korean mainland and Jeju Island [15, 16]. In this study, the Chinese *Ae. koreicus* population exhibited slightly higher stability values than the Korean population, suggesting that it may represent an additional potential source of European populations (Table 2).

To date, genetic reference data representing native populations have been largely limited to a small number of Korean samples of two species [136, 137], and these datasets are predominantly based on analyses of a restricted set of genetic markers. The limited representation of native populations, together with the inherent limitations of marker-based approaches, suggests that previous interpretations regarding the origin of European invasive *Ae. koreicus* populations may have been influenced by incomplete geographic sampling. Future studies incorporating whole-genome comparisons

across multiple native populations will therefore be essential for accurate inference of the origins of invasive *Ae. koreicus* populations.

Influence of underlying data on the niche prediction

Our results underscore the importance of incorporating native occurrence data for accurate prediction of the potential global distribution of these two invasive species. Expansion values of 0.179–0.224 observed in comparisons between native and non-native populations indicate that having non-native occurrence records alone do not fully capture the environmental niche of the native range (Table 2). Despite this importance, previous studies have been limited by the unavailability of reliable native occurrence data. Native occurrence records for *Ae. japonicus* were overrepresented in native ranges [4], and those for *Ae. koreicus* have been constrained by a limited number of occurrence records given their wide geographic extent [7, 8]. To address these limitations, we compiled a comprehensive dataset of native occurrences by integrating published literature, public databases, and previously unpublished field collections conducted by the authors across Korea and Japan. In particular, we incorporated records from literature that have been underutilized in previous studies due to language barriers. At the same time, we carefully evaluated the taxonomic validity of the records to ensure that the occurrence data for both species were compiled as accurately as possible. By incorporating native occurrence data that were previously underutilized, our study provides a more comprehensive characterization of the environmental niche of these two important invasive mosquito species that have crossed continental boundaries. These improved niche representations can enhance not only SDM performance, but also other niche-based predictive modelling frameworks used to support surveillance and management of invasive mosquito species.

Despite our effort, this study may not have fully captured the full extent of native niche. Occurrence records from North Korea are extremely limited. However, given that both species are present in South Korea, it is highly likely that the two species also occur in North Korea. Therefore, this limitation may lead to incomplete representation of the native niche. In addition, the distribution of *Ae. japonicus* in China and Russia remains uncertain. Literature from the 1980s and 1990s reported its presence in these regions [138–140], but it is unclear whether these records represent *Ae. japonicus* or other species of the Japonicus group that were previously treated as subspecies. As we couldn't find subsequent records confirming the presence of *Ae. japonicus* in China and Russia, we assumed that these earlier records likely represent other species within the Japonicus group, such as *Ae. shintienensis*. Clarifying the distributional status of species of the Japonicus group would improve understanding of niche dynamics and prediction.

Conclusion

This study examined niche shift and dynamics in two closely related invasive mosquito species, *Ae. japonicus* and *Ae. koreicus*, which represent rare cases of mosquitoes crossing continental boundaries

and establishing in non-native regions. Our results revealed three main findings. First, although the two species occupied distinct environmental niches in their native ranges, their niches showed convergence in the non-native ranges. Second, non-native populations of both species occupied niches that differed significantly from those of their native populations. Subtle but significant differences in environmental preferences between native and non-native populations imply that invasive populations may represent only a subset of the native niche or may undergo local adaptation following introduction. Third, specific native subpopulations may have contributed to shaping the niches of the non-native populations. Higher niche stability between Japanese and non-native populations of *Ae. japonicus* supports Japan as a source region. In contrast, results for *Ae. koreicus* suggest that Chinese populations may represent an additional potential source for the European populations. Overall, incorporating comprehensive native occurrence data is essential for accurately characterizing environmental niches and improving predictive models used for surveillance and management of invasive mosquito species.

Declarations

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Competing interests

The authors declare that they have no competing interests.

Funding

We acknowledge funding support of the National Institute of Health (R35GM156217), the Southern Integrated Pest Management Center (Project S24-050) as part of United States Department of Agriculture (USDA) National Institute of Food and Agriculture (NIFA) Crop Protection and Pest Management (CPPM) Regional Coordination Program (Agreement No. 2022-70006-38002), the USDA NIFA Hatch project 7007941. This work was also supported by the Global-LAMP Program of the National Research Foundation of Korea (KRF) grant funded by the Ministry of Education (No. RS-2023-00301976, RS-2023-00237351).

Author Contribution

SS: Conceptualization; Methodology; Formal analysis; Investigation; Data Curation; Writing – Original Draft; Writing – Review & Editing; Visualization; Project administration. JS: Investigation; Validation; Writing – Review & Editing. WJB: Investigation; Validation; Writing – Review & Editing. MM: Conceptualization; Investigation; Writing – Review & Editing. YL: Writing – Review & Editing; Supervision; Funding acquisition

Data Availability

The occurrence data used in this study are available in the Supplementary Table.

References

1. Reaser JK, Burgiel SW, Kirkey J, Brantley KA, Veatch SD, Burgos-Rodríguez J. The early detection of and rapid response (EDRR) to invasive species: a conceptual framework and federal capacities assessment. *Biol Invasions*. 2020;22:1–19. <https://doi.org/10.1007/s10530-019-02156-w>
2. Whelan PI, Kurucz N, Pettit WJ, Krause V. Elimination of *Aedes aegypti* in northern Australia, 2004–2006. *J Vector Ecology*. 2020;45:118–126. <https://doi.org/10.1111/jvec.12379>
3. Vazquez-Prokopec GM, Chaves LF, Ritchie SA, Davis J, Kitron U. Unforeseen costs of cutting mosquito surveillance budgets. *PLoS Neglect Trop D*. 2010;4:e858. <https://doi.org/10.1371/journal.pntd.0000858>
4. Cunze S, Kochmann J, Klimpel S. Global occurrence data improve potential distribution models for *Aedes japonicus japonicus* in non-native regions. *Pest Manag Sci*. 2020;76:1814–1822. <https://doi.org/10.1002/ps.5710>
5. Peach DAH, Almond M, Pol JC. modeled distributions of *Aedes japonicus japonicus* and *Aedes togoi* (Diptera: Culicidae) in the United States, Canada, and northern Latin America. *J Vector Ecology*. 2019;44:119–129. <https://doi.org/10.1111/jvec.12336>
6. Outammassine A, Zouhair S, Loqman S. Global potential distribution of three underappreciated arboviruses vectors (*Aedes japonicus*, *Aedes vexans* and *Aedes vittatus*) under current and future climate conditions. *Transbound Emerg Dis*. 2022;69:e1160-e1171. <https://doi.org/10.1111/tbed.14404>
7. Liu Q, Xie J-W, Wang M, Du Y-T, Yin Z-G, Zhou N-X, et al. Potential global distribution of the invasive mosquito *Aedes koreicus* under a changing climate. *Trop Med Infect Dis*. 2023;8:471. <https://doi.org/10.3390/tropicalmed8100471>
8. Seok S, Kim Z, Nguyen VT, Lee Y. The potential invasion into North America and Europe by non-native mosquito, *Aedes koreicus* (Diptera: Culicidae). *J Med Entomol*. 2023;60:1305–1313. <https://doi.org/10.1093/jme/tjad116>
9. Pearman PB, Guisan A, Broennimann O, Randin CF. Niche dynamics in space and time. *Trends Ecol Evol*. 2008;23:149–153. <https://doi.org/10.1016/j.tree.2007.11.005>

10. Fernández M, Hamilton H. Ecological niche transferability using invasive species as a case study. PLoS One. 2015;10:e0119891. <https://doi.org/10.1371/journal.pone.0119891>
11. Kaufman MG, Fonseca DM. Invasion biology of *Aedes japonicus japonicus* (Diptera: Culicidae). Annu Rev Entomol. 2014;59:31–49. <https://doi.org/10.1146/annurev-ento-011613-162012>
12. Seok S, Mogi M, Lee Y. Resolving confusion in the native distribution of *Aedes* (*Hulecoeteomyia*) *koreicus* (Diptera: Culicidae). J Med Entomol. 2024;61:1077–1080. <https://doi.org/10.1093/jme/tjae078>
13. Wilkerson RC, Somboon P, Harbach RE. Reconsideration of the status of subspecies in the Japonicus Group of the subgenus *Hulecoeteomyia* Theobald of *Aedes* Meigen (Diptera: Culicidae). Zootaxa. 2022;5162:198–200. <https://doi.org/10.11646/zootaxa.5162.2.8>
14. Kampen H, Werner D. Out of the bush: the Asian bush mosquito *Aedes japonicus japonicus* (Theobald, 1901) (Diptera, Culicidae) becomes invasive. Parasite Vector. 2014;7:59. <https://doi.org/10.1186/1756-3305-7-59>
15. Versteirt V, Pecor JE, Fonseca DM, Coosemans M, Bortel WV. Confirmation of *Aedes koreicus* (Diptera: Culicidae) in Belgium and description of morphological differences between Korean and Belgian specimens validated by molecular identification. Zootaxa. 2012;3191:21–32.
16. Pfitzner WP, Lehner A, Hoffmann D, Czajka C, and Becker N. First record and morphological characterization of an established population of *Aedes* (*Hulecoeteomyia*) *koreicus* (Diptera: Culicidae) in Germany. Parasite Vector. 2018;11:662. <https://doi.org/10.1186/s13071-018-3199-4>
17. Jansen S, Cader D, Lühken R, Pfitzner WP, Jöst H, Oerther S. Vector competence of the invasive mosquito species *Aedes koreicus* for arboviruses and interference with a novel insect specific virus. Viruses. 2021;13:2507. <https://doi.org/10.3390/v13122507>
18. Gierek M, Ochała-Gierek G, Woźnica AJ, Zaleśny G, Jarosz A. Winged threat on the offensive: a literature review due to the first identification of *Aedes japonicus* in Poland. Viruses. 2024;16:703. <https://doi.org/10.3390/v16050703>
19. Hill MP, Gallardo B, Terblanche JS. A global assessment of climatic niche shifts and human influence in insect invasions. Global Ecol Biogeog. 2017;26:679–689. <https://doi.org/10.1111/geb.12578>
20. Cunze S, Kochmann J, Koch LK, Klimpel S. Niche conservatism of *Aedes albopictus* and *Aedes aegypti* – two mosquito species with different invasion histories. Sci Rep. 2018;8:7733. <https://doi.org/10.1038/s41598-018-26092-2>
21. Nie P, Feng J. Niche and range shifts of *Aedes aegypti* and *Ae. albopictus* suggest that the latecomer shows a greater invasiveness. Insects. 2023;14:810. <https://doi.org/10.3390/insects14100810>
22. Armistead JS, Arias JR, Nishimura N, Lounibos LP. Interspecific larval competition between *Aedes albopictus* and *Aedes japonicus* (Diptera: Culicidae) in Northern Virginia. J Med Entomol. 2008;45:629–637. <https://doi.org/10.1093/jmedent/45.4.629>
23. Armistead JS, Nishimura N, Arias JR, Lounibos LP. Community ecology of container mosquitoes (Diptera: Culicidae) in Virginia following invasion by *Aedes japonicus*. J Med Entomol.

- 2012;49:1318–1327. <https://doi.org/10.1603/ME11261>
24. Arnoldi R, Negri A, Soresinetti L, Brambilla M, Carraretto D, Montarsi F et al. Assessing the distribution of invasive Asian mosquitoes in Northern Italy and modelling the potential spread of *Aedes koreicus* in Europe. *Acta Trop.* 2022;232:106536. <https://doi.org/10.1016/j.actatropica.2022.106536>
 25. Baharmand I, Coatsworth H, Peach DAH, Belton P, Lowenberger C. Molecular relationships of introduced *Aedes japonicus* (Diptera: Culicidae) populations in British Columbia, Canada using mitochondrial DNA. *J Vector Ecol.* 2020;45:285–296. <https://doi.org/10.1111/jvec.12399>
 26. Balestrino F, Schaffner F, Forgia DL, Paslaru AI, Torgerson PR, Mathis A, et al. Field evaluation of baited traps for surveillance of *Aedes japonicus japonicus* in Switzerland. *Med Vet Entomol.* 2016;31:64–72. <https://doi.org/10.1111/mve.12152>
 27. Bang WJ, Won MH, Cho ST, Ryu J, Choi KW. A multiplex PCR assay for six Aedini species, including *Aedes albopictus*. *Parasite Vector.* 2021;14:380. <https://doi.org/10.1186/s13071-021-04871-7>
 28. Bradt D, Coburn L, Bradley KK, Noden BH. First record of *Aedes japonicus japonicus* in Oklahoma, 2017. *J Am Mosquito Contr.* 2018;34:380. <https://doi.org/10.2987/17-6690.1>
 29. Campbell M, Mullin M, Connelly R, Super PE, Byrd BD. *Aedes japonicus*: a tenant invader in the Great Smoky Mountains National Park, USA. *J Am Mosquito Contr.* 2025;41:34–38. <https://doi.org/10.2987/24-7203>
 30. Catapano PL, Falcinelli M, Damiani C, Cappelli A, Koukouli D, Rossi P, et al. De novo genome assembly of the invasive mosquito species *Aedes japonicus* and *Aedes koreicus*. *Parasites Vectors.* 2023;16:427. <https://doi.org/10.1186/s13071-023-06048-w>
 31. Day CA, Lewandowski K, Vonesh JR, Byrd BD. Phenology of rock pool mosquitoes in the southern Appalachian Mountains: surveys reveal apparent winter hatching of *Aedes japonicus* and the potential for asymmetrical stage-specific interactions. *J Am Mosquito Contr.* 2020;36:216–220. <https://doi.org/10.2987/20-6964.1>
 32. Eastwood G, Donnellycolt AK, Shepard JJ, Misencik MJ, Bedoukian R, Cole L et al. Evaluation of novel trapping lures for monitoring exotic and native container-inhabiting *Aedes* spp. (Diptera: Culicidae) mosquitoes. *J Med Entomol.* 2020;57:534–541. <https://doi.org/10.1093/jme/tjz200>
 33. Ejiri H, Sato Y, Sawai R, Sasaki E, Matsumoto R, Ueda M et al. Prevalence of avian malaria parasite in mosquitoes collected at a zoological garden in Japan. *Parasitol Res.* 2009;105:629–633. <https://doi.org/10.1007/s00436-009-1434-9>
 34. Ejiri H, Sato Y, Kim KS, Tsuda Y, Murata K, Saito K et al. Blood meal identification and prevalence of avian malaria parasite in mosquitoes collected at Kushiro wetland, a subarctic zone of Japan. *J Med Entomol.* 2011;48:904–908. <https://doi.org/10.1603/ME11053>
 35. Eritja R, Ruiz-Arrondo I, Delacour-Estrella S, Schaffner F, Chachero JÁ, Bengoa M et al. First detection of *Aedes japonicus* in Spain: an unexpected finding triggered by citizen science. *Parasite Vector.* 2019;12:53. <https://doi.org/10.1186/s13071-019-3317-y>

36. Eritja R, Delacour-Estrella S, Ruiz-Arrondo I, González MA, Barceló C, García-Pérez AL et al. At the tip of an iceberg: citizen science and active surveillance collaborating to broaden the known distribution of *Aedes japonicus* in Spain. *Parasite Vector*. 2021;14:375. <https://doi.org/10.1186/s13071-021-04874-4>
37. Fonseca DM, Campbell S, Crans WJ, Mogi M, Miyagi I, Toma Takako et al. *Aedes (Finlaya) japonicus* (Diptera: Culicidae), a newly recognized mosquito in the United States: analyses of genetic variation in the United States and putative source populations. *J Med Entomol*. 2001;38:135–146. <https://doi.org/10.1603/0022-2585-38.2.135>
38. Gallitano S, Blaustein L, Vonesh J. First occurrence of *Ochlerotatus japonicus* in Missouri. *J Vector Ecol*. 2005;30:347.
39. Gaspar JP, McKay T, Huss MJ. First record of *Aedes japonicus* in natural and artificial habitats in Northeastern Arkansas. *J Am Mosquito Contr*. 2012;28:38–42. <https://doi.org/10.2987/11-6196.1>
40. González MA, Delacour-Estrella S, Bengoa M, Barceló C, Bueno-Marí R, Eritja R et al. A survey on native and invasive mosquitoes and other biting dipterans in Northern Spain. *Acta Parasitol*. 2022;67:867–877. <https://doi.org/10.1007/s11686-022-00529-1>
41. Gray EW, Harrison BA, Womack ML, Kerce J, Neely CJ, Noblet R. *Ochlerotatus japonicus japonicus* (Theobald) in Georgia and North California. *J Am Mosquito Contr*. 2005;21:144–146. [https://doi.org/10.2987/8756-971X\(2005\)21\[144:OJJTIG\]2.0.CO;2](https://doi.org/10.2987/8756-971X(2005)21[144:OJJTIG]2.0.CO;2)
42. Hayakawa H, Yamashita N, Hasegawa T, Tsubaki Y, Iwane K, Shinjo G. Notes on the construction and use of animal-baited traps for sampling haematophagous Diptera. *Med Entomol Zool*. 1990;41:121–125.
43. Harwood JF, Fiorenzano JM, Gerardo E, Black T, LaPointe DA, Hasty J. Seasonal surveillance confirms the range expansion of *Aedes japonicus japonicus* (Theobald) (Diptera: Culicidae) to the Hawaiian Islands of Oahu and Kauai. *J Asia-Pacific Entomol*. 2018;21:1366–1372. <https://doi.org/10.1016/j.aspen.2018.10.015>
44. Hirabayashi K. mosquito fauna in Karuizawa Town in Nagano Prefecture. *Pestology*. 2020;35:5–7. <https://doi.org/10.7601/mez.71.271>
45. Horváth C, Cazan CD, Mihalca AD. Emergence of the invasive Asian bush mosquito, *Aedes (Finlaya) japonicus japonicus*, in an urban area, Romania. *Parasite Vector*. 2021;14:192. <https://doi.org/10.1186/s13071-021-04698-2>
46. Hoshino K, Isawa H, Tsuda Y, Kobayashi M. Laboratory colonization of *Aedes japonicus japonicus* (Diptera: Culicidae) collected in Narita, Japan and the biological properties of the established colony. *Jpn J Infect Dis*. 2010;63:401–404. <https://doi.org/10.7883/yoken.63.401>
47. Huber K, Jansen S, Leggewie M, Badusche M, Schmidt-Chanasit J, Becker N et al. *Aedes japonicus japonicus* (Diptera: Culicidae) from Germany have vector competence for Japan encephalitis virus but are refractory to infection with West Nile virus. *Parasitol Res*. 2014;133:3195–3199. <https://doi.org/10.1007/s00436-014-3983-9>

48. Hughes TH, Irwin PM, Kaufman A, Sage H, Pagac BB, Paskewitz SM. First records of *Aedes japonicus japonicus* in Wisconsin. J Am Mosquito Contr. 2008;24:583–584.
<https://doi.org/10.2987/5735.1>
49. Ibáñez-Justicia A, Kampen H, Braks M, Schaffner F, Steeghs M, Werner D et al. First report of established population of *Aedes japonicus japonicus* (Theobald, 1901) (Diptera: Culicidae) in the Netherlands. J Am Mosquito Contr. 2014;32:9–13.
50. Iriarte WLZ, Tsuda Y, Wada Y, Takagi M. Distribution of mosquitoes on a hill of Nagasaki City, with emphasis to the distance from human dwellings. Trop Med. 1991;33:55–60.
51. Janssen N, Graovac N, Vignjević G, Bogojević MS, Turić N, Klobučar A et al. Rapid spread and population genetics of *Aedes japonicus japonicus* (Diptera: Culicidae) in southeastern Europe (Croatia, Bosnia and Herzegovina, Serbia). PLoS One. 2020;15:e0241235.
<https://doi.org/10.1371/journal.pone.0241235>
52. Johnson KA, Brogren SJ, Crane DM, Lamere CA. Status of *Aedes japonicus* in the metropolitan mosquito control district, Minnesota. J Am Mosquito Contr. 2010;26:328–331.
<https://doi.org/10.2987/10-6018.1>
53. Juma EO, Allan BF, Kim CH, Stone C, Dunlap C, Muturi E. The larval environment strongly influences the bacterial communities of *Aedes triseriatus* and *Aedes japonicus* (Diptera: Culicidae). Sci Rep. 2021;11:7910. <https://doi.org/10.1038/s41598-021-87017-0>
54. Kalan K, Ivović V, Glasnović P, Buzan E. Presence and potential distribution of *Aedes albopictus* and *Aedes japonicus japonicus* (Diptera: Culicidae) in Slovenia. J Med Entomol. 2017;54:1510–1518.
<https://doi.org/10.1093/jme/tjx150>
55. Kampen H, Kuhlisch C, Fröhlich A, Scheuch DE, Walther D. Occurrence and spread of the invasive Asian bush mosquito *Aedes japonicus japonicus* (Diptera: Culicidae) in West and North Germany since detection in 2012 and 2013, respectively. PLoS One. 2016;11:e0167948.
<https://doi.org/10.7601/mez.71.271>
56. Kawada H, Maekawa Y, Abe M, Ohashi K, Ohba S, Takagi M. Spatial distribution and pyrethroid susceptibility of mosquito larvae collected from catch basins in parks in Nagasaki City, Nagasaki, Japan. Jpn J Infect Dis. 2010;63:19–24. <https://doi.org/10.7883/yoken.63.19>
57. Kim HC, Wilkerson RC, Pecor JE, Lee WJ, Lee JS, O’Guinn ML et al. New records and reference collection of mosquitoes (Diptera: Culicidae) on Jeju Island, Republic of Korea. Entomol Res. 2005;35:55–66. <https://doi.org/10.1111/j.1748-5967.2005.tb00137.x>
58. Klobučar A, Lipovac I, Žagar N, Mitrović-Hamzić S, Tešić V, Vilibić-Čavlek T et al. First record and spreading of the invasive mosquito *Aedes japonicus japonicus* (Theobald, 1901) in Croatia. Med Vet Entomol. 2019;33:171–176. <https://doi.org/10.1111/mve.12337>
59. Kosone K, Kanayama A. Kanagawa Pest Control Association, Yokohama Naka Ward Public Health and Welfare Center. Species of mosquitoes collected with CDC light trap in Yokohama (2004). Pestol (Pest Control Res). 2005;20:89–94. https://doi.org/10.24486/pestology.20.2_89

60. Kosone K, Ito M, Usuku S. Survey of adult mosquitoes in Umi no Koen (Marine Park) in Yokohama (2014). *Pestol (Pest Control Res)*. 2015;30:69–71. https://doi.org/10.24486/pestology.30.2_69
61. Krebs T, Bindler P, L'Ambert G, Toty C, Perrin Y, Jourdain F. First establishment of *Aedes japonicus japonicus* (Theobald, 1901) (Diptera: Culicidae) in France in 2013 and its impact on public health. *J Vector Ecol*. 2014;39:437–440. <https://doi.org/10.1111/jvec.12119>
62. Krupa E, Henon N, Mathieu B. diapause characterization and seasonality of *Aedes japonicus japonicus* (Diptera, Culicidae) in the northeast of France. *Parasite*. 2021;28:45. <https://doi.org/10.1051/parasite/2021045>
63. Larish LB, Savage HM. Introduction and establishment of *Aedes (Finlaya) japonicus japonicus* (Theobald) on the Island of Hawaii: implications for arbovirus transmission. *J Am Mosquito Contr*. 2005;21:318–321. [https://doi.org/10.2987/8756-971X\(2005\)21\[318:IAEOAF\]2.0.CO;2](https://doi.org/10.2987/8756-971X(2005)21[318:IAEOAF]2.0.CO;2)
64. Lowe A-M, Forest-Bérard K, Trudel R, Lo E, Gamache P, Tandonnet M et al. Mosquitoes know no borders: surveillance of potential introduction of *Aedes* species in Southern Québec, Canada. *Pathog*. 2021;10:998. <https://doi.org/10.3390/pathogens10080998>
65. Maekawa Y, Ogawa K, Komagata O, Tsuda Y, Sawabe K. DNA barcoding for molecular identification of Japanese mosquitoes. *Med Entomol Zool*. 2016;67:183–198. <https://doi.org/10.7601/mez.67.183>
66. Maekawa Y, Tsuda Y, Sawabe K. A nationwide survey on distribution of mosquitoes in Japan. *Med Entomol Zool*. 2016;67:1–12. <https://doi.org/10.7601/mez.67.1>
67. Maekawa Y, Sanjoba C, Minagawa K, Sawabe K, Kasai S. Faunal and genetic studies of mosquitoes on Sado Island, Niigata Prefecture, Japan. *Med Entomol Zool*. 2022;73:15–23. <https://doi.org/10.7601/mez.73.15>
68. Maekawa Y, Komagata O, Yamanouchi S, Okuyama H, Fujii S, Ishida K, et al. Invading toward the North: status of the spread of the native mosquito species *Aedes albopictus* in northern Japan. *Med Entomol Zool*. 2025;76:135–143. <https://doi.org/10.7601/mez.76.135>
69. Martinet J-P, Ferté H, Sientzoff P, Krupa E, Mathieu B, Depaquit J. Wing morphometrics of *Aedes* mosquitoes from North-Eastern France. *Insects*. 2021;12:341. <https://doi.org/10.3390/insects12040341>
70. Matsumoto R, Ueda M, Murata K, Higa Y, Sawabe K, Tsuda Y, et al. Survey of mosquito species and their potential as vectors of mosquito-borne diseases in a zoological garden in Yokohama. *Jpn J Zoo Wildlife Med*. 2010;15:79–86.
71. Melaun C, Werblow A, Cunze S, Zotzmann S, Koch LK, Mehlhorn H, et al. Modelling of the putative distribution of the arbovirus vector *Ochlerotatus japonicus japonicus* (Diptera: Culicidae) in Germany. *Parasitol Res*. 2015;114:1051–1061. <https://doi.org/10.1007/s00436-014-4274-1>
72. Mizuta H. Occurrence of two rare mosquito species, *Aedes bekkui* and *Verrallina nobukonis* (Diptera: Culicidae) in southern Osaka Prefecture, Japan. *Med Entomol Zool*. 2011;62:195–198. <https://doi.org/10.7601/mez.62.195>

73. Nakazawa M, Nariai E, Nakamura S, Kuramoto S. Monitoring of mosquito vectors and arboviruses in Kanazawa, Ishikawa Prefecture, western central Japan. *Med Entomol Zool.* 2024;75:5–11. <https://doi.org/10.7601/mez.75.5>
74. Nihei N, Komagata O, Mochizuki K, Kobayashi M. Geospatial analysis of invasion of the Asian tiger mosquito *Aedes albopictus*: competition with *Aedes japonicus japonicus* in its northern limit area in Japan. *Geospatial Health.* 2014;8:417–427.
75. Niizuma J, Osato S, Shoji Y, Madokoro K, Fujiwara N, Nakagawa E, et al. Vector surveillance at Narita International Airport in 2021: the detection of Japanese encephalitis virus genotype I from *Culex tritaeniorhynchus* and the vector control conducted by Narita Airport Quarantine Station. *Med Entomol Zool.* 2022;73:43–51. <https://doi.org/10.7601/mez.73.43>
76. Niizuma J, Kanasugi T, Watanabe M, Sasaki H. Mosquito larvae collected at the Ozegahara wetland, Gunma, Japan. *Med Entomol Zool.* 2024;75:17–19. <https://doi.org/10.7601/mez.75.17>
77. Noda S. Survey of mosquito larvae on Kuro Island, Mishima village, Kagoshima Prefecture. *Occas Pap.* 2011;51:19–20.
78. Odagawa T, Inumaru M, Sato Y, Murata K, Higa Y, Tsuda Y. A long-term field study on mosquito vectors of avian malaria parasites in Japan. *J Vet Med Sci.* 2022;84:1391–1398. <https://doi.org/10.1292/jvms.22-0211>
79. Peyton EL, Campbell SR, Candeletti TM, Romanowski M, Crans WJ. *Aedes (Finlaya) japonicus japonicus* (Theobald), a new introduction into the United States. *J Am Mosquito Contr.* 1999;15:238–241.
80. Riles MT, Day CA, Killingsworth D. Field observations of invasive species *Aedes japonicus* and larval contemporaries in Escambia County, Florida. *J Am Mosquito Contr.* 2020;36:269–271. <https://doi.org/10.2987/20-6981.1>
81. Sardelis MR, Turell MJ. *Ochlerotatus j. japonicus* in Frederick County, Maryland: discovery, distribution, and vector competence for West Nile virus. *J Am Mosquito Contr.* 2001;17:137–141.
82. Sato T, Matsumoto F, Abe T, Nihei N, Kobayashi M. Recent distribution of *Aedes albopictus* in Iwate Prefecture, northern Japan and analysis of climatic conditions for northern limit of geographic distribution by geographic information systems. *Med Entomol Zool.* 2012;63:195–204. <https://doi.org/10.7601/mez.63.195>
83. Sato H, Miyake S. Mosquito fauna in the Nature Observation Park in Saitama Prefecture (2014 ~ 2019). *Pestol (Pest Control Res).* 2022;37:1–7. https://doi.org/10.24486/pestology.37.1_1
84. Schaffner F, Chouin S, Guilloteau J. First record of *Ochlerotatus (Finlaya) japonicus japonicus* (Theobald, 1901) in metropolitan France. *J Am Mosquito Contr.* 2003;19:1–5.
85. Schaffner F, Ries C. First evidence and distribution of the invasive alien mosquito *Aedes japonicus* (Theobald, 1901) in Luxembourg. *B Lux Nat Soc.* 2019;121:169–183.
86. Schaffner F, Kwaśnik M, Myczko Ł, Rożek W, Eritja R, Lippert S, et al. A survey targeting exotic *Aedes* mosquito species in Central Europe, summer 2023, reveals the extensive occurrence of *Aedes*

- japonicus* in Poland. J Europe Mosquito Contr. 2025;43:1–15. <https://doi.org/10.52004/2054930X-20241010>
87. Seidel B, Montarsi F, Huemer HP, Indra A, Capelli G, Allerberger F, et al. First record of the Asian bush mosquito, *Aedes japonicus japonicus*, in Italy: Invasion from an established Australian population. Parasite Vector. 2016;9:284. <https://doi.org/10.1186/s13071-016-1566-6>
 88. Seidel B, Nowotny N, Bakonyi T, Allerberger F, Schaffner F. Spread of *Aedes japonicus japonicus* (Theobald, 1901) in Austria, 2011–2015, and first records of the subspecies for Hungary, 2012, and the principality of Liechtenstein, 2015. Parasite Vector. 2016;9:356. <https://doi.org/10.1186/s13071-016-1645-8>
 89. Seok S, Jacobsen CM, Romero-Weaver AL, Wang X, Nguyen VT, Collier TC, et al. Complete mitogenome sequence of *Aedes (Hulecoeteomyia) japonicus japonicus* from Hawai'i Island. Mitochond DNA Part B Res. 2023;8:64–68. <https://doi.org/10.1080/23802359.2022.2161328>
 90. Shimooka M, Sakurai Y, Muramatsu Y, Uchida. Isolation and characterization of mosquito-associated *Spiroplasma cantharicola* from *Aedes japonicus* collected in Hokkaido, Japan. Insects. 2021;12:1056. <https://doi.org/10.3390/insects12121056>
 91. Shiraishi S. Field collections of mosquito larvae in 2009 and 2010 in Ehime Prefecture, western Japan. Med Entomol Zool. 2011;62:109–116. <https://doi.org/10.7601/mez.62.109>
 92. Shirotani A, Shibata A, Ejiri H, Sato Y, Hatakeyama Y, Iwano H, Tsuda Y, et al. Detection of avian malaria DNA from mosquitoes in Kanagawa in Japan. J Jpn Vet Med Assoc. 2009;62:73–79.
 93. Situmorang T, Bakran-Lebl K, Unterköfler MS, Püschel U, Knobloch L, Fuehrer H-P. Monitoring of alien Asian mosquitoes in Linz, Austria. J Europe Mosquito Contr. 2025;43:97–104. <https://doi.org/10.52004/2054930x-20251026>
 94. Sota T, Mogi M, Hayamizu E. Habitats stability and the larval mosquito community in treeholes and other containers on a temperature island. Res Popul Ecol. 1994;36:93–104.
 95. Sunahara T, Mogi M. Drought and overwintering success of *Tripteroides bambusa* (Diptera: Culicidae) larvae and eggs in a bamboo grove. Med Entomol Zool. 1997;48:295–302.
 96. Sunahara T. Extremely high biting densities of *Aedes albopictus* (Skuse) (Diptera: Culicidae) at a university campus in Nagasaki, Japan. Jpn J Infect Dis. 2019;72:368–373. <https://doi.org/10.7883/yoken.JJID.2019.047>
 97. Tanaka K, Mizusawa K, Saugstad ES. A revision of the adult and larval mosquitoes of Japan (including the Ryukyu Archipelago and the Ogasawara Islands) and Korea (Diptera: Culicidae). Vol 16. Contributions of the American Entomological Institute; 1979.
 98. Thorn M, Varnado WC, Goddard J. First record of *Aedes japonicus japonicus* in Mississippi. J Am Mosquito Contr. 2012;28:43–44. <https://doi.org/10.2987/11-6204.1>
 99. Tsuda Y, Takagi M, Wada Y. Ecological study on mosquito communities in tree holes in Nagasaki, Japan, with special reference to *Aedes albopictus* (Diptera; Culicidae). Med Entomol Zool. 1994;45:103–111.

100. Tsuda Y, Kim KS. Results of mosquito collections at Izumo, Shimane, Japan. *Med Entomol Zool.* 2023;74:113–118. <https://doi.org/10.7601/mez.74.113>
101. Turell MJ, Byrd BD, Harrison BA. Potential for populations for *Aedes j. japonicus* to transmit Rift Valley Fever virus in the USA. *J Am Mosquito Contr.* 2013;29:133–137. <https://doi.org/10.2987/12-6316r.1>
102. Versteirt V, Schaffner FS, Garros C, Dekoninck W, Coosemans M, van Bortel W. Introduction and establishment of the exotic mosquito species *Aedes japonicus japonicus* (Diptera: Culicidae) in Belgium. *J Med Entomol.* 2009;46:1464–1467. <https://doi.org/10.1603/033.046.0632>
103. Watanabe M. Surveillance study of mosquitoes on cow-house at Hietsu highland in Gifu prefecture. *Med Entomol Zool.* 2009;60:147. https://doi.org/10.7601/mez.60.147_2
104. Watanabe M, Watanabe H, Tabaru Y, Hirao M, Roychoudhury S, Sawabe J, et al. Occurrence of vector mosquitoes at tsunami disaster areas of the Great East Japan Earthquake. *Med Entomol Zool.* 2012;63:31–43. <https://doi.org/10.7601/mez.63.31>
105. Watanabe M, Watanabe H. Survey results of mosquito outbreaks in the 2023 Okunoto earthquake disaster area. *Pestol* 2024;39:27–29. https://doi.org/10.24486/pestology.39.1_27
106. Watanabe M, Watanabe H, Oikawa Y, Murakami M, Sawabe K, Higa Y. Occurrence of mosquitoes, in particular *Culex tritaeniorhynchus* in the Noto Peninsula, Honshu, Japan. *Med Entomol Zool* 2024;75:59–67. <https://doi.org/10.7601/mez.75.59>
107. Werner D, Kronefeld M, Schaffner F, Kampen H. Two invasive mosquito species, *Aedes albopictus* and *Aedes japonicus japonicus*, trapped in south-west Germany, July to August 2011. *Eurosurveillance.* 2012;19:pii20067. <https://doi.org/10.5167/uzh-61698>
108. Yamanishi H. Seasonal fluctuation of the parous rate of *Aedes albopictus* at a thicket in Kobe City, Japan from 2015 to 2019. *Med Entomol Zool.* 2021;72:67–73. <https://doi.org/10.7601/mez.72.67>
109. Yamanishi H. Observation of parous rate, shedding of scales in the single white stripe on the scutum in *Aedes albopictus* females at a thicket in Kobe City. *Med Entomol Zool.* 2022;73:161–166. <https://doi.org/10.7601/mez.73.161>
110. Yamashita N. Occurrence and feeding activity of *Aedes japonicus* in Iwate Prefecture. *Med Entomol Zool.* 2001;52(supplement):134. https://doi.org/10.7601/mez.52.134_3
111. Yamauchi T. Mosquito species (Diptera: Culicidae) collected from the inhabited islands and trunk of Uwajima City, Shikoku, Japan. *Med Entomol Zool.* 2010;61:121–124. <https://doi.org/10.7601/mez.61.121>
112. Yamauchi T. Mosquitoes found along the coast of Toyama Prefecture, Japan. *Pestol (Pest Control Res).* 2013;28:17–20. https://doi.org/10.24486/pestology.28.1_17
113. Zielke DE, Werner D, Schaffner F, Kampen H, Fonseca DM. Unexpected patterns of admixture in German populations of *Aedes japonicus japonicus* (Diptera: Culicidae) underscore the importance of human intervention. *PLoS ONE.* 2014;9:e109471. <https://doi.org/10.1371/journal.pone.0099093>
114. GBIF. 2026. GBIF Occurrence Download <https://doi.org/10.15468/dl.mxjkc7>. Accessed 02 Feb 2026.

115. Soresinetti L, Naro G, Arnoldi I, Mosca A, Adam K, Kim HC, et al. The genetic trail of the invasive mosquito species *Aedes koreicus* from the east to the west of Northern Italy. *PLoS Neglect Trop D*. 2025;19:e0012945. <https://doi.org/10.1371/journal.pntd.0012945>
116. Peñazziová KL, Pivka S, Barbušinová E, Jalili NA, Kiss V, Kurucz K, et al. First molecular evidence and phylogenetic characterization of *Aedes (Hulecoeteomyia) koreicus* (Diptera: Culicidae) in Slovakia. *Parasitol Res*. 2016;125:11. <https://doi.org/10.1007/s00436-026-08628-y>
117. GBIF 2026. GBIF Occurrence Download <https://doi.org/10.15468/dl.8mpku8>. Accessed 02 Feb 2026.
118. Aiello-Lammens ME, Boria RA, Radosavljevic A, Vilela B, Anderson RP. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography* 2015;38:541–545. <https://doi.org/10.1111/ecog.01132>
119. Krupa E, Grehal AL, Esnault J, Bender C, Mathieu B. Laboratory evaluation of flight capacities of *Aedes japonicus* (Diptera: Culicidae) using a flight mill device. *J Insect Sci*. 2021;21:18. <https://doi.org/10.1093/jisesa/ieab093>
120. Fick SE, Hijmans RJ. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. *Int J Climatol*. 2017;37:4302–4315. <https://doi.org/10.1002/joc.5086>
121. Amatulli G, Domisch S, Tuanmu MN, Parmentier B, Ranipeta A, Malczyk J, et al. A suite of global, cross-scale topographic variables for environmental and biodiversity modeling. *Sci Data*. 2018;5:180040. <https://doi.org/10.1038/sdata.2018.40>
122. Danielson JJ, Gesch DB. Global multi-resolution terrain elevation data 2010 (GMTED2010). U.S. Geological Survey. 2011. <https://doi.org/10.3133/ofr20111073>
123. Broennimann O, Fitzpatrick MC, Pearman PB, Petitpierre B, Pellissier L, Yoccoz NG, et al. Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecol Biogeogr*. 2012;21:481–497. <https://doi.org/10.1111/j.1466-8238.2011.00698.x>
124. Warren DL, Glor RE, Turelli M. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution*. 2008;62:2868–2883. <https://doi.org/10.1111/j.1558-5646.2008.00482.x>
125. Petitpierre B, Kueffer C, Broennimann O, Randin C, Daehler C, Guisan A. Climatic niche shifts are rare among terrestrial plant invaders. *Science*. 2012;335:1344–1348. <https://doi.org/10.1126/science.1215933>
126. Di Cola V, Broennimann O, Petitpierre B, Breiner FT, D'Amen M, Randin C, et al. ecospat: an R package to support spatial analyses and modeling of species niches and distributions. *Ecography*. 2017;40:774–787. <https://doi.org/10.1111/ecog.02671>
127. R Core Team, R: A language and environment for statistical computing. R Foundation for statistical computing, Vienna, Austria. 2018. <https://www.R-project.org/>
128. Seok S, Kim W, Kim J, Doung CV, Sareein N, Bae YJ. Role of the predaceous mosquito *Toxorhynchites christophi* (Diptera: Culicidae) in treehole ecosystems in a Korean forest. *J Vector Ecology*. 2022;47:202–209. <https://doi.org/10.52707/1081-1710-47.2.202>

129. Rödder D, Engler JO. Quantitative metrics of overlaps in Grinnellian niches: advances and possible drawbacks. *Global Ecol Biogeogr.* 2011;20:915–927. <https://doi.org/10.1111/j.1466-8238.2011.00659.x>
130. Crips MD, Cook LG. Phylogenetic niche conservatism: what are the underlying evolutionary and ecological causes. *New Phytol.* 2012;196:681–694. <https://doi.org/10.1111/j.1469-8137.2012.04298.x>
131. Wassem A, Chan P, Chang K, Lee WJ. Comparative association of species of Culicinae (Diptera) at various altitudes in Republic of Korea. *Afr J Microbiol Res.* 2012;6:6958–6968.
132. Tang X, Yuan Y, Liu X, Zhang J. Potential range expansion and niche shift of the invasive *Hyphantria cunea* between native and invasive countries. *Ecol Entomol.* 2021;46:910–925. <https://doi.org/10.1111/een.13028>
133. Liu C, Wolter C, Xian W, Jeschke JM. Most invasive species largely conserve their climatic niche. *Proc Natl Acad Sci USA.* 2020;117:23643–23651. <https://doi.org/10.1073/pnas.2004289117>
134. Fonseca DM, Widdell AK, Hutchinson M, Spichiger S-E, Kramer LD. Fine-scale spatial and temporal population genetics of *Aedes japonicus*, a new US mosquito, reveal multiple introductions. *Mol Ecol.* 2010;19:1559–1572. <https://doi.org/10.1111/j.1365-294X.2010.04576.x>
135. Cardador L, Carrete M, Gallardo B, Tella JL. Combining trade data and niche modelling improves predictions of the origin and distribution of non-native European populations of a globally invasive species. *J Biogeogr.* 2016;43:967–978. <https://doi.org/10.1111/jbi.12694>
136. Cameron EC, Wilkerson RC, Mogi M, Miyagi I, Toma T, Kim H-C, et al. Molecular phylogenetics of *Aedes japonicus*, a disease vector that recently invaded Western Europe, North America, and the Hawaiian Islands. *J Med Entomol.* 2012;47:527–535. <https://doi.org/10.1093/jmedent/47.4.527>
137. Shin J, Jung J. First record of the complete mitochondrial genome of *Aedes koreicus* (Edwards, 1917) (Diptera: Culicidae) in South Korea. *Mitochond DNA Part B Res.* 2020;5:2000–2001. <https://doi.org/10.1080/23802359.2020.1756947>
138. Chen H. The mosquito fauna of Guizhou volume one (Culicinae and Toxorhynchitinae). Guizhou People's Publishing House, Guizhou; 1987.
139. Lu B, Chen H, Xu R, Shuhong J. A checklist of Chinese mosquitoes (Diptera: Culicidae). Guizhou People's Publishing House, Guizhou; 1988.
140. Lu B. Fauna Sinica Insecta vol 8. Diptera: Culicidae 1. Science Press, Beijing; 1997.

Figures

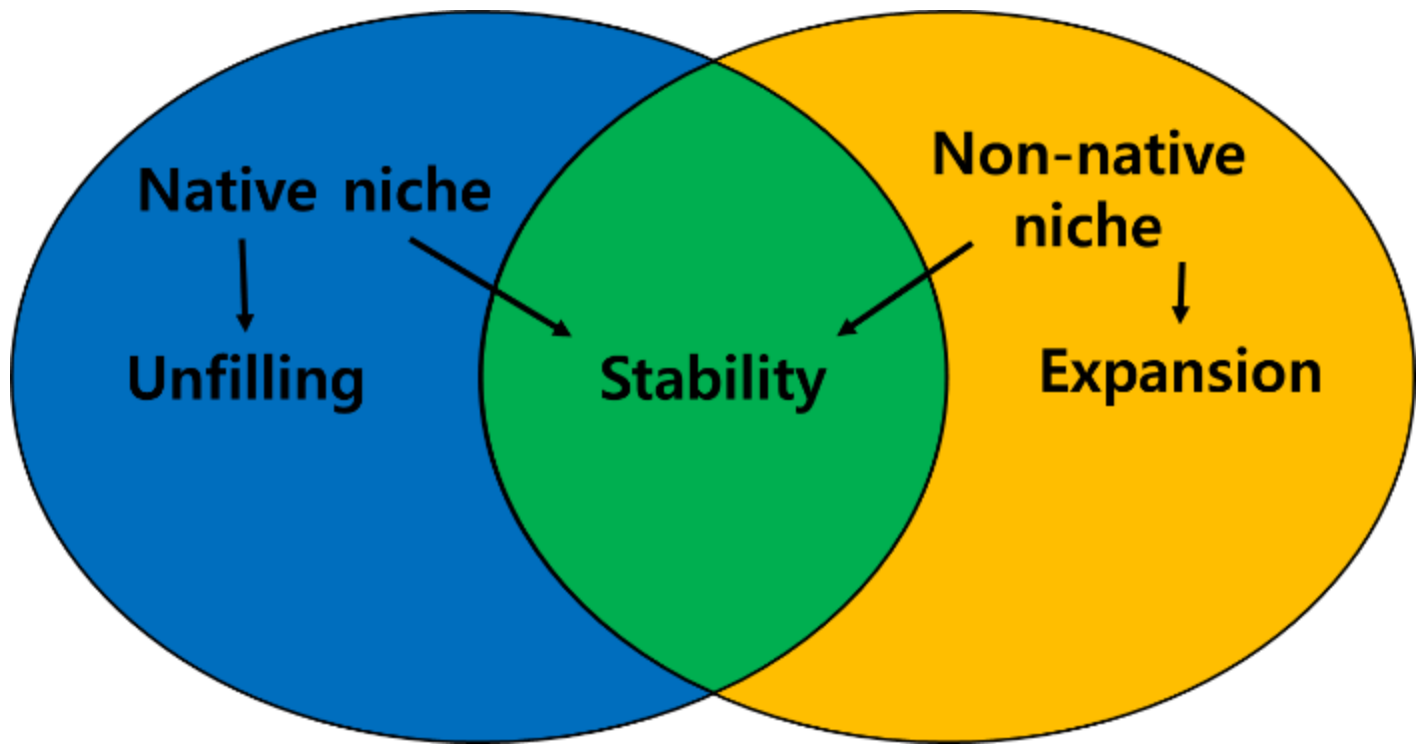


Figure 1

Conceptual illustration of three niche dynamics: unfilling, stability, and expansion.

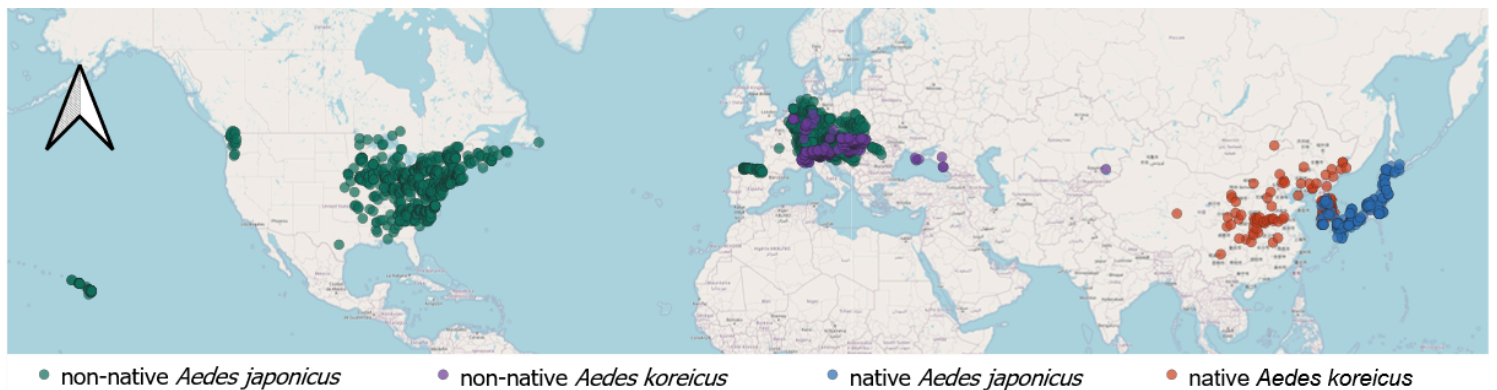


Figure 2

Global occurrence records of *Aedes japonicus* and *Aedes koreicus*. *Aedes japonicus* (native: blue, non-native: green) and *Aedes koreicus* (native: red, non-native: purple).

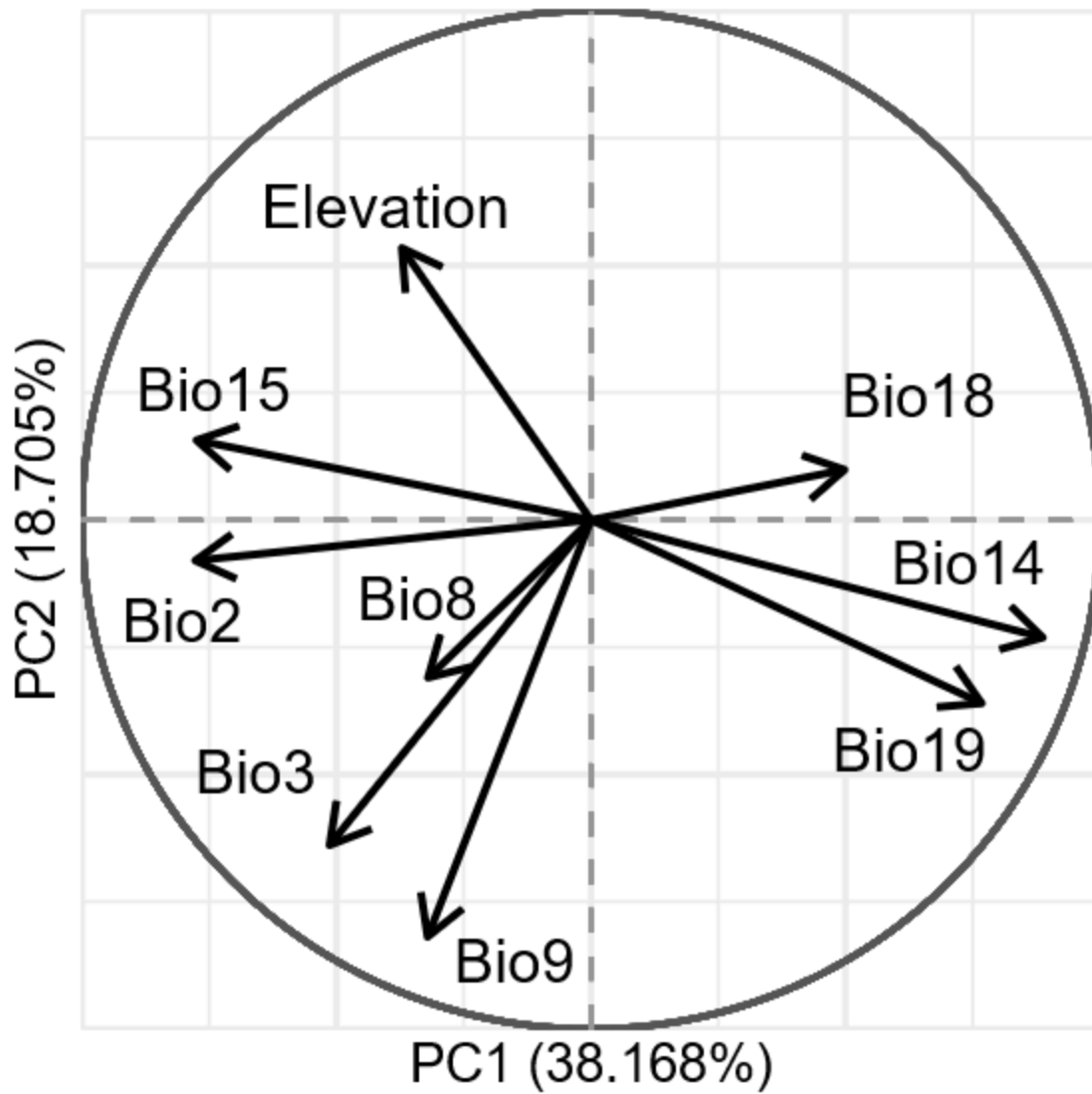


Figure 3

PCA correlation circle showing variable loadings on PC1 and PC2.

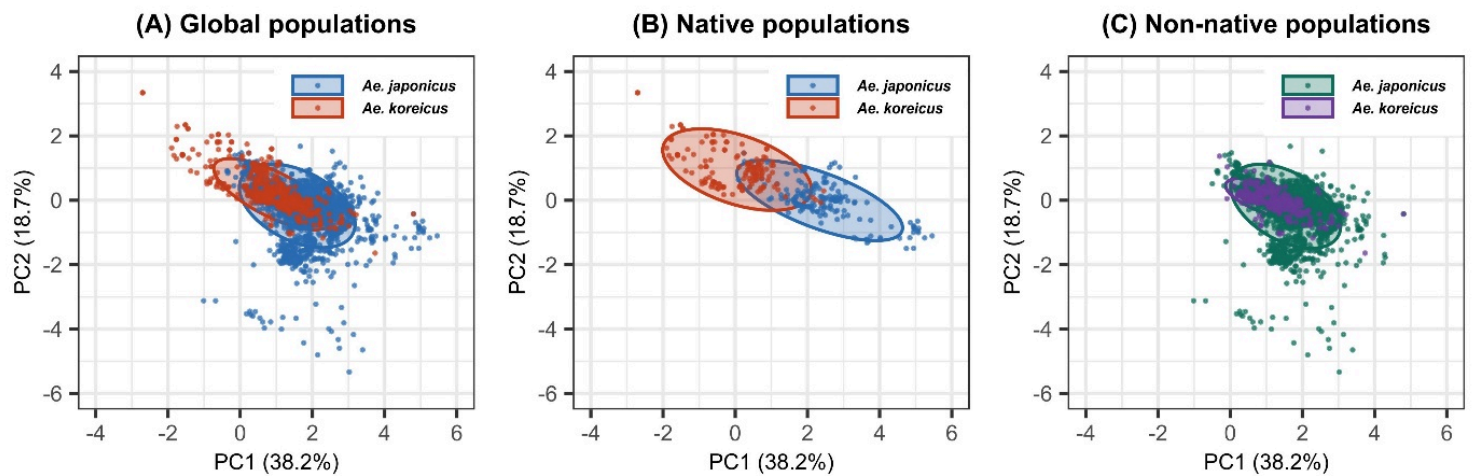


Figure 4

PCA-based environmental niche comparisons of *Aedes japonicus* and *Aedes koreicus*: (A) global populations; (B) native populations; (C) non-native populations. Shaded ellipses represent 95% confidence regions for each species.

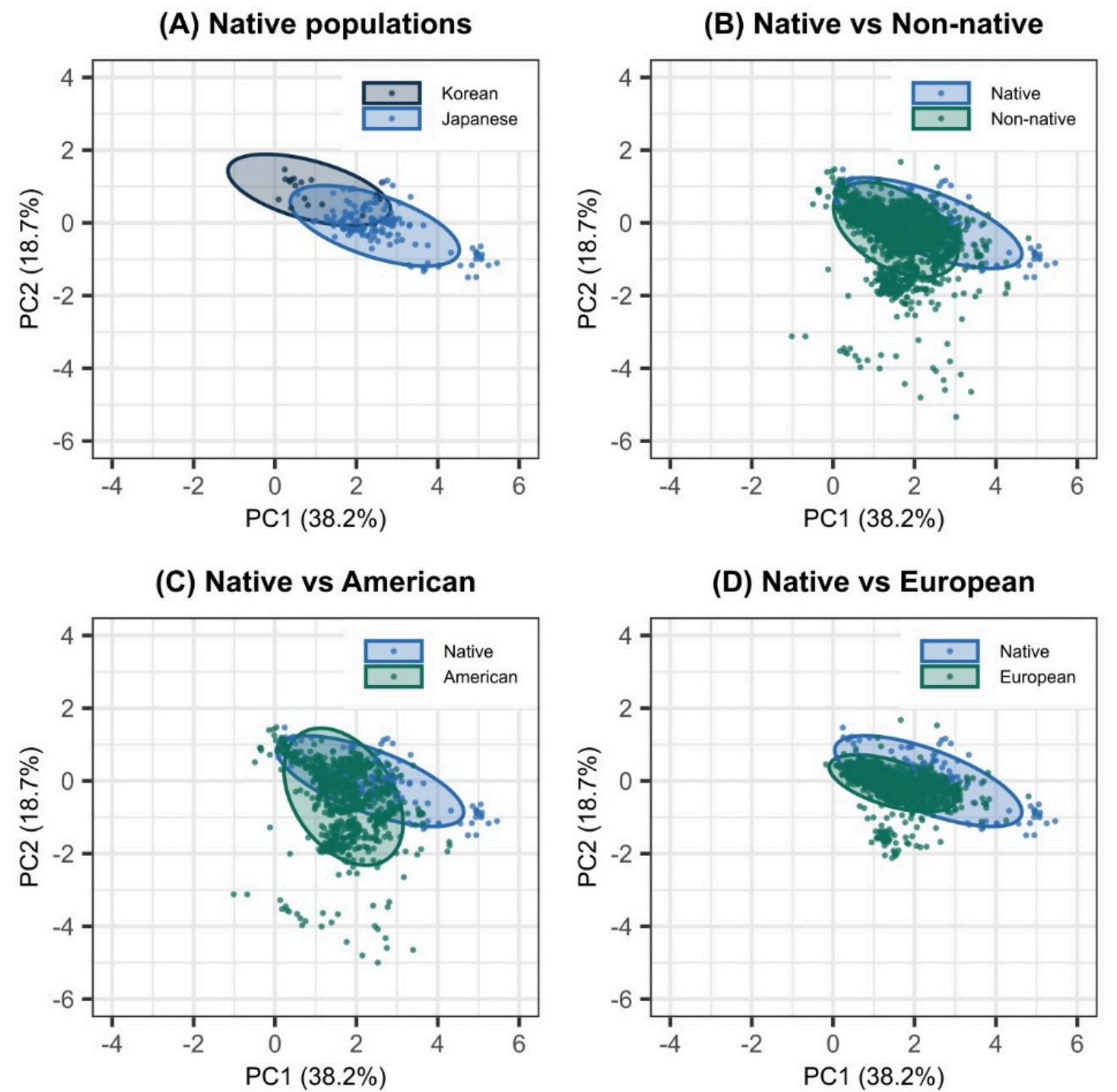


Figure 5

PCA-based environmental niche comparisons of *Aedes japonicus* population: (A) Japanese vs Korean populations; (B) native vs non-native populations; (C) native vs American populations; (D) native vs European populations; Shaded ellipses represent 95% confidence regions for each population.

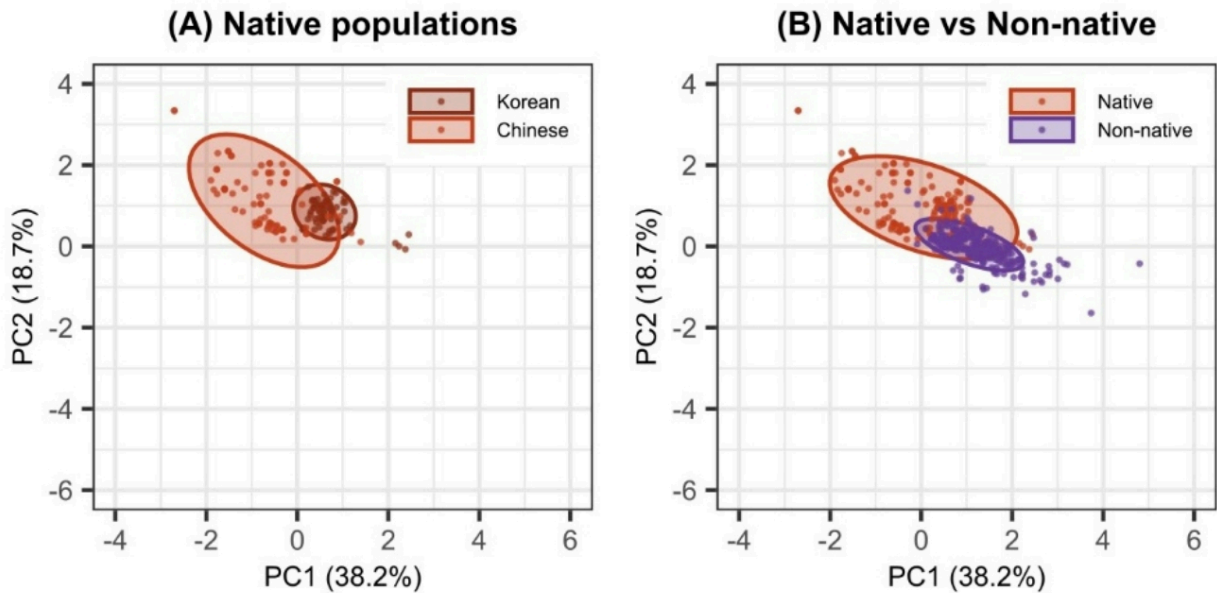


Figure 6

PCA-based environmental niche comparisons of *Aedes koreicus* population: (A) Chinese vs Korean populations; (B) native vs non-native populations. Shaded ellipses represent 95% confidence regions for each population.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [TableS1.xlsx](#)
- [TableS2.xlsx](#)
- [FigureS2.svg](#)
- [FigureS1.svg](#)