



Colonizing the east and the west: distribution and niche properties of a dwarf Asian honey bee invading Africa, the Middle East, the Malay Peninsula, and Taiwan

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Abstract – Species invasions are expected to increase continuously with undeniable impact upon native biodiversity, being an important process in relation to the decline of native pollinators. We used species distribution models and multivariate analyses to assess the climatic niche properties of the red dwarf honey bee, *Apis florea* Fabricius (Apidae: Apini), an open-nesting species native to southern Asia and parts of the Middle East, currently invading East Africa, Sundaic tropical Southeast Asia (Peninsular Malaysia and Singapore), and East Asia (Taiwan). The species' niche was relatively conserved, with the climatic conditions in all its invaded range overlapped by those from its native one. Its potential distribution in Africa and the Indomalayan region is broad, with anthropogenic areas likely providing new habitats and dispersal corridors in areas that were formerly too arid or too heavily forested to allow its dispersal. Future studies to evaluate the potential impacts of *A. florea* in invaded ranges are encouraged.

species distribution models / macroecology / invasion process / Asia / Africa

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1. INTRODUCTION

Species invasions constitute one of the main drivers of biodiversity loss today, along with habitat loss and fragmentation, environmental deposition of nitrogen and phosphorus, and the expected climate change due to the emission of CO₂ and

other greenhouse gases (Tylianakis et al. 2008). Invasive species may cause significant ecological problems in the regions they invade, since they generally are important competitors and may eventually become abundant in such adventive areas, altering species interspecific interactions and the availability of natural resources (Pejchar and Mooney 2009). This may significantly impact humanity's relationship with nature and thereby cause economic losses in the scale of billions of dollars per annum (Pimentel et al. 2005).

The invasion process is usually divided into different phases (Richardson et al. 2000; Blackburn et al. 2011). In the initial phase, propagules of the invasive species trespass geographic barriers that keep them in their native ranges and, consequently, reach new distributional areas, although most of these propagules do not establish in the new localities. Eventually, those propagules that survive and reproduce may establish a stable population within the newly invaded localities. In the final invasion period, this newly naturalized population will produce new propagules from within invaded areas, and these new propagules may restart the whole process in a series of new locations.

Explaining why certain species can invade new areas is challenging. Two non-mutually compatible hypotheses attempt to explain such successes. One hypothesis assumes that invasive species go through a process of "enemy-release" while invading new ranges, temporarily freed of competitors and natural enemies that are otherwise capable of controlling the species' populations within its native range (Keane and Crawley 2002; Müller-Schärer and Schaffner 2008). The alternative hypothesis postulates that invasive species experience adaptive shifts that eventually lead to niche changes that allow for and explain their success while occupying new localities and ranges.

Another possibility is that anthropogenic creation of novel habitats provides new suitable areas, including dispersal corridors, in locations that did not originally have the climatic conditions tolerated by invading species. Such new habitats may allow invading species to transverse formerly unsuitable areas so as to reach formerly inaccessible sites with naturally more favorable climatic conditions. The creation of novel habitats can be due to deliberate urban greening (Hennig and Ghazoul 2012;

Braaker et al. 2014; Threlfall et al. 2017), as in the case of Arabian cities and Singapore, but can also be a by-product of larger-scale phenomena such as deforestation of the Thai-Malay Peninsula (Liow et al. 2001; Oldroyd and Nanork 2009), replacing unsuitable continuous humid forests with suitable more open habitats and drier microclimates.

From this perspective, current macroecological approaches unifying multivariate climatic analyses and species distribution models (SDM hereon) attempt to answer what occurs with the niche of an exotic species as it invades new areas (Guisan et al. 2014). These analyses make use of the increasing amount of collection occurrence records (Pyke and Ehrlich 2010) available from online databases (e.g., Global Biological Information Facility – GBIF; Centro de Referência em Informação Ambiental – CRIA's Species Link), along with historical climatic data easily available from the internet (e.g., WorldClim; Hijmans et al. 2005). This framework has been recently applied to several insect species and revealed that invasion success is usually dependent on different invasion histories, but also different ecological perspectives (Di Cola et al. 2017; Hill et al. 2017).

Considering bee species, some historic invasion events are well documented and studied, and a few studies use species distribution models to predict their distribution ranges in the recent literature. As for many other invasive species, these studies show that invasive bees are expected to invade large regions (e.g., Hinojosa-Díaz et al. 2005; Strange et al. 2011; Vital et al. 2012; Jamevich et al. 2014). For instance, the European woolcarder bee *Anthidium (Anthidium) manicatum* (Linnaeus, 1758) (Megachilidae: Anthidiini), the woodborer bee *Lithurgus huberi* Duce, 1907 (Lithurginae), and the giant resin bee *Megachile (Callomegachile) sculpturalis* Smith, 1853 (Megachilini) expanded their ranges from their native ranges and invaded different regions around the world (Hinojosa-Díaz et al. 2005; Strange et al. 2011; Silva et al. 2014). Recently, it has been suggested that *M. sculpturalis* is establishing new populations in Europe (e.g., Quaranta et al. 2014; Westrich et al. 2015; Le Feón et al. 2018), along with *M. (Callomegachile) disjunctiformis* Cockerell, 1911 (Hymenoptera: Megachilidae), a related species in the same subgenus (Bortolotti et al. 2018).

Perhaps the most famous invasion among bees, however, is the Africanized honey bee, i.e., escaped populations derived from *Apis* (*Apis*) *mellifera scutellata* Lepeletier, 1836 (Apidae: Apini), which are intensively used in agricultural ecosystems. This species is claimed to cause significant ecological problems in its now widespread New World range (Butz-Huryn 1997; Goulson 2003; Paine 2004). Another species of subgenus *Apis*, the cavity-nesting *A.* (*Apis*) *cerana* Fabricius, 1793 (Apidae: Apinae) of South, Southeast, and East Asia has been introduced to islands of Melanesia (e.g., New Guinea, Solomon Islands) and has recently expanded its range to tropical Australia (Shield 2007). This species is expected to control resources to almost the same intensity observed for *A. mellifera* in Africa (Koetz 2013).

Finally, the red dwarf honey bee *A.* (*Micrapis*) *florea* Fabricius, 1787 (Apini), a species originally from western and southern Asia and monsoonal Southeast Asia (Radloff et al. 2011), has been reported to have gradually expanded its range into the Middle East (Mossageh 1993) and Arabia, and has more recently been discovered to be extending its range in eastern Africa (Bezabih et al. 2014; Shebl 2017), in regions of Sundaic Southeast Asia including the Malay Peninsula that were formerly too forested and instead occupied by its sister species *A.* (*Micrapis*) *andreniformis* Smith, 1858, and in Taiwan. Considering this new case of range increase in multiple continents by an invasive bee species, we explored the invasion history of *A. florea* in both African and Indomalaya ranges. Specifically, we (1) evaluate using multivariate analyses whether the climatic niche of the species shifted or was conserved during its invasion process, and (2) use SDMs to estimate the species' distribution in both its native and invaded areas.

2. METHODS

2.1. Occurrences dataset

We obtained occurrence records for *A. florea* from various data sources, including the Global Biological Information Facility (GBIF.org), CRIA's Species Link (<http://splink.cria.org.br>), and iNaturalist (<http://www.inaturalist.org>;

identifications were made or verified by JSA). We also obtained records from major entomological collections: the Division of Entomology of the University of Kansas Natural History Museum (SEMC: Lawrence, KS), the American Museum of Natural History (AMNH: New York, NY), and the Department of Biological Sciences of the National University of Singapore (NUS). Occurrences with unreliable geographic information were disregarded. For the occurrences that had locality cited but no specific geographic information, we used Google Earth (Google Inc. 2018) to obtain geographic coordinates for the nearest municipality. In total, we obtained 1012 occurrences for the species, with 930 from the species' native distribution and 98 from areas outside its original distribution range (Figure 1). For all occurrences of *A. florea* we gathered, we provided the original source from where they were obtained in our supplementary materials. In Table S1, we provided the countries' names from where each occurrence was obtained. All occurrences are provided in a Supplementary File.

2.2. Environmental variables and species distribution models

We obtained environmental variables from the Worldclim database (Hijmans et al. 2005), considering a grid cell size resolution of 2.5 arc-min (0.041° or 4 Km at the equator), and the whole study area across both Africa and Asia (minimum longitude, -18° ; maximum longitude, 122° ; minimum latitude, -35° ; maximum latitude, 42°). To reduce model overfitting in the distribution models for the species (Jiménez-Valverde et al. 2011), we applied a principal components analysis (PCA hereon) to create new orthogonal climatic variables (principal components; PCs hereon) to be used as the environmental predictors to estimate the distribution of *A. florea*. The seven selected PCs explained almost 96% of the original climatic variation.

We modeled the species' distribution with the obtained occurrence records using six different modeling methods: (1) the method of maximum entropy implemented in MaxEnt (MAX hereon; Phillips et al. 2006; Phillips and Dudík 2008), (2) Gaussian Model (GAU; Vanhatalo et al. 2012),

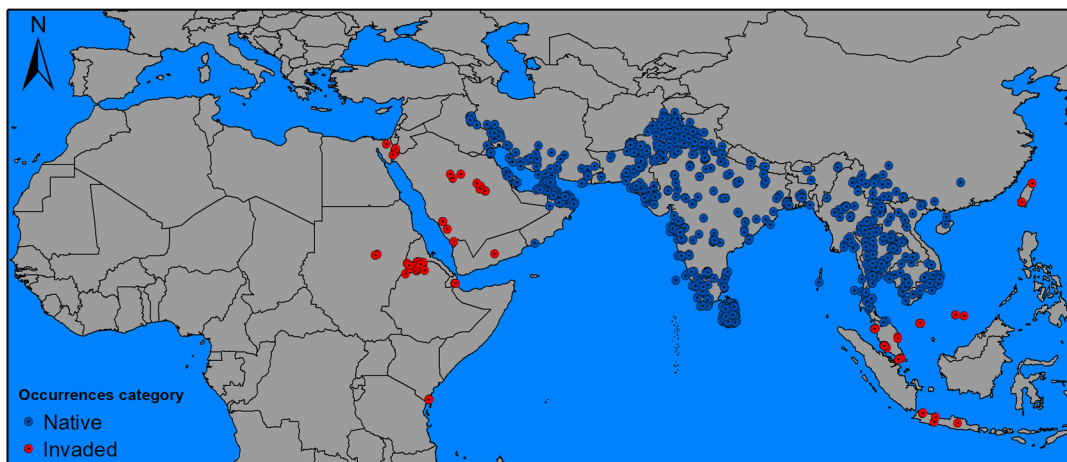


Figure 1. Occurrence data for *Apis florea* in its native (blue circles) and invaded (red circles) range within Africa and Asia.

(3), Generalized Linear Models (GLM hereon; Guisan et al. 2002), (4) Random Forest (RF hereon; Breiman 2001), (5) Generalized Additive Models (GAM; Hastie and Tibshirani 1986), and (6) Support Vector Machines (SVM hereon; Schölkopf et al. 2001; Tax and Duin 2004; Guo et al. 2005).

We used all spatially unique occurrences to generate the models and partitioned them in a checkerboard fashion, with an aggregation factor of two. In this partition method, the occurrences are divided into two datasets, one of which is used to predict the species distribution and the other to evaluate the first distribution model produced. The latter dataset is also used to produce a second distribution model for the species, which is then evaluated by the dataset initially used to produce the species distribution in the first step (Muscarella et al. 2014; Roberts et al. 2017). We also used a shapefile of world ecoregions, obtained from World Wildlife Fund website (<http://www.worldwildlife.org/biomes>), to restrict the training area of our distribution models to climatic conditions of the ecoregions where known occurrences of the species are available. By using such methods, we decrease the effects of a random pseudo-absence allocation in the geographic space that may produce unreliable distributions for the target species (VanDerWal et al. 2009; Lobo and Tognelli 2011).

We considered the threshold that balances both omission and commission errors in order to cut the suitability matrices into presence/absence maps (Jiménez-Valverde and Lobo 2006, 2007). To evaluate the goodness-of-fit of our model, we used the true skill statistic (TSS hereon; Allouche et al. 2006), a threshold-dependent metric that varies from -1 to $+1$, where models reaching values near to 0.5 are considered as acceptable and predictions reaching 0.7 or higher values are considered as excellent. Finally, we used all models with TSS values above the mean TSS value to produce the ensemble distribution for *A. florea* (Araújo and New 2007).

2.3. Multivariate niche analyses

We considered the 19 environmental variables from Wordclim to perform the niche analysis and compared the environmental properties of *A. florea* in both its native and invaded ranges using the R package *ecospat* (Di Cola et al. 2017). We considered the same grid cell size and study extent used before. To establish a background area before starting the analyses, we created a 150-km buffer around the species occurrences, where we sampled 1000 points (as done in Silva et al. 2016).

We performed the analyses based on the PCA-env methods proposed by the framework of Broennimann et al. (2012). This method considers

pairwise comparisons of both niche and the density of occurrences, correcting for collection biases on occurrence records. It uses a smooth kernel density function and calculates a niche overlap score between each range (native vs. introduced ranges) of the species by using the Schoener's D metric (Schoener 1970). This metric varies from 0 to 1, where 0 represents a complete dissimilarity between the compared ranges and 1 represents a complete similarity between the compared ranges. The method performs two different randomization tests of the occurrence records to evaluate whether the climatic niche of the species shifted when it invaded the new range. In the first, it performs niche equivalence tests to check whether the observed niche overlap value is different than what would be expected by chance alone. The second randomization test computes niche similarity tests and compares the niche overlap of one range distributed at random over its background area, while keeping the other range unchanged (native range → invaded range). The method is also capable of performing the same analysis with the range which was originally kept unchanged in the first procedure (native range ←invaded range). Nonetheless, since this comparison is not of our interest, since the invasion process occurs from the native to the invaded ranges, we did not consider this analysis direction in our study. In this test, these comparisons are repeated 100 times to allow the production of a null distribution of random overlap values to be compared with the value from the real occurrences of the species in each of its ranges, as proposed by Warren et al. (2008). In the event where the observed overlap is significantly smaller than those values obtained at random, it means the species occupies different segments of environmental space in both occupied ranges. Following these procedures, we obtained the proportion of the climatic niches from the compared ranges that suffered expansion, remained stable, or were unfilled during the invasion process.

We measured the amount of niche stability, niche expansion, and niche unfilling between both native vs. invaded ranges of *A. florea* (*sensu* Guisan et al. 2014). In these analyses, we do comparisons of the available analog climatic conditions in areas that may or may not be occupied

by the species, but that are available for its colonization within both ranges with those in fact occupied by the species in both ranges. If there is a high overlap of available and occupied analog climatic conditions between both ranges, there is a high proportion of stabilized niche for the species in each range. If the overlap of climatically analog and occupied conditions in both ranges is low, the species would have a high proportion of its niche unfilled. In both scenarios, the general expectation is that no niche shift is expected to have occurred. Finally, if the overlap of analog climatic conditions available is high between each range, but the overlap of occupied conditions by the species is low or nonexistent, then we can assume the species' niche is expanding in the invaded range, with a consequent niche shifting/unfilling if compared with the native range.

3. RESULTS

3.1. Distribution models for *Apis florea*

Our species distribution models for *A. florea* reached a mean TSS value of 0.927 ± 0.026 (mean \pm standard deviation; $n = 6$ models). The RDF method yielded the highest TSS value (0.960), followed by MAX (0.948), SVM (0.937), GAU (0.910), GAM (0.898), and GLM (0.879). Only MAX (Figure 2d) showed more overprediction of the distribution of *A. florea* and included several suitable areas in the Sahara Desert.

Based on all methods, the predictions produced for *A. florea* show suitable regions currently without reported occurrences of the species. For instance, several regions in east and southeast China, Indonesia (e.g., Sumatra, Kalimantan, and Sulawesi), and also Taiwan, where *A. florea* has been recently reported, were indicated as potentially suitable. Additionally, regions from the Middle East (e.g., Saudi Arabia, Israel) and the sub-Saharan Africa (several countries) and North Africa (Morocco to Egypt) were predicted as suitable for the species (Figure 2a–f). Several areas in western, sub-Saharan, and southern Africa were also indicated as suitable for potential invasion by *A. florea*. The species' final ensemble distribution model, based on the weighted distribution that considered the independent results produced

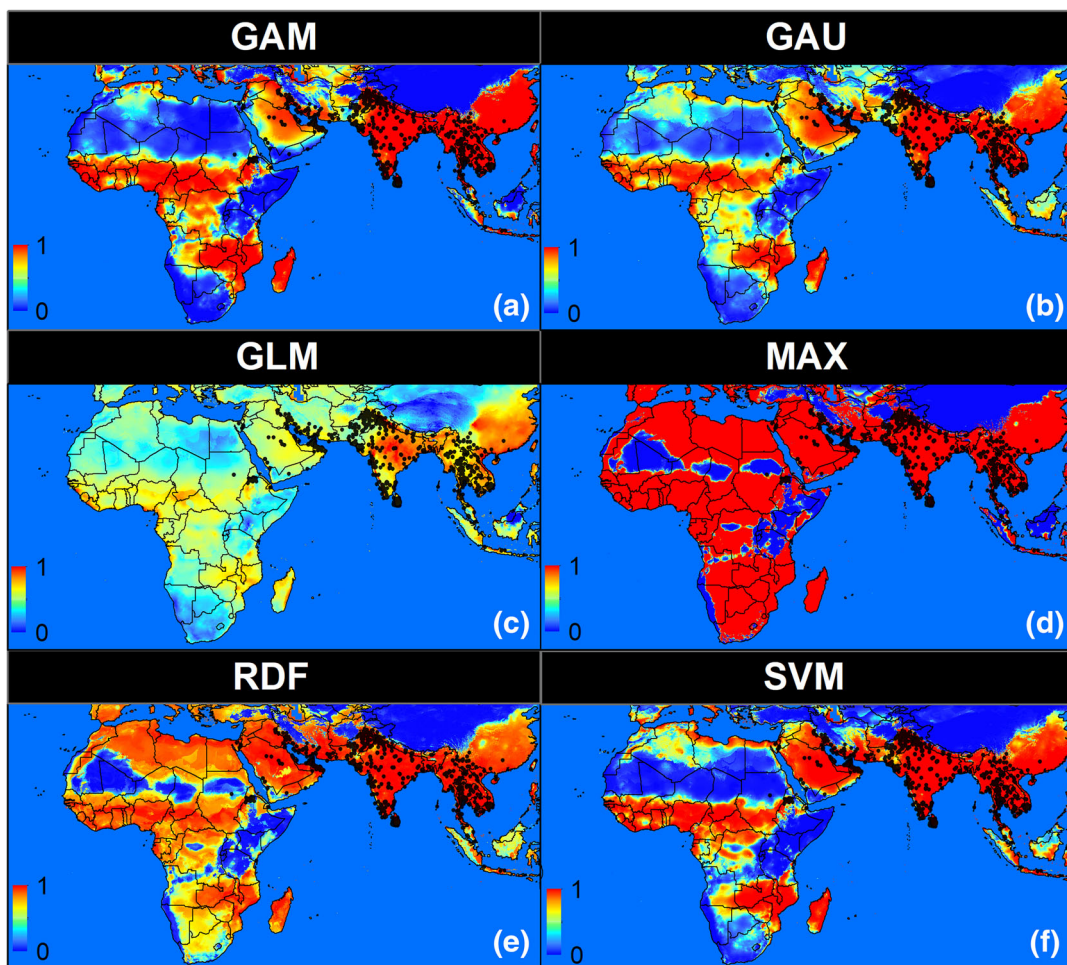


Figure 2. Model predictions for *Apis florea* based on the six modeling methods: **a** GAM, **b** GAU, **c** GLM, **d** MAX, **e** RDF, and **f** SVM. Warmer colors represent high suitability for each method employed to predict the bee's current distribution range, while colder colors represent areas with low suitability. Scale bar represents the suitability map. Occurrences for *A. florea* are depicted with black dots in all maps.

by all modeling methods, is shown in Figure 3 a (mean suitability values map) and b (presence/absence maps).

3.2. Multivariate niche properties of *Apis florea*

In our multivariate niche analyses, the first two PCA axes explained ~ 70% (42.06% and 27.48%, respectively) of the original environmental variables considered. The contributions of each variable for each one of the PCA axes are shown in Figure 4a, b and the composed PCA plot is shown in Figure 4c.

The pairwise comparisons between the native and invaded ranges of *A. florea* yielded a relatively low Schoener's *D* value of 0.089, indicating a low niche overlap proportion between the two distribution range classes (Figure 4d). The niche similarity test indicated no changes in the niche of *A. florea* as it invaded previously unoccupied regions (*p* value from the native range to the invaded one was 0.198). The proportion of unfilled niche from the native to the exotic range was 0.506 and that of expansion was 0 from the native to the invaded range. In summary, these values indicate that climatic conditions for the species in

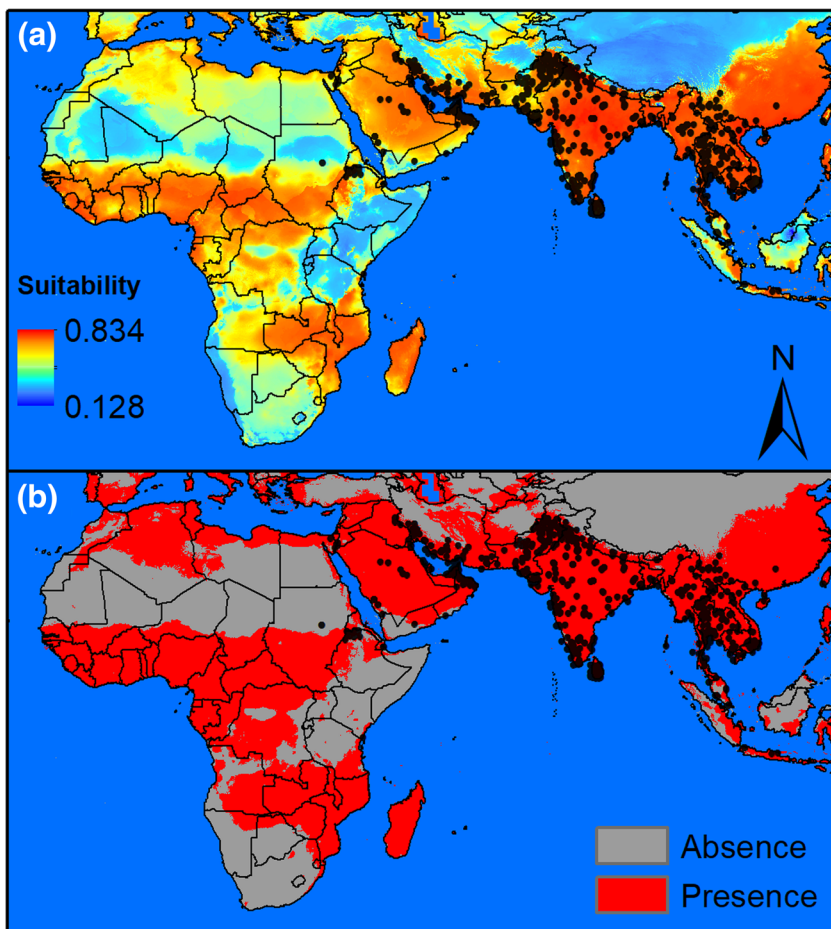


Figure 3. Results of the species distribution models obtained for *Apis florea*, considering **a** the species' suitability gradient and **b** the presence/absence map. In **a**, warmer colors represent high suitability for each method employed to predict the bee's current distribution range, while colder colors represent areas with low suitability. Scale bar represents the suitability map. Occurrences for *A. florea* are depicted with black dots in both maps.

its invaded range are not different from those in its native one. All these results are shown in Table I.

4. DISCUSSION

Using multivariate analyses, we demonstrated that the climatic niche of *A. florea* is generally conserved, even though there was a significant proportion of niche unfilling (0.506) when we compared the climatic conditions in areas occupied by the bee in both of its native and invaded ranges. In general, the species showed a small proportion of overlap between the

climatic conditions within its native and invaded ranges, but all the climatic conditions from the invaded niche were found within the native one. Therefore, in general, the climatic conditions in the invaded range are essentially the same as those in the native one. Such climatic conditions occurred even with a broad potential geographic range of the species, as detected by our distribution modeling procedures. We showed in our SDMs that the potential distribution of this species is wide, extending from its core range in South and Southeastern Asia to include to southern China and Taiwan,

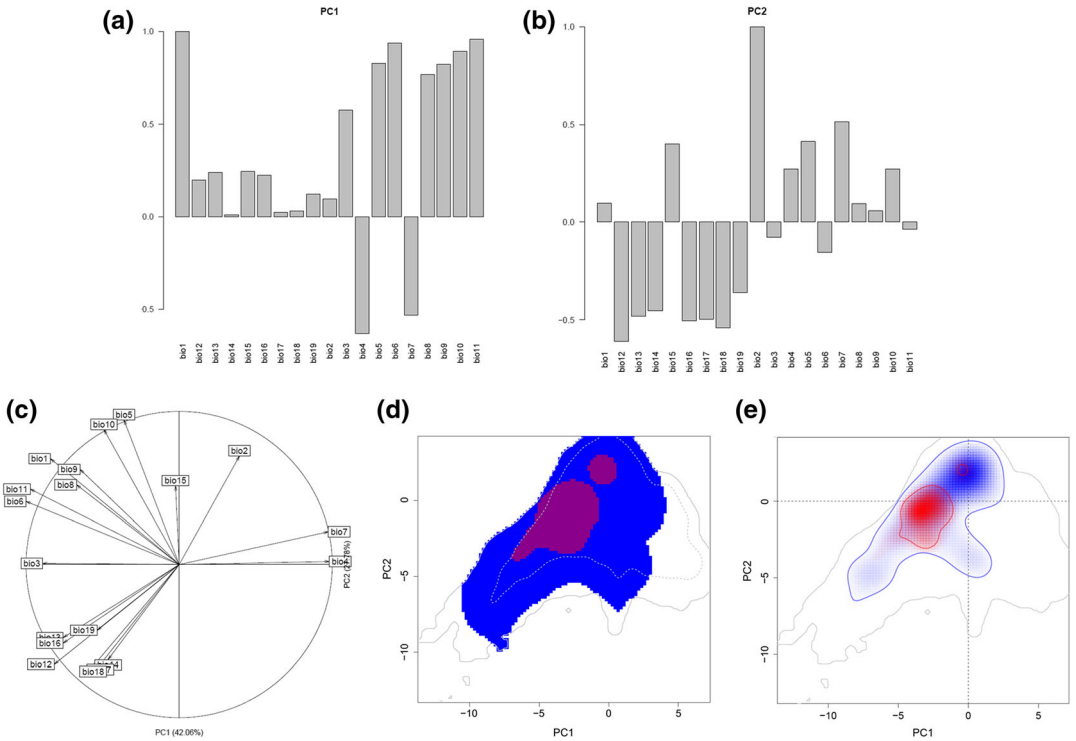


Figure 4. Results of multivariate niche analyses. Explanation of the original climatic variation by the **a** first and **b** second PCA axes from the PCA-env analyses from Broennimann et al. (2012). **c** The first two PCA axes and orientation of all environmental variables in each axis. **d** Overlap of the realized climatic niches of *Apis florea*, representing the stable (purple) and unfilled (red) niche proportions, when comparing its invaded with its native ranges. There was no niche expansion. Outermost and thicker line represent 100% of available climatic conditions for the species in each range. Dotted middle lines correspond to 50% of available climatic conditions for the species in each range. **e** Overlap of the realized niches of *Apis florea* in all its considered (native and invaded) ranges. Native: blue; invaded: red. The solid lines represent 10% of the occurrences density in each range.

Table I. Pairwise comparisons of niche overlap (*D*), niche similarity *p* value, niche unfilling, niche stability, and niche expansion between the native and invaded ranges (direction: native range → invaded range) of *Apis florea* following Broennimann et al. (2012). The direction invaded range → native range was not considered, since the invasion process does not occur in this fashion

Statistic	Direction Native → invaded
Schoener's <i>D</i>	0.089
Similarity test (<i>p</i> value)	0.198
Niche unfilling	0.506
Niche stability	0.494
Niche expansion	0.000

Peninsular Malaysia, Singapore, and most of the African continent.

One major issue when discussing the effects of invasive pollinators is their potential impact on native species inhabiting the invaded regions. Although estimations of their effects are generally lacking, when considering *A. mellifera*, Cane and Tepedino (2017) were able to estimate that the amount of resources gathered by a single colony of this species would prevent the production of 100,000 native bees. Such pernicious and pervasive effects are in agreement with previous analyses (Butz-Huryn 1997; Goulson 2003; Paini 2004; Paini et al. 2016).

Considering the known floral resource control and monopolization by *A. mellifera* [in the Americas (Cane and Tepedino 2017)] and *A. cerana* [in Southeast Asia (Koetz 2013)], if the behavior of *A. florea* overlaps with that of its related species, native pollinators are expected to suffer some competition.

Evaluating the niche conservatism we obtained for *A. florea* from its native range to its invaded one and the predicted distribution in Africa and Southeast Asia, we expect that this bee is able to expand its range considerably. Particularly, the establishment of new populations is expected to occur in those locations where human activity is intense, i.e., among plantings and irrigated lands within urban green spaces (Hennig and Ghazoul 2012; Braaker et al. 2014; Threlfall et al. 2017), as well as in areas where the native dipterocarp forests have been removed (Liow et al. 2001; Oldroyd and Nanork 2009). For the distribution of *A. florea* in Africa, we also expect that such processes (human activities and forest deforestation) may, in some degree, allow this species to increase its distribution. Regarding the new occurrence records reported for Taiwan, extensive trade involving the island has probably led to ship transportation of swarms to its major ports and establishment of new populations in an environment that is suitable but was previously unreachable for the species.

In the analyses we used here, we only dealt with the climatic conditions of the areas occupied by the species in each one of its ranges, and no deeper considerations related to the biotic interactions and dispersal capacities of the species were covered. Considering the BAM (Biotic-Abiotic-Dispersal) diagram proposed by Soberón (2007), alongside with abiotic environmental conditions, the distribution of a species is also determined by the biotic interactions it maintains with other species and by its dispersal capabilities. Therefore, even though our models predicted a wide potential distribution range, biotic interactions with native species already established in the areas it is invading may, in the end, prevent the species from effectively occupying these areas and developing viable populations.

The native habitats for *A. florea* in the Middle East, without human interference, were unsuitable under the current natural conditions due to aridity and lack of adequate vegetation that might provide year-round floral resources. Nonetheless, massive planting of irrigated gardens has created unprecedented favorable habitat in what would otherwise be climatically suitable areas. These anthropogenic sites may help *A. florea* to reach formerly inaccessible natural oases with favorable conditions.

In Southeast Asia, *A. florea* along with a potentially large number of Hymenoptera and other animals are adapted to more seasonal conditions, where more open vegetation prevails (e.g., in Central Thailand). Under natural conditions, southernmost Thailand and the Malay Peninsula were unsuitable to this species due to the occurrence of dense, humid, dipterocarp rainforest. Nonetheless, widespread deforestation of the Thai-Malay Peninsula has removed unsuitable dense forests and replaced them with far more open vegetation with a drier microclimate, thus rendering vast newly suitable (and/or accessible) areas for *A. florea*. Due to lack of data for key areas, such as conflict zones in southern Thailand, it is difficult to assess whether recent occurrences in the Malay Peninsula are the result of continuous spread of the bees from their core range in south Thailand through deforested landscapes, or if populations in places like Singapore were founded by colonies transported by ship. These scenarios, which are potentially testable using phylogeographic or population genomic datasets, are not mutually exclusive and both are plausible considering the known colonization of *A. florea* of Taiwan and Jakarta by ship.

Both in its native and in its introduced range (e.g., Singapore), *A. florea* thrives alongside large populations of three other species of *Apis*, including its closest relative *A. andreniformis*. Clearly, these species do not exclude each other at large spatial scales. At local scales, *A. andreniformis* predominates in the most mesic and densely forested semi-natural sites, whereas *A. florea* thrives in more open, drier, human-modified sites and is

so far undetected in Singapore's most intact primary forest remnant (Ascher et al. 2019). It is not clear to what extent if any direct competition explains this pattern as opposed to differing niches.

Whether the invasive species' niche is conserved or shifting needs to be assessed to better predict if and how the invasion may impact local bee communities. The Multivariate and SDM methods used to study the invasion of *A. florea* have been used previously to evaluate the how invasion processes took place when considering other taxa in new ranges (Petitpierre et al. 2012; Strubbe et al. 2013; Silva et al. 2016). For 22 invasive insect species, Hill et al. (2017) showed that 12 had expanded their climatic niches in comparison to the climatic conditions within their native range. Moreover, among those 22 species, 15 also showed a significant level of niche unfilling, meaning that they still do not occupy the same climatic conditions they do in their native ranges, which indicates they may still yet go on to occupy even larger geographic areas. The unfilled proportion of climatic conditions of *A. florea*'s niche when comparing the native and invaded ranges is a clear indication that this species is in climatic equilibrium with the climatic conditions available in its native range. Still, considering the amount of climatic conditions it occupies in its native range that is still not occupied in its invaded one, the large distribution range for *A. florea* we predicted with our SDMs is possible to occur in the future.

Based on our results, we encourage new studies attempting to evaluate the potential impacts of *A. florea* upon the community of native pollinators in Africa, and whether this bee has the potential to cause the same kind of harm to native species as its larger-bodied, cavity-nesting relatives *A. mellifera* and *A. cerana* are doing elsewhere. Lastly, considering the available toolbox to determine climatic niche shift/conservatism and a recent publication enumerating several invasive bee species throughout the world (Russo 2016), we also believe a proper analysis of the invasive potential of these bee species is

greatly needed. It is impossible to precisely determine at the moment the degree to which *A. florea* may impact co-occurring native pollinators in the sub-Saharan African and Southeast Asian regions predicted by our SDMs as suitable for the species. Nonetheless, the potential of this and other exotic species to impose a negative impact on native bees should serve as a call to critically evaluate the influence of exotic bees and other Hymenoptera.

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AUTHOR CONTRIBUTION

DPS and MSE conceived this research and designed the experiments; MSE, JSA, JCT, ASA, and MSE provided the data; DPS, ACFC, and BV analyzed the data; and DPS, ACFC, BV, JSA, JCT, ASA, XRO, and MSE wrote the paper.

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modèles de répartition des espèces / macroécologie / processus d'invasion / Asie / Afrique.

Sie kolonisiert den Osten und den Westen: Verbreitung und Nischeneigenschaften einer Zwerghonigbiene, die nach Afrika, in den Mittleren Osten, in die malaiische Halbinsel und nach Taiwan einwandert.

**Artverbreitungsmodelle / Makroökologie /
Invasionsprozess / Asien / Afrika.**

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