Analysis of potential niche shifts in alien pairs of mantis species (Insecta, Mantodea) with comments on the current taxonomic and ecological knowledge

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Academic editor: Matan Shelomi | Received 12 August 2023 | Accepted 5 February 2024 | Published 11 June 2024

Abstract

Due to the pet and goods trade, several animals are now present in regions outside of their traditional native ranges. A peculiar situation has arisen in mantises, insects that are becoming more popular as pets: two genera (Hierodula and Tenodera) have begun to spread around the world, with two Hierodula species overlapping in Europe and two Tenodera species doing the same in North America. Such an event can lead to possible competition with both local taxa and alien congeneric sister species; the latter may reduce the impact of one of the invaders. Additionally, the situation allows the comparisons of niche shifts in displaced mantises, allowing us to understand whether such animals respect general patterns shown in terrestrial ectothermic invasive species. To do this, I adapted scripts from previous publications for analyzing niche overlap (Schoener’s D), niche expansion (E), and unfilling (U) through the centroid shift, overlap, unfilling, and expansion (COUE) scheme using presence records from GBIF and iNaturalist Research-Grade observations and bioclimatic variables available in BIOCLIM, selected according to variance inflation factor (VIF) values. I also evaluated the overlap between the sister species in the non-native range with D. Overall, there was relatively high niche expansion and unfilling patterns shared among the taxa, although species tended to have low abiotic overlap between native and alien ranges, and a relatively high niche overlap was present among congeneric species in the shared non-native area. However, such analyses may be biased due to chosen variables, taxonomic uncertainty, and lack of information on mantises’ ecology; particularly, the situation regarding H. tenuidentata/teno transcaucasica should be monitored and clarified, given the higher potential invasion risk of these species compared to other mantises and the uncertainties regarding which populations have reached Europe. Additionally, the biology of alien mantises should be studied in more detail in both native and non-native environments given the current critical lack of information.

Keywords

COUE, generalist predator, Hierodula, overlap, Tenodera

Introduction

The increase in global trade has allowed several species to be present outside their native ranges, leading to the presence of more than 37,000 alien species globally (IPBES 2023) and to an exponential increase of invasive taxa (Meurisse et al. 2019, Mormul et al. 2022). The establishment of an alien species starts with overcoming the dispersal barrier, which is aided by humans through accidental transportation or species traded for commercial reasons (Seebens et al. 2015, Meurisse et al. 2019, Sinclair et al. 2020, Mormul et al. 2022, IPBES 2023, Pili et al. 2023). For example, several animals are imported through the pet market, which is known to have a strong influence on their invasiveness (Lockwood et al. 2019, Maceda-Veiga et al. 2019, Gippet and Bertelsmeier 2021).

Insects are usually introduced in non-native environments by accidental means (e.g., Meurisse et al. 2019). Among them, mantises (Mantodea) were probably introduced in different parts of the world by both accidental transportation (Battistion et al. 2018, 2020, Moulin 2020, Connors et al. 2022) and pet mismanagement (Battistion et al. 2022, Connors et al. 2022), although the introduction pathway of each species may be different (Battistion et al. 2022). Non-native mantises may compete with native Mantodea taxa (e.g., Fea et al. 2013) and may also have secondary ecosystem effects, such as feeding on pollinators (Anderson 2019), herbivores, and intra-guild species (Snyder and Evans 2006, Crowder and Snyder 2010). At the same time, alien (i.e., non-native, e.g., Almena et al. 2023) mantises sharing non-native environments may also compete with each other (e.g., Snyder and Hurd 1995). Competition between introduced species has been shown to potentially reduce the impact of an invasive species (e.g., Van Riel et al. 2009, Russell et al. 2014).
Although it is known that several mantises are now present in regions outside their known native ranges (e.g., Fea et al. 2013, Battiston et al. 2017, 2018, 2020, 2022, Schwarz and Ermann 2018, Anderson 2019, Shcherbakov and Govorov 2020, 2021, Connors et al. 2022, Martinović et al. 2022), to the best of my knowledge, it has never been analyzed if their alien niches are similar to their native ones or if these niches have shifted. Generally, such analyses are based on the centroid shift, overlap, unfilling, and expansion (COUE) scheme, which was first presented by Broennimann et al. (2012) and later modified by Petitpierre et al. (2012) (Liu et al. 2020). This scheme is based on first reducing the environmental space in two dimensions through principal component analysis (PCA) and then splitting said space into three parts: stability (S), which is the space that the species occupies in both the native and introduced range; unfilling (U), which is the space occupied in the native range and also present but not occupied in the alien one; and expansion (E), which is the area occupied only in the alien range and also present but not occupied in the native range (Broennimann et al. 2012, Liu et al. 2020). To avoid issues caused by different sampling efforts and strategies, a kernel density function is used to smooth the occurrence densities in both native and introduced environments (Broennimann et al. 2012, Liu et al. 2020). The COUE scheme is important for the quantification of niche space and for understanding the niche shift of invasive species. E provides the niche shift magnitude, given that U shows a potential condition that species may colonize in the alien range after some time (Liu et al. 2020). Furthermore, the COUE scheme allows for the testing of niche conservatism as a binary pattern and checks if both native and alien niches are significantly similar to each other (niche equivalency test; Bates et al. 2020, Liu et al. 2020) and if such resemblance is caused by chance by randomly allocating the occurrences in one range (niche similarity test) (Liu et al. 2020).

COUE analyses can be helpful for understanding the potential ecological patterns of alien species. For example, it is known that ectothermic terrestrial species considered as invasive may tend to conserve their climatic niche compared to those regarded as alien (introduced outside their native range) but non-invasive (Bates et al. 2020, Liu et al. 2020). This pattern is probably explained by the biotic, abiotic, movement (BAM) model introduced by Soberon and Peterson (2005); according to this model, species distribution is constrained by factors linked to biotic (B) and abiotic (A) interactions, coupled with the need of the species to reach certain places (M) (Soberon and Peterson 2005). Therefore, species might need more overlapping of such factors in alien environments to become invasive (Bates et al. 2020, Mormul et al. 2022). Therefore, species that are introduced to climates similar to their native ones may be able to establish populations in such environments (Liu et al. 2020). At the same time, methods for analyzing niche shifts may also be biased by several factors. For example, the chosen metric thresholds and variables have been shown to hugely influence results and interpretations (Bates and Bertelsmeier 2021; Lo Parrino et al. 2023). It is also important to note that incomplete ecological niches may be suitable for one population of a non-native species to colonize while excluding a second, closely related population (Liu et al. 2020). In fact, it is recognized that different populations or subspecies of the same species may have different ecological niches (e.g., Weaver et al. 2022) or plasticity to colonize different environments (Bates and Bertelsmeier 2021).

A curious situation arose in recent years with at least two species of giant Asian mantises (genus Hierodula Burmeister, 1838) colonizing environments in Europe (Battiston et al. 2018, 2020, Moulin 2020, Martinović et al. 2022, Sevgili and Yilmaz 2022, Moulin and Rouard 2023) and two species of Tenodera Burmeister, 1838 colonizing North America, particularly Northeastern United States (Snyder and Hurd 1995, Snyder and Evans 2006, Anderson 2019). Such a situation may allow us not only to compare the possibility of niche shifts in such insects but also to evaluate potential differences between congeneric taxa sharing a non-native range, which may lead to potential competition between the invaders (e.g., Snyder and Hurd 1995). It could be possible that the native conditions for species spreading more easily, such as one of the Hierodula species in Europe (Sevgili and Yilmaz 2022), are similar to those in its non-native one, while species with more difficulty in dispersal could exhibit less overlap if the generic pattern observed for ectothermic species is respected (Bates et al. 2020, Liu et al. 2020). In addition, different climatic requirements may lead the species to occupy different environments, as happened with other sister pairs in a different taxonomic group (Summers et al. 2023).

I ran niche shift analyses on the two clades, Hierodula and Tenodera, to evaluate possible patterns in alien Mantodea sister species. First, I considered the native and alien ranges of a single species and calculated overlap and niche shifts, and then I compared the alien ranges shared by sister taxa. Based on previous observations (Anderson 2019, Battiston et al. 2020, Sevgili and Yilmaz 2022), I expected that the most widespread alien species of each genus would have high overlap between their own alien and native niche, as happens in other ectothermic terrestrial animals (Bates et al. 2020, Liu et al. 2020), and that can lead to a competitive advantage, as has happened in other taxa. Such tasks were complicated and influenced by taxonomic (Battiston et al. 2018, 2021, Shcherbakov and Battiston 2020, Liu et al. 2021, Shim et al. 2021, van der Heyden and Schwarz 2021) and ecological uncertainties (Anderson 2019). Furthermore, the analyses relied on citizen science data, which are very helpful in tracking invasions (e.g., Battiston et al. 2020, Moulin 2020, Connors et al. 2022, Martinović et al. 2022, Sevgili and Yilmaz 2022, Moulin and Rouard 2023) and generating observational records (iNaturalist Blog 2023, GBIForg 2023a, 2023b) but may have limitations in terms of identifying insects at the species level (Gardiner et al. 2012, Ratnieks et al. 2016). I briefly review these issues here given that they will influence possible future studies.

Materials and methods

Considered species and caveats.—I conducted analyses on the following taxa: the Transcaucasian Giant Mantis Hierodula transcaucasica Brunner de Wattenwyl, 1878 and/or the Giant Asian Mantis H. tenuidentata Saussure, 1869 (see sections below); the Indochina mantis H. patellifera Serville, 1839; the narrow-winged mantis Tenodera angustipennis Saussure, 1869; and the Chinese mantis Tenodera sinensis (Saussure, 1871).

Species of the genus Hierodula are naturally distributed in the Oriental, Palaeartic, and Australian biogeographic regions but mostly in Asia (Leong 2009, Liu et al. 2021). H. tenuidentata, in particular, is thought to be distributed from Indonesia to Caucasus, with alien populations from Northern Ukraine to Spain (Pushkar and Kavurka 2016, Shcherbakov and Battiston 2020, Sevgili and Yilmaz 2022, Mizzaee et al. 2023, Pintilioaie et al. 2023). However, the presence of this species in Indonesia is doubtful (Shcherbakov and Battiston 2020). Battiston et al. (2018) officially synonymized H. transcaucasica with H. tenuidentata, given the high morphological similarities between the two. H. transcaucasica is generally defined as present in the Caucasus region from Iran to Georgia (Kolnegari 2023). While synonymy has been used in some works (e.g.,
It is known that *H. patellifera* actually represents a species complex distributed in several South, South-East, and East Asia regions (Liu et al. 2021, Chih-Ting Hsu pers. comm.). It also presents high intra-specific morphological variation, even in terms of the white coaxal marks that are usually used for species identification (Leong 2009, Battiston et al. 2020, Oshima 2021, Shim et al. 2021). Therefore, the limits of the taxon are unclear. After discussing with a taxonomic expert (Chih-Ting Hsu), I decided to run the intra-species analyses with two datasets: one in which I removed potentially problematic localities (India, Nepal, Philippines) and another in which I kept the data from these countries (Suppl. material 1: fig. S4). It must be noted that the niche similarity between the India, Nepal, and Philippines datasets and the one with the rest of the native area was low \( (D = 0.294, p = 0) \) (Suppl. material 1: figs S5–S7). It should also be noted that I considered points from areas outside of Europe (e.g., Seychelles and Hawaii) for the intra-species comparisons in this taxon, given that such observations seem to represent *H. patellifera sensu stricto* (Nguyen and Maxwell 2008, Seychelles Nation 2009, Chih-Ting Hsu pers. comm.). In addition, given that the population from Christmas Island is unlikely to represent *H. patellifera sensu stricto* (Connors 2023, Chih-Ting Hsu pers. comm.), those data were not included in my analyses (Suppl. material 1: fig. S4). Furthermore, given that the status of *H. patellifera* in Korea is unclear (Taewoo Kim, pers. comm.), I considered the Korean population as native, although this species was not recorded in the region before 1999 (Shin et al. 2023).

The species of the genus *Tenodera* are naturally distributed in the eastern hemisphere in various biogeographical realms from Africa to Australasia (Jensen et al. 2009; Anderson 2019). *T. sinensis* was introduced in North America around 1896 and *T. angustipennis* around 1926 in the same region (Snyder and Hurd 1995, Anderson 2019). Both taxa are naturally distributed in East Asia, with *T. sinensis* being more spread in both the native and non-native areas (Anderson 2019, GBIF.org 2023b) and known to be more biologically competitive in North America (Hurd 1988, Snyder and Hurd 1995, Anderson 2019). It is unclear if these species are capable of establishing populations outside of the Northeastern area of the United States, although some individuals can overcome such geographical barrier (Anderson 2019, iNaturalist 2023). Therefore, I analyzed the data first with all the available points and again omitting the points according to the distribution maps made by Anderson (2019), which considered the continental United States and Canada (Suppl. material 1: figs S8–S11). Taxonomic issues are also present within this genus, given that mostly citizen-science observations (e.g., iNaturalist records) were used and that such mantises can be morphologically similar to each other with few characters available for distinguishing them (Jensen et al. 2009, Anderson 2019).

Given the considerations in the paragraphs above, identification of such animals based on citizen science might be biased. However, since 2020, iNaturalist has provided at least 64% of the insect data present in GBIF (iNaturalist Blog 2023), which is one of the most used archives for biological data (Heberling et al. 2021). Conversely, if all the Mantodea data with coordinates and uncertainty less than or equal to 10 km (limits set given the specificiations used for “spThin”; see sections below) are considered, iNaturalist Research-Grade observations are responsible for approximately 81,647 observational data out of the 111,728 available in GBIF (GBIF.org 2023a), accounting for roughly 73.08% of such.

**Fig. 1.** Presence records used in the analyses for *H. tenuidentata sensu Battiston et al. (2018). The maps for the other species are available in Suppl. material 1: figs S4, S8–S11.**
data in the archive. Critically, such a percentage increases to approximately 98.1% if only the evaluated taxa are taken into consideration (GBIF.org 2023b). Therefore, citizen-sciente records might currently be regarded as the best method for obtaining as many observation points for mantises as possible.

Presence records and environmental variables.—Presence records from the focal species were downloaded from Research-Grade iNaturalist (iNaturalist 2023) observations, which means that at least two-thirds of the users who tried to identify the animal agreed on the species ID (https://www.inaturalist.org/pages/help#quality), and from GBIF (GBIF.org 2023b). Such records were then filtered using the R package “spThin” (version 0.2.0: Aiello-Lammens et al. 2015) to reduce potential sampling bias and also remove duplicated coordinates, with each point set at least 10 km apart, one maximum possible output file, and 100 repetitions for getting an optimal number of presence points. The records were then converted to spatial points with the “sp” package (version 1.4-7; Bivand et al. 2013). Potential erroneous points, points representing potential single escaped pets, or records of single instances of species in regions with no literature available (e.g., a single point of *H. patellifera* in California: https://www.inaturalist.org/observations/93123522) were removed from the datasets. In the case of doubtful records (e.g., the ones for Oceanian *Hierodula*), the possible species ID was checked in collaboration with a mantis taxonomist (Chih-Ting Hsu). For the analyses regarding the statuses of *H. tenuidentata*, I also added Chinese observation points from Liu et al. (2021).

For building the climatic niche of the species, I downloaded the 19 bioclimatic variables from WorldClim2 (Fick and Hijmans 2017) at 30s (~1 km2) resolution. Then, the value of each climatic variable for each spatial point was extracted with the extract() function of the “raster” package (version 3.5-15; Hijmans 2022). I then removed all the records with at least one missing environmental variable with the na.omit() function of the “stats” package (version 1.1.1; R Core Team 2022). After that, I merged all the values of the variables together with the rbind() function of the “base” package (version 4.1.1; R Core Team 2022) and submitted them by removing collinear ones; collinearity was evaluated by variance inflation factor (VIF) matrices, with 5 as a threshold, using the vifstep() function implemented in the “usdm” R package (version 2.1-6; Naimi et al. 2014), and I chose to use all the metrics with VIF < 5 (Table 2). It must be noted that the chosen variables can influence the results of the analyses (Bates and Bertelsmeier 2021, Lo Parrino et al. 2023). However, the majority of the variables used here were also used for niche modeling of mantises in past publications (e.g., Steger et al. 2020, De Vivo and Huang 2022, Pintilioae et al. 2023, Shin et al. 2023), and they should also be relevant for the studied taxa. For example, it is known that temperature can influence the biology of *H. patellifera* (Shin et al. 2023) and *Tenebroides* species (Snyder and Hurd 1995, Hurd et al. 2020) and therefore including a variable such as BIO5 (max temperature of warmest month) is biologically meaningful. Potential spatial autocorrelation was evaluated by Mantel correlograms through the ecospat.mantel.correlogram() function of the ecospat” package (version 3.2.2; Di Cola et al. 2017).

Niche shift and overlap analyses.—To identify potential niche shifts and congreneric competition, while also checking on potential patterns shared by those taxa, I adapted and used scripts from Bates et al. (2020) and ran the analyses in R (version 4.1.3; R Core Team 2022). The variables were reduced through the use of a principal component analysis (PCA) with functions from the “ade4” package (version 1.7-19; Dray and Dufour 2007). Then, I ran a between-class analysis with 10 axes from said PCA using a priori classes (i.e., native vs non-native for all the taxa or *H. tenuidentata sensu stricto* vs *H. transcaucasica sensu stricto*) to identify which axis separated the two categorical ranges the most for each of the considered groups (i.e., the same species in two different ranges or two species sharing the alien range). These axes were then converted into densities of occurrences using the “ecospat” package (Di Cola et al. 2017). To understand which factors were the most impactful on the difference in native and alien distributions of the mantises, I plotted the contributions of the variables for the first two PCs with the frvz_pca_var() and the frvz_contrib() functions of the “factoextra” package (version 1.0.7: Kassambara and Mundt 2020). Particularly, the last function also detects which variables are significantly important in the considered PCs with a reference line: every variable above said line should be regarded as important (Kassambara and Mundt 2020).

Overlap of occurrence densities in the environmental space was evaluated by Schoener’s Δ (De Schoener 1968), which ranges from 0 (no overlap) to 1 (totally overlapping). Niche expansion (E) followed the definition of Bates et al. (2020), which regards it as the percentage of abiotic features in the non-native range that are not present in the colonized one. I considered E as significant if its value was > 10%. Unfilling (U) followed the definition of Peitipiere et al. (2012), and I considered it significant if it was > 10%, as done with E in previous studies (Peitipiere et al. 2012, Lo Parrino et al. 2023). To evaluate if similarities/differences were caused by random effects, I ran niche equivalency tests following Bates et al. (2020).

I calculated a potential correlation between the number of native or alien points and D overlap for each intra-specific analysis using Kendall’s rank correlation (τ: Kendall 1938), following Bates et al. (2020), using the “stats” package (version 4.1.1; R Core Team 2022).

Results

If analyzed as *H. transcaucasica sensu stricto*, the alien *Hierodula* species seemed to have moderately high overlap with its native range, low levels of expansion, and no unfilling (*D* = 0.5, *E* = 3.06%, and *U* = 0%; Table 1, Fig. 2A, Suppl. material 1: fig. S12A). When considered as *H. tenuidentata sensu stricto*, there was low overlap between native and alien ranges, high expansion, and very high unfilling (*D* = 0.119, *E* = 21.55%, and *U* = 84.37%; Table 1, Suppl. material 1: figs S13, S14). When considered as *H. tenuidentata sensu stricto* Battiston et al. (2018), the native-alien niche overlap was lower than the one considered for *H. transcaucasica sensu stricto*, and there was no expansion, while unfilling was high (*D* = 0.476, *E* = 0%, and *U* = 47.77%; Table 1, Suppl. material 1: figs S15, S16). For *H. patellifera*, overlap was low and both expansion and unfilling were high when using both the dataset with no dubious (i.e., the previously mentioned uncertain data from Nepal, India, and Philippines) points (*D* = 0.18, *E* = 24.05%, and *U* = 20.97%; Table 1, Fig. 2B, Suppl. material 1: fig. S12B) and the one with all the points of specimens regarded as the same species (*D* = 0.179, *E* = 18.39%, and *U* = 23.72%; Table 1, Suppl. material 1: figs S17, S18). *T. angustipennis* showed almost no overlap between native and alien ranges and extremely significant expansion and unfilling with both the full dataset (*D* = 0.01, *E* = 96.56%, and *U* = 97.35%; Table 1, Fig. 3A, Suppl. material 1: fig. S19A) and with the one using the Anderson (2019) distribution map (*D* = 0.009, *E* = 98.51%, and *U* = 98.85%; Table 1, Suppl. material 1: figs S20, S21). *T. sinensis* also had very low overlap with its native range and sig-
significant expansion and unfilling in the alien one, both when the whole possible range was evaluated \((D = 0.022, E = 36.62\%, U = 66.59\%\); Table 1, Fig. 3B, Suppl. material 1: fig. S19B) and when only the trimmed distribution was considered \((D = 0.02, E = 54.04\%, U = 95.97\%\); Table 1, Suppl. material 1: figs S22, S23).

All the intra-species analyses were significant according to niche equivalency tests \((p < 0.0001\); Table 1). Therefore, their \(D\) values were not generated by random chance. Furthermore, none of the \(\tau\) values were significantly different from random, both for native points-\(D\) correlation \((\tau = 0.229, p = 0.3991)\) and for alien points-\(D\) correlation \((\tau = 0, p = 1\); Table 1). These results highlight the lack of effect the number of occurrence points had on the results. In addition, the Mantel tests proved that there was no spatial autocorrelation at 10 km (Suppl. material 1: figs S24–S27).

In terms of the importance of the variables in the intra-species analyses, BIO19 (Precipitation of Coldest Quarter) was the most important variable if we considered one of the \(Hierodula\) species as \(H.\ transcaucasica\) sensu stricto (Table 3, Suppl. material 1: figs S28, S29), followed by BIO18 (precipitation of warmest month), BIO13 (Precipitation of Coldest Quarter), BIO9 (mean temperature of warmest quarter), BIO3 (isothermality), and BIO5 (Table 3, Suppl. material 1: fig. S28). When the taxon was regarded as \(H.\ patellifera\) sensu stricto, BIO9 was the most important variable (Table 3, Suppl. material 1: figs S28, S29), followed by BIO18 (precipitation of warmest quarter), BIO5, BIO14, and BIO3 (Table 3, Suppl. material 1: fig. S28). BIO5 was the most important for the difference between native and alien niches when one of the \(Hierodula\) species was considered as \(H.\ tenuidentata\ sensu Battiston et al. (2018)\) (Table 3, Suppl. material 1: figs S32, S33), followed by BIO18,

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Alien points ((p = 1, \tau = 0))</th>
<th>Native points ((p = 0.3991, \tau = 0.229))</th>
<th>(D)</th>
<th>(E)</th>
<th>(U)</th>
<th>(p)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(H.\ transcaucasica) sensu stricto</td>
<td>347</td>
<td>173</td>
<td>0.5</td>
<td>3.06%</td>
<td>0%</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>(H.\ tenuidentata) sensu stricto</td>
<td>347</td>
<td>180</td>
<td>0.119</td>
<td>21.55%</td>
<td>84.37%</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>(H.\ tenuidentata) sensu Battiston et al. (2018)</td>
<td>347</td>
<td>353</td>
<td>0.476</td>
<td>0%</td>
<td>47.77%</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>(H.\ patellifera) (no dubious points)</td>
<td>89</td>
<td>835</td>
<td>0.18</td>
<td>24.05%</td>
<td>20.97%</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>(H.\ patellifera) (all)</td>
<td>89</td>
<td>852</td>
<td>0.179</td>
<td>18.39%</td>
<td>23.72%</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>(T.\ angustipennis) (full dataset)</td>
<td>292</td>
<td>161</td>
<td>0.01</td>
<td>96.56%</td>
<td>97.35%</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>(T.\ angustipennis) (trimmed)</td>
<td>262</td>
<td>161</td>
<td>0.009</td>
<td>98.51%</td>
<td>98.85%</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>(T.\ sinensis) (full dataset)</td>
<td>3315</td>
<td>462</td>
<td>0.022</td>
<td>36.62%</td>
<td>66.59%</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>(T.\ sinensis) (trimmed)</td>
<td>3065</td>
<td>462</td>
<td>0.02</td>
<td>54.04%</td>
<td>95.97%</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

Table 1. Number of points and metric values per each evaluated taxon. \(D\) is rounded up to the third decimal number. The \(p\) and \(\tau\) values reported in the native and alien points’ columns come from the Kendall test, while the \(p\) values in the last columns come from the niche equivalency tests.
For *H. patellifera*, the dataset trimming did not lead to a change in inferences given that BIO9 was the most important variable; the other significant ones were, in order of importance, BIO5, BIO14, BIO8, and BIO19 for both datasets (Table 3, Suppl. material 1: figs S34–S37).

For *T. angustipennis*, if the full dataset was considered, BIO18 was the most important variable (Table 3, Suppl. material 1: figs S38, S39), while the other important ones were BIO13, BIO19, BIO2 (mean diurnal range), and BIO9 (Table 3, Suppl. material 1: fig. S38). If only the Anderson (2019) distribution was considered, BIO2 was the most important variable (Table 3, Suppl. material 1: figs S40, S41), followed by BIO19, BIO14, BIO13, BIO18, BIO9, and BIO3 (Table 3, Suppl. material 1: fig. S40).

Concerning *T. sinensis*, BIO13 was the most important variable in both the full and trimmed datasets (Table 3, Suppl. material 1: figs S42–S45). In the analyses with the full dataset, BIO18 followed suit, with a seemingly negligible difference between it and the most important variable, while the other significant ones were BIO19, BIO9, and BIO2 (Table 3, Suppl. material 1: fig. S42). In the trimmed analysis, the other important variables were BIO18, BIO19, BIO9, and BIO3 (Table 3, Suppl. material 1: fig. S44).

In the inter-taxa analyses, the two *Hierodula* taxa in Europe had high overlap (\(D \approx 0.57\)), and the analysis was not significantly influenced by random chance (\(p = 0.008\); Fig. 4A). The *Tenodera* species also had high overlap according to both whole (\(D \approx 0.665\), \(p < 0.0001\); Suppl. material 1: fig. S44), BIO13 was the most important variable for the comparison between the two *Hierodula* followed by BIO18, BIO9, BIO19, and BIO14 (Table 4, Suppl. material 1: figs S47, S48). In the comparison between the two *Tenodera* species, BIO13 was the most important variable for both analyses (Table 4, Suppl. material 1: figs S49–S52). When the full dataset was used, BIO5, BIO2, BIO9, and BIO3 were the other important variables, while BIO8, BIO3, BIO14, BIO2, BIO9, and BIO3 were the other important variables in the trimmed dataset (Table 4, Suppl. material 1: figs S49, S51).

### Table 3. Important variables in the intra-species analyses.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Most important variable</th>
<th>Other important variables</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>H. transcaucasica sensu stricto</em></td>
<td>BIO19</td>
<td>BIO18, BIO13, BIO14, BIO9, BIO3, BIO5</td>
</tr>
<tr>
<td><em>H. tenuidentata sensu stricto</em></td>
<td>BIO9</td>
<td>BIO8, BIO5, BIO14, BIO3</td>
</tr>
<tr>
<td><em>H. tenuidentata sensu</em> Battiston et al. (2018)</td>
<td>BIO5</td>
<td>BIO18, BIO3, BIO13, BIO14</td>
</tr>
<tr>
<td><em>H. patellifera</em> (no dubious points)</td>
<td>BIO9</td>
<td>BIO5, BIO14, BIO9, BIO19</td>
</tr>
<tr>
<td><em>H. patellifera</em> (all)</td>
<td>BIO9</td>
<td>BIO5, BIO14, BIO8, BIO19</td>
</tr>
<tr>
<td><em>T. angustipennis</em> (full dataset)</td>
<td>BIO18</td>
<td>BIO13, BIO19, BIO2, BIO9</td>
</tr>
<tr>
<td><em>T. angustipennis</em> (trimmed)</td>
<td>BIO2</td>
<td>BIO19, BIO14, BIO13, BIO18, BIO9, BIO3</td>
</tr>
<tr>
<td><em>T. sinensis</em> (full dataset)</td>
<td>BIO13</td>
<td>BIO18, BIO19, BIO3, BIO14, BIO2</td>
</tr>
<tr>
<td><em>T. sinensis</em> (trimmed)</td>
<td>BIO13</td>
<td>BIO18, BIO19, BIO9, BIO14, BIO2, BIO3</td>
</tr>
</tbody>
</table>

**Fig. 3.** Intra-species niche dynamics analyses for the *Tenodera* species with the full datasets. A. Results for *T. angustipennis*; B. Results for *T. sinensis*. Blue: niche stability. Red: niche expansion. Green: unfilling. \(U\) and \(E\) values are in Table 1. The analyses with the trimmed points are available in Suppl. material 1: figs S21, S23.

### Table 4. Important variables in the inter-species analyses.

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Most important variable</th>
<th>Other important variables</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Hierodula</em> in Europe</td>
<td>BIO13</td>
<td>BIO18, BIO9, BIO19, BIO14</td>
</tr>
<tr>
<td><em>Tenodera</em> in North America (full dataset)</td>
<td>BIO19</td>
<td>BIO5, BIO2, BIO9, BIO3</td>
</tr>
<tr>
<td><em>Tenodera</em> in North America (trimmed)</td>
<td>BIO19</td>
<td>BIO8, BIO3, BIO14, BIO2, BIO9, BIO13</td>
</tr>
</tbody>
</table>
Results for Tenodera. In addition, the Tenodera species showed high levels of unfilling and different degrees of expansion, with T. angustipennis showing an $E$ larger than that of T. sinensis, although the metric was significant for both taxa. This may seem counterintuitive given that T. sinensis is generally thought to have a higher impact in the United States than T. angustipennis (Snyder and Hurd 1995, Hurd et al. 2004, Anderson 2019). However, it must be noted that potential impacts may not be related to expansion (Petipierre et al. 2012, Bates et al. 2020), and species with smaller native ranges may experience greater niche shifts (Bates et al. 2020). At the same time, it seems that T. sinensis is constrained by abiotic and movement variables in certain areas given the doubts about its ability to establish populations outside of the northeast of the United States (Anderson 2019) and the reports of very high rates of nymph mortality in dry conditions (Hurd et al. 2004). The last point also explains the importance of precipitation variables such as BIO13 for this species in the intra-species analyses. Thus, a low $D$ overlap and high unfilling may imply that Tenodera species are constrained by abiotic and movement factors in the United States, and the high expansion may be explained by a relatively small native range (Bates et al. 2020) or by the chosen variables (see Lo Parrino et al. 2023). However, it is also recognized that T. sinensis shifted its maturation period over the years in the United States, showing a degree of biological plasticity potentially triggered by temperature changes, which may also lead to a range expansion in this species (Hurd et al. 2020).

In terms of T. angustipennis, the two datasets showed different variables as the most important (BIO18, a precipitation-related variable, for the full dataset and BIO2, a temperature-related variable, for the trimmed dataset). This might mean that this species is constrained by more factors than the congeneric species. However, two precipitation variables always ranked among the three most important for both Tenodera, highlighting the importance of rain to this genus in North America. Given the potential increase in rainfall in some eastern areas of the United States in the future (Harp and Horton 2023), it is possible that both species may increase their non-native range. It must be noted that T. sinensis also feeds on T. angustipennis (Hurd 1988, Snyder and Hurd 1995), and it seems to be more prolific in nymph production (Anderson 1999). These biological factors, together with movement ones, may reduce the impact and the dispersal of T. angustipennis in the United States and show how the competition between two alien species shapes the distribution of sister species in non-native ranges.

It is possible that the two Hierodula taxa occupy niches that are not occupied by other European mantises, given their arboreal ecology (Battiston et al. 2020). At the same time, these niches might be only a small part of their native ones, and therefore they may survive in Europe only by expanding them (if one of the taxa is considered as H. tenientata sensu stricto). However, such results may be influenced by taxonomic status. For example, considering the most taxonomically problematic Hierodula taxon as H. transcaucasica sensu stricto, H. tenientata sensu stricto, or H. tenientata sensu Battiston et al. (2018) clearly changed the value of the examined metrics and the inference about this taxon. Specifically, when one of the Hierodula taxon was considered as H. tenientata sensu Battiston et al. (2018) or H. transcaucasica sensu stricto, its alien niche tended to be relatively similar to its native one, hinting at higher potential invasiveness if mantises respect the general pattern in terrestrial ectotherms (Bates et al. 2020, Liu et al. 2020). However, the higher $D$ and the smaller $E$ in H. transcaucasica sensu stricto is surprising given the smaller range compared to H. tenientata sensu Battiston et al. (2018). This, together with the lack of U, might imply a potential natural expansion of said species/population that started in the past, as suggested by Pintilioaei et al. (2023), which was also considered as a hypothesis for the Crimean and Balkan populations (Pushkar and Kavurka 2016, Battiston et al. 2018, Shcherbakov and Battiston 2020). Critically, the

**Discussion**

**Intra-species analyses and the impact of taxonomic impediments.**—It seems that there is both little overlap between the native and alien ranges in the considered mantises and high levels of unfilling and expansion if one of the Hierodula taxa is regarded as H. tenientata sensu stricto. Potentially, a low $D$ overlap might be caused by recent introduction (Liu et al. 2020), which would explain the alien–native overlap and high unfilling for H. tenientata sensu stricto and H. patellifera (Battiston et al. 2018, 2020). However, the given time period in which T. angustipennis and T. sinensis were introduced in continental North America (Snyder and Hurd 1995, Anderson 2019), it seems unlikely that time is a factor for the low $D$ in Tenodera. In addition, the Tenodera species showed high levels of unfilling and different degrees of expansion, with T. angustipennis showing an $E$ larger than that of T. sinensis, although the metric
taxon (regardless of the controversial taxonomy) has been shown to be more widespread in Europe than *H. patellifera* (Sevgili and Yilmaz 2022), potentially due to its better ability to circumvent movement barriers (Battiston et al. 2020, Moulin 2020, William Di Pietro pers. comm.). Therefore, the higher *D*, lower *E*, and lack of *U* may highlight a higher BAM overlap than that of the sister species. However, it is unclear if the population that is traditionally regarded as *H. transcaucasia* is the source one for the European alien range given that such a hypothesis can only be tested by molecular means (Bates and Bertelsmeier 2021) and the fact that the lower *D* in *H. patellifera* or *H. tenuidentata sensu stricto* may also be explained by recent introduction (Battiston et al. 2018, 2020, Liu et al. 2020). In addition, it is unclear whether the observations of this *Hierodula* complex belong to one or more lineages (i.e., populations from both South Asia and Caucasus).

In terms of the abiotic factors, the importance of the variables in the controversial *Hierodula* taxon seemed to vary according to the taxonomic assignment. Generally, the *Hierodula* species had temperature variables as the most important, which makes sense particularly for *H. patellifera* (Shin et al. 2023). However, if we consider the *Hierodula* taxon to be *H. transcaucasia*, BIO19 was the most relevant variable for explaining the difference between native and non-native ranges. Previous modeling attempts have shown that both temperature and precipitation are important for *H. tenuidentata sensu stricto* Battiston et al. (2018), and it is thought that the taxon could spread further in Europe due to climate change (Pintilioaie et al. 2023). Particularly, it is recognized that precipitation in cold months has been increasing due to increased temperature in several European areas (Hynčica and Huth 2019), and therefore both factors (increased temperature and increased precipitation in coldest months) might have been important in the dispersal in the mantis, regardless of the source population.

*Inter-species analyses.*—There is relatively high overlap between sister taxa occupying the same alien range. This may not be surprising given that such species potentially share areas in their native ranges as well (Snyder and Hurd 1995, Anderson 2019, Liu et al. 2021).

As stated above, the natural spreading ability of *H. patellifera* in Europe, where it seems to be most likely to be in places where it is transported through anthropogenic means (Battiston et al. 2020, Moulin 2020, William Di Pietro pers. comm.), appears to be less than the spreading of the other *Hierodula* taxon, which seems to be able to become more widespread in this continent (Battiston et al. 2018, Shcherbakov and Battiston 2020, van der Heyden and Schwarz 2021, Sevgili and Yilmaz 2022, Moulin and Rouard 2023, Pintilioaie et al. 2023), although *H. patellifera* was probably able to reach Croatia from Italy by natural means (Martinovič et al. 2022). Precipitation variables mostly explained the difference between the two non-native species in Europe, particularly BIO13. Therefore, precipitation might be a factor explaining the difference between the two. The ecology of these two species/taxa is mostly known from laboratory observations in areas in which they do not co-exist (Leong 2009, Kharabadze et al. 2022, Mirzaee et al. 2023), and therefore it is challenging to make assumptions about potential competition and differences in abiotic requirements between the taxa, particularly in non-native environments where different populations of two species from non-shared environments may meet for the first time. However, given that it is also observed in *Tenodera* species (Anderson 2019), it would not be surprising if BAM factors shape the distribution of *Hierodula* species in Europe. Critically, given what is observed by the distribution of *H. patellifera*, it seems that the other *Hierodula* taxa might have a competitive movement advantage that may result in a reduction in the impact of the former species, as observed in other taxa (e.g., Van Riel et al. 2009, Russell et al. 2014).

Concerning the *Tenodera* species, the high overlap is consistent with the observations regarding their distribution (Anderson 2019) and competition (Hurd 1988, Snyder and Hurd 1995). Therefore, a high overlap in the area they share is expected, although *T. sinensis* is more widespread for biological reasons (Anderson 2019), highlighting the effect of competition on the distribution of alien sister species. In both the datasets used, BIO19 was the variable that explained more of the difference between the two, which may be a limiting factor for *T. angustipennis* given its reduced geographical range in both native and non-native environments compared to *T. sinensis* coupled with the biological and movement constraints discussed in the previous section.

*Limitations of the study.*—As I stated in the previous sections, taxonomic statuses and misidentification could radically change the results of this study. In the future, an integrative taxonomic approach in which both morphological and molecular characters are used (e.g., Shim et al. 2021) is needed to understand which species and which populations are present as an alien taxon, which is very important for tracking potential changes between the original native niche and the non-native one (Liu et al. 2020, Bates and Bertelsmeier 2021).

Another issue is the lack of information on mantis ecology. Specifically, although several mantises have been called “invasive” in some studies (e.g., Snyder and Evans 2006, Crowder and Snyder 2010, Fea et al. 2013, Battiston et al. 2018, Schwarz and Ehrmann 2018, Moulin 2020, Shcherbakov and Govorov 2020, Moulin and Rouard 2023, Pintilioaie et al. 2023), no Mantodea species is currently present in the Global Invasive Species Database (GSID) made by the Invasive Species Specialist Group (ISSG) of IUCN (GSID 2023). IUCN defines species as invasive if they are “negatively impacting native biodiversity, ecosystem services or human economy and well-being” (IUCN 2023). However, the impact of alien mantises on ecosystems is not very well understood (Fea et al. 2013, Battiston et al. 2020, 2022, Connors et al. 2022), and few studies have evaluated the impact of displaced Mantodea species on native taxa in the same order or niche (see Snyder and Evans 2006 and Fea et al. 2013). This causes serious problems with the possible listing of mantises as alien or invasive alien; specifically, a lack of baseline may cause concerns in analyzing potential patterns shared by non-native mantises and differentiating potential invasive ones (Liu et al. 2020). That being said, several alien mantises (e.g., all the species evaluated in this study) would be regarded as invasive if looser definitions are used (e.g., Gippet and Bertelsmeier (2021) regard all the species “with at least one established population outside of the native range” as invasive, even if no potential impact is known), but finding a unified definition is still challenging, and only recently has a framework been proposed for finding a shared terminology among ecologists (Almema et al. 2023). Critically, by using shared terminology, we should consider all the mantises analyzed here as “invasive non-native” species, which are “established non-native species” spreading and establishing populations further from their introduction points (Almema et al. 2023).

In addition, there are biases toward some countries for both research efforts (Battiston et al. 2022) and presence records. For example, there were almost nine times more observation points for *T. sinensis* in the United States than in Asia (Table 1). Critically, some areas of the world need to be studied due to potential invasions of mantises or to better understand the ecology of invading mantises. For example, I found several points on iNaturalist of a mantis identified as *H. patellifera sensu stricto* in the Seychelles (identification by Chih-Ting Hsu), but the only alternative source I could find about its presence in the nation was an online news
source (Seychelles Nation 2009). Therefore, it is not known whether such species had any impact on the Seychellois ecosystems. Another potential example is *Sphodromantis viridis* (Forskål 1775), which is becoming widespread in Europe (Battistone et al. 2017, Martinovic et al. 2022). Despite its increasing presence in this area, we still know very little about its ecology (Battistone et al. 2017), and in both iNaturalist and GBIF, there are a very limited number of records from its native range (GBIF 2023a, iNaturalist 2023).

**Conclusions**

Overall, the analyzed mantises did not exhibit high overlap between their native and alien niches, while showing high expansion and unfilling, which shows that mantises can establish populations in environments dissimilar to their native ones while having limits in their spread at the same time. However, the situation for *H. tenuidentata/transcaucasica* must be clarified given the potential change of results and inferences caused by the taxonomic issues in such species complex. Given these considerations, I argue that future taxonomic and ecological studies are critically needed to better understand mantis ecology and taxonomy, especially in less studied areas of the world and in natural environments where alien species are present, which would also help to understand whether the invasion was started by different or specific populations of the same species with different requirements. However, given my results, coupled with previous modeling attempts and inferences by other research teams, it is highly likely that the unclear *Hierodula* taxon could be the population/species referred to as *H. transcaucasica*, given its niche overlap that seems to resemble the general pattern of invasive ectothermic terrestrial species, although only genetic studies could prove these assumptions.

**Data availability statement**

The scripts and the elaborated presence points with the values per each variable are present in Zenodo (https://zenodo.org/records/10101384, DOI: 10.5281/zenodo.10101384).

**Acknowledgements**

I thank Chih-Ting Hsu (National Chung Hsing University, Taichung, Taiwan) for discussion and suggestions on the taxonomy of the evaluated species, William Di Pietro (World Biodiversity Association Onlus, Verona, Italy) for discussion regarding the presence of *H. patellifera* in Italy, Howon Rhee (University of Trier, Trier, Germany) and Taewoo Kim (National Institute of Biological Resources, Incheon, South Korea) for discussion regarding *H. patellifera* in Korea, Trevor Padgett (Taiwan International Graduate Program on Biodiversity and Tunghai University, Taichung, Taiwan) for revising both the grammar and the content of the manuscript, Jen-Pan Huang (Academia Sinica, Taipei, Taiwan) for suggestions on the manuscript, and the Orthopterists’ Society for the fee waiver. For this study, I was supported by the Taiwan International Graduate Program (TIGP) through the TIGP Research Performance Fellowship 2022 and by internal research support from Academia Sinica and the University of Trier.

**References**


iNaturalist Blog (2023) Thank you for helping generate most GBIF records for most species since 2020. https://www.inaturalist.org/blog/76606


**Supplementary material 1**

Author: Mattia De Vivo

Data type: pdf

Explanation note: 52 supplementary images for the study.

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Link: https://doi.org/10.3897/jor.33.111057.suppl1